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1160 W. Orange Grove Ave., Arcadia, California, U.S.A. 91006

SEASONAL CHANGES IN ORGANIZATION OF TROPICAL RAIN FOREST BUTTERFLY POPULATIONS IN PANAMA

THOMAS C. EMMEL and CHARLES F. LECK
Department of Zoology, University of Florida, Gainesville 32601
Section of Neurobiology and Behavior, Cornell University, Ithaca 14850

SEASONALITY IS USUALLY CONSIDERED a distinctive feature of temperate zone communities, with their fluctuating annual climates, while the wet lowland tropics are relatively constant in most environmental conditions. Yet major seasonal changes in tropical plant communities have been demonstrated for even rain forest areas and the selective reasons for this seasonality are beginning to be explored (e.g., see Janzen 1967). The possible existance of seasonality in the animals of tropical communities has barely been touched upon to date, most available data being on birds (e.g., Skutch 1950, Moreau 1950, Miller 1954, Ricklefs 1966, Leck 1970), certain tropical lizards (Hirth 1963, Alcala 1966, Sexton 1967) and foliage-inhabiting insects (Janzen, unpublished; Hespenheide, unpublished). These studies have shown there may be significant changes in vertebrate population size and reproductive activities even in tropical forests with a constant annual climate. Differences in population density and species composition of foliage-inhabiting insect communities have been shown (by Janzen and Schoener 1968) between wetter and drier sites in a tropical deciduous forest, while the dry season has been shown to decrease population density of inflorescence-feeding *Drosophila* in Panama (Pipkin, Rodríguez and León 1966). Most mosquito species studied by Bates (1945) in tropical eastern Colombia showed seasonal fluctuations in population density. Yet there has been little documentation of the recent textbook assertion (Boughley 1968: p. 40) that "Marked seasonal fluctuations in population density are encountered as frequently

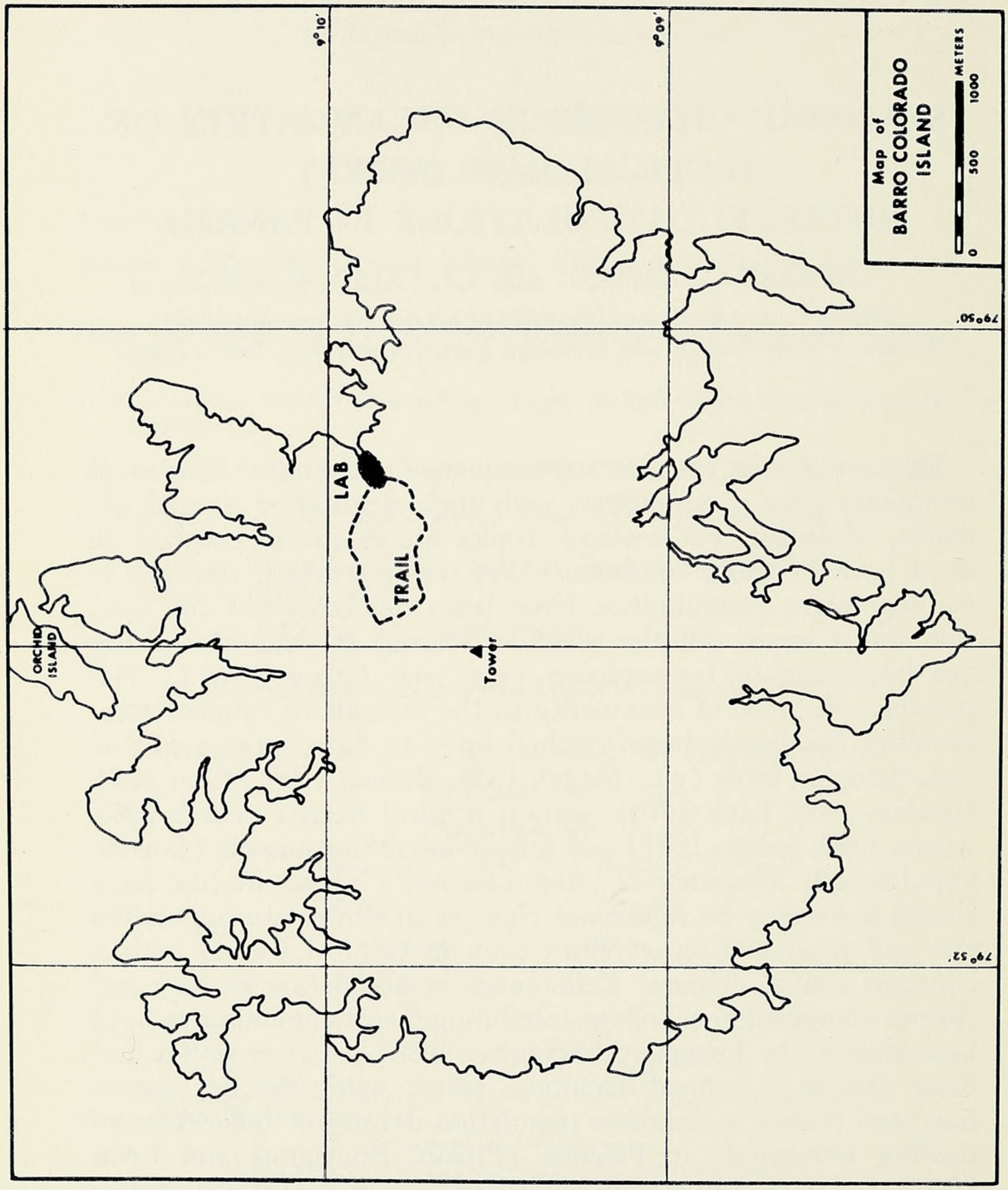

Fig. 1.—Map of Barro Colorado Island, Canal Zone, showing location of 1968-69 study areas (Laboratory Clearing and Forest trail).

in tropical . . . regions as they are in temperate." Moreover, detailed data on seasonal changes in species composition of a major animal group aside from birds (Slud 1960) are lacking for the tropical rain forest in the Americas.

The existance of seasonal change in species composition, as well as number of individuals, is a standard feature of temperate communities, especially among the arthropods but even vertebrates (e.g., birds). One group of insect species is characteristic of the spring fauna, another group of species replaces them in early summer, and so on with the changing temperature regime and food availability. However, the tropical species in rain forests would be expected to breed all year if constant temperature was the principal requirement for continuous breeding. A stable species composition in any one area should result; that is, the same group of species should be present all year. On the other hand, fluctuations in population density and even species composition could be expected from possible seasonal variation of rainfall, humidity, light intensity as affected by cloudiness, and other environmental conditions in the rain forest.

With about 4,000 species in tropical America (Seitz 1913) out of a world fauna of 12-15,000 species and their suggested impact upon evolution of the angiosperms (Ehrlich and Raven 1965), butterflies definitely qualify as a major tropical animal group of considerble ecological interest. This study examines the dynamics of faunal composition in the resident butterflies of the tropical rain forest in Barro Colorado Island, Panama, with respect to seasonal changes in active species and changes in population density from the latter half of the wet season (October-November 1968) through the major portion of the dry season (December 1968-March 1969). The viewpoint that tropical species diversity may be influenced by a "seasonal ecotone" or edge effect at the period of wet-to-dry-season transition is suggested by these faunal changes in Panamanian butterflies.

DESCRIPTION OF STUDY AREAS AND METHODS

This research was conducted on Barro Colorado Island in Gatun Lake, Canal Zone, Isthmus of Panama, from October 1, 1968, through April 12, 1969. The island is largely covered with rain forest having a canopy starting at about ninety feet, The annual rainfall is about 2700 mm at the Smithsonian Tropical Research Institute station (Moynihan, 1968). Further descriptions of the general vegetation and climate may be found in Allee (1926a, 1926b).

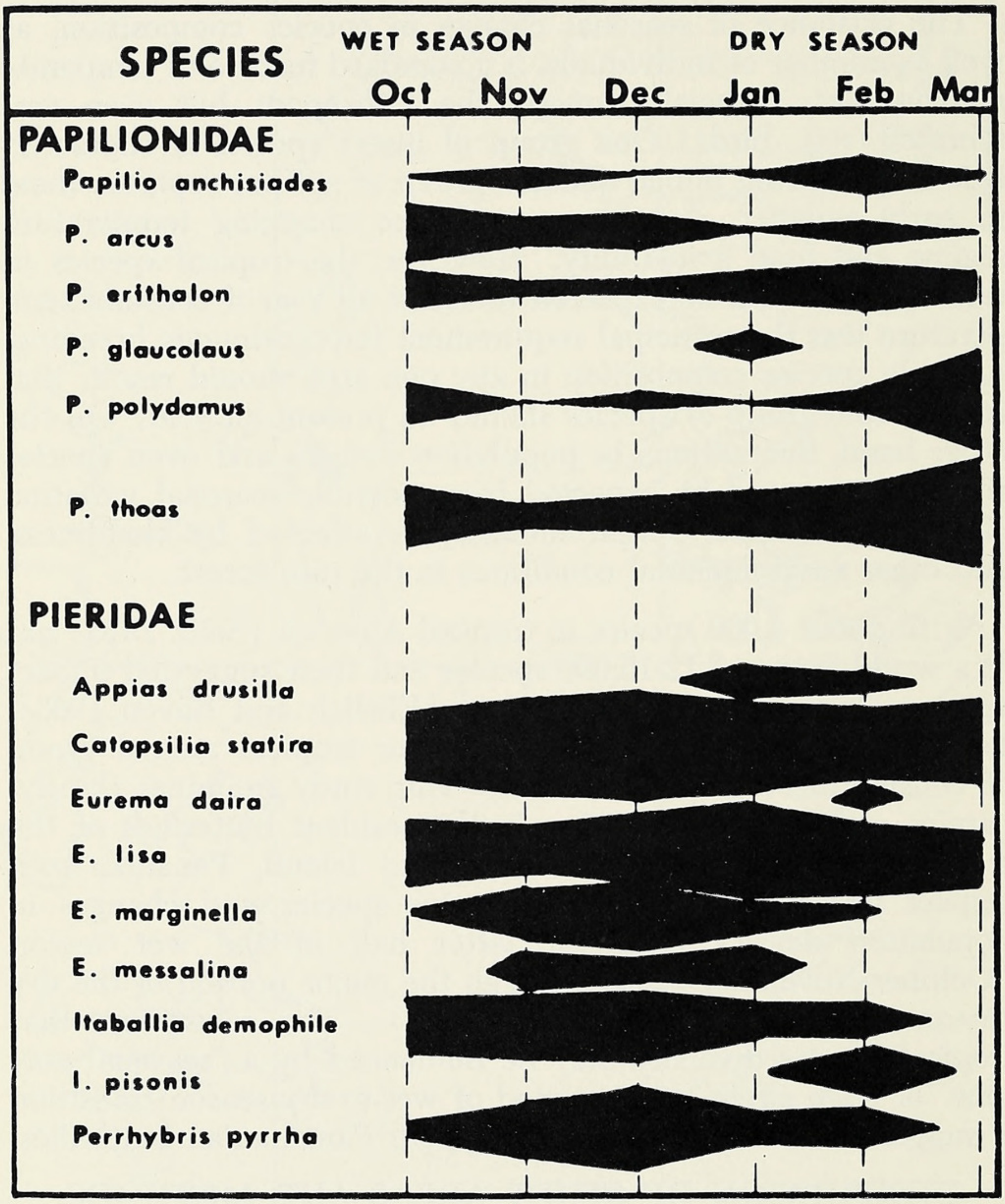

Fig. 2.—Patterns of flight activity of adult populations of butterflies in the Families Papilionidae and Pieridae, Clearing study area, October 1968 to the end of February 1969. The width of the bar indicates relative adult population density for a given species during each month (number of days species was observed out of total number of observation days).

Clearing Study Area. Most of the data reported herein were collected in the clearing extending from slightly southwest of the Smithsonian Tropical Research Institute field station northeastward to the shore of Gatun Lake, at 9°09′50″ north latitude and 79°50′25″ west longitude (see Fig. 1). This clearing measures about 778 m by approximately 286 m (the width varies considerably); the elevation at the southwestern end is 35 m higher than the northestern end at the Gatun Lake shore line (26 m above sea level). Since its establishment, the size and condition of the clearing has varied considerably through the years. Presently it is maintained in the early stages of succession, much as described by Kenoyer (1929): (1) In small areas about the buildings frequent cutting permits only grasses and annual weeds. (2) In much of the clearing where cutting occurs infrequently, plants of the second-year association are common (e.g. *Heliconia* and *Piper*). (3) Along the edges and in neglected patches throughout the clearing, species of the "pioneer forest" (e.g. *Cecropia, Ochroma,* and *Tetracera*) dominate. (4) Within the whole area introduced plants are important (e.g. *Citrus, Hibiscus, Ixora, Musa, Psidium,* and others).

Censusing of butterfly species was carried out for two hours daily on census days: one hour between 0900 and 1200, and one hour between 1300 and 1500. Specific hour periods were rotated regularly. Only 4 lycaenid and 2 hesperiid species were censused; otherwise, all species present were recorded. Field identification of flying butterflies was considered quite accurate (all species identifications were originally verified by collected specimens). All censusing was done by the second-named author (C.F.L.).

Forest Study Area. Within the rain forest species censuses were conducted weekly to record changes in forest-restricted butterfly populations. The 2,050 m trail route indicated in Figure 1 was censused from 0800 to 1030; no afternoon censuses were taken. This route ran west of the C.C.I. Laboratory on the Lathrop trail, then south and east on the Miller, Wheeler, and Snyder-Molino trails, and north on the last-named trail to the laboratory again.

RESULTS

The Clearing study area provided census data on 92 species of butterflies; these are summarized in Table 1. The relative abundance or relative population density of each species per

TABLE 1

Flight activity patters in wet and dry seasons for butterfly species in Clearing study area, October 1968 through February 1969. Figures represent percentage of total census days in a month that each species was recorded.

FAMILY Species	Relative Adult Population Density of Species*				
	WET SEASON		DRY SEASON		
	October	November	December	January	February
PAPILIONIDAE: 6 species					
Papilio anchisiades	--	4	--	--	4
P. arcus	58	22	20	--	14
P. erithalon	25	9	5	13	27
P. glaucolaus	--	--	--	9	--
P. polydamus	12	--	5	--	11
P. thoas	17	9	14	35	68
PIERIDAE: 10 species					
Appias drusilla	--	--	--	26	14
Phoebis statira and argante	42	74	82	87	77
Eurema daira	--	--	--	--	9
E. lisa	75	61	77	87	64
E. marginella	--	31	55	12	5
E. messalina	--	9	5	17	--
Itaballia demophile	50	83	86	13	18
I. pisonis	--	--	--	--	18
Perrhybris pyrrha	4	57	68	13	23
DANAIDAE: 21 species					
Dabaus gilippus	4	--	--	--	5
Lycorea cleobaea	8	--	--	--	--

Table 1: Continued

	Oct.	Nov.	Dec.	Jan.	Feb.
ITHOMIIDAE: 6 species					
Aeria eurimedia	--	--	5	--	11
Hypoleria libera	--	--	5	--	--
Hypothyris euclea	--	4	5	4	--
Mechanitis franis	--	--	9	--	--
M. isthmia	--	--	--	35	9
Tithorea tauracina	--	--	--	13	--
SATYRIDAE: 10 species					
Antirrhaea miltiades	--	--	5	--	--
Callitaera menander	17	17	9	4	--
Euptychia antonoe	--	--	--	9	14
E. gulnare	4	--	5	13	5
E. hermes	96	87	100	87	45
E. hesione	4	9	5	4	--
E. juani	--	4	--	--	9
E. labe	--	--	5	--	--
E. molina	75	43	53	65	68
Pierella luna	13	17	14	9	18
BRASSOLIDAE: 4 species					
Caligo sp.	8	--	5	--	--
Eryphanis polyxena	--	4	5	13	9
Orsiphanes fabricii	--	--	5	--	--
O. xanthicles	13	4	--	4	--
MORPHIDAE: 3 species					
Morpho peleides and amathonte	50	44	41	39	50
M. theseus	--	4	18	17	--

Table 1: Continued

	Oct.	Nov.	Dec.	Jan.	Feb.
HELICONIIDAE: 13 species					
Colaenis (Dryas) julia	42	52	91	70	64
Dione juno	29	13	9	--	--
D. vanillae	--	--	--	--	5
Heliconius (Eueides) aliphera	--	13	--	9	--
H. (E.) isabella	17	--	--	4	27
H. (E.) lybius	--	--	--	4	--
Heliconius cydno	54	70	68	50	59
H. doris	--	--	5	30	5
H. erato	88	70	77	78	86
H. ethillius	58	35	32	35	17
H. sappho	--	--	--	--	9
H. sara	71	70	68	57	23
Metamorpha dido	4	--	--	--	--
NYMPHALIDAE: 21 species					
Adelpha iphicleola	--	4	5	4	5
A. marcia	8	4	14	22	9
Ageronia (Hamadryas) februa	4	13	--	--	5
Anartia fatima	100	100	100	100	100
A. jatrophae	71	13	23	74	91
Callicore sp.	--	4	5	--	--
Catagramma sp. (peralta?)	4	--	--	--	--
C. titheas	--	4	--	4	--
Catonephele numilia	--	9	5	--	--
Myscelia cyaniris	--	--	9	--	5
Phyciodes clio	--	--	5		

Table 1: Continued

	Oct.	Nov.	Dec.	Jan.	Feb.
P. leucodesma	8	--	9	4	--
P. ofella	--	--	9	--	--
Precis lavinia	--	4	5	--	--
Prepona sp.	--	--	--	4	--
Protogonius fabius	13	--	--	4	--
Pyrrhogyra crameri	--	--	5	4	--
Taygetis uncinata	8	--	--	9	5
Temenis libera	4	48	27	30	14
Marpesia chiron	8	--	9	17	--
Victorina steneles	--	4	27	26	--
RIODINIDAE: 11 species					
Calephelis virginiensis	--	4	--	--	--
Charis chrysus	--	4	--	--	--
Eurybia patrona	--	--	5	--	--
Euselasia sp.	--	--	5	--	--
Hades noctula	--	--	5	--	--
Ithomeis eulema	--	--	--	--	9
Mesosemia sp.	4	--	--	4	--
M. telegone	13	13	--	--	--
Nymula phylleus	--	--	--	--	4
Oleria paula	4	4	--	--	9
Zelotaea pellex	--	--	5	--	--
LYCAENIDAE: 4 species tallied					
Strymon yojoa	--	--	--	--	4
Thecla hemon	--	--	--	--	4
T. jalan	--	--	--	--	4

Table 1: Continued

	Oct.	Nov.	Dec.	Jan.	Feb.
T. togarna	--	--	--	--	14
HESPERIIDAE: 2 species tallied					
Eudamus sp.	--	4	5	65	27
Hesperia syrichtus	50	13	32	52	77
TOTAL: 92 species tallied in Clearing					

*The index of relative population density of each species is recorded as the frequency of occurrence out of the total number of census days each month (see text). The numbers of census days per month, 1968-69, were: October (24), November (23), December (22), January (23), February (22). The wet season extends from June to mid December, the dry season from late December to May (see text).

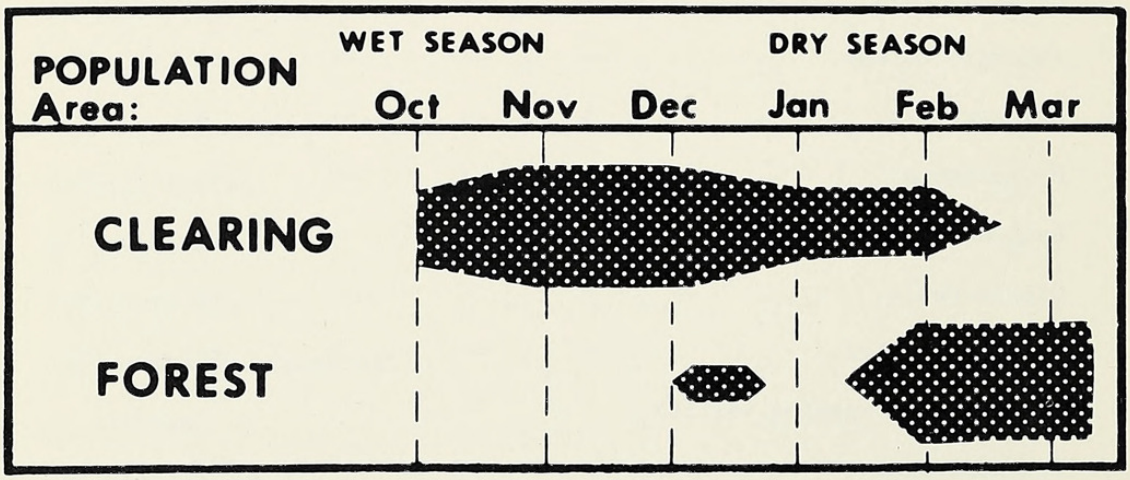

Fig. 3.—Pattern of relative flight activity in the Clearing and Forest areas. of the pierid butterfly, *Itaballia demophile*.

month is indicted as a percentage:

$$\frac{\text{Number of days sp. recorded}}{\text{Total no. of census days that month}} = \begin{array}{c}\text{Index of Relative Abundance} \\ \text{(Percentage of census days} \\ \text{each sp. was recorded).}\end{array}$$

That is, the commoner a species the higher the probability that it will show up in all census periods. For example, *Anartia fatima* (Nymphalidae) was the only species observed on all census days every month (index value of 100%), while *Papilio anchisiades* was only seen on one out of 23 days in November (index = 4%) and one out of 22 census days in February (Table 1); hence the latter species' population density was comparatively very low. The Clearing area was too large and time too limited for capture-recapture determinations of absolute population densities. However, the present method at least allowed an accurate estimate of variations in adult population density from month to month. The data for the period from October 1968 to February 1969 were collected on a comparable number of days (22 to 24; see Table 1). Only five census days were available for March 1969, and the data are not tabulated here though they support the same general trends already evident in the dry-season censuses.

The Forest study area supported a much smaller fauna; census data on the 23 species observed are given in Table 2. Here, actual numbers are given because of the variable number of census days per month and the low forest population densities which made sampling errors relatively more important.

The average rainfall and duration of wet and dry seasons for the last forty years on Barro Colorado Island are given in Table 3. The rainfall during the present study, September 1968 to March 1969, is given in Table 4. It is clear from a comparison of the two tables that the dry season began somewhat earlier than usual in 1968-69, but that December is a transition period between the end of the heaviest rains (in November) and the start of the dry season which come towards the end of December.

The data in Table 5 indicate that our censusing procedure included a full representation of the butterfly fauna of Barro Colorado Island, with the exception of the two groups of small, often secretive or fast-flying species in the families Lycaenidae and Hesperiidae.

TABLE 2. Flight activity patterns in wet and dry season for butterfly populations in Forest study area, October 1968 through March 1969.

	Forest Route:	Number of Individuals Censused on Each Date:																				
		Oct.	Nov.				Dec.			Jan.				Feb.				Mar.				
	Species*	14	1	9	16	28	5	16	30	7	14	21	27	2	8	16	22	1	8	15	22	28
1.	Callitaera menander	1	1	2		1																1
2.	Pierella luna		5	7	3	4	4	1		2	1		2	3	2	1	2	4		1	1	4
3.	Caligo sp.	1																	1		1	1
4.	Morpho sp. (blue)	3			1	1	1			1			1			1	2	1	5	4	2	1
5.	Adelpha iphicleola		1																			
6.	Myscelia cyaniris								1													
7.	Itaballia demophile							1	1				2	5	8	6	5	7	1	6	4	7
8.	Heliconius cydno								1	2											1	2
9.	Euptychia hesione								1					2				1	1	3	5	1
10.	Taygetis uncinata												2					1	3			
11.	Eriphanes polyxena												1									
12.	Euptychia juani													1								
13.	Heliconius sappho													2								
14.	Aeria eurimedia													1				1	2			1
15.	Itahallia pisonis													2	3	5	1		1			
16.	Antirrhaea miltiades																	1				
17.	Mechanitis sp.																			1		
18.	Euptychia antonoe																			2	2	1
19.	Thecla sp.																			1	1	1
20.	Catagrama denina																			1		
21.	Terias lisa																				1	
22.	Colaenis julia																				1	
23.	Temenis libera																					1

*Species arranged in order of appearence during forest-survey period, not in taxonomic groups.

TABLE 3. Rainfall in wet and dry seasons on Barro Colorado Island, Canal Zone, Isthmus of Panama (Station average, 1925 or 1926 to 1966; data calculated from Moynihan, 1968).

Month		Station Average Rainfall in mm.
WET SEASON		
May		276.6
June		276.9
July		293.9
August		329.7
September		262.6
October		347.5
November		461.3
December		269.2
DRY SEASON*		
January		57.7
February		32.5
March		29.2
April		88.4
ANNUAL TOTAL		2,712.7
DRY SEASON:	TOTAL:	207.8
WET SEASON:	TOTAL:	2,504.9

*Dry season generally starts in latter half of December. The median date for the beginning of the dry season is about December 20.

Table 4

Rainfall in the 1968-69 study period on Barro Colorado Island, Canal Zone (unpublished data from Panama Canal Company, Engineering and Construction Bureau, Meteorological and Hydrographic Branch).

Month	Station Rainfall in mm.
September 1968	179.8
October	474.0
November	262.1
December	46.2
January 1969	44.2
February	13.2
March	10.9

DISCUSSION AND CONCLUSIONS

There were far greater number of butterfly species and individuals active in the Clearing than in the Forest study areas, both in the wet season and dry season. Part of the explanation is likely an "overflow" effect, where many of the species that normally fly high in the forest canopy come down low over the clearing and are noted, but remain on top of the canopy and thus unrecorded in the forest. Further reasons for the abundance of species in the clearing undoubtedly lie in the heliothermic and thus heliophillic nature of butterfly physiology and behavior (Emmel and Emmel 1962, 1963, 1964; Clench 1966; Watt 1968). Most species, even in the tropics, require direct sunlight to raise their body temperatures above ambient levels for flight. The clearing also provides a much greater variety of nectar sources for adult feeding, and a much greater variety of of second-growth plants commonly used as larval foodplants in such groups as the Pieridae, Nymphalidae and Heliconiidae.

1. *Seasonal fluctuations in population size*

There were considerable fluctuations in population size from month to month for most species of butterflies on Barro Colorado Island. These changes were usually associated with the change from wet season to dry season, species flying mainly in one season (within the limits of the present survey). However, many species reached their population peaks during the transition period between wet and dry seasons. Fluctuations in populations of papilionid and pierid butterflies are shown in Figure 2. These changes may be due partly to changes in condition of larval food, such as has been advanced as an explanaton of fluctuations in tropical *Drosophila* populations (Pipkin 1953) where major variations in population size follow variations in the local food supply.

It is clear that later in the dry season, by the month of March, the grasses and herbs of the Clearing area become very dry or if still green, new growth has halted. Populations of some butterflies, such as the pierid *Itaballia demophile*, actually shift their activity into the cooler more humid forest from the clearing when the dry season is well underway (see Fig. 3). This shift from open areas to the forest probably accounts for the increase in number of species in the forest fauna in the dry season (Fig. 4, lower portion), although the dry season also probably presents more favorable environmental conditions for adult flight

Table 5. Comparison of species recorded in the butterfly fauna of Barro Colorado Island by Huntington (1932) and those censused in the present study.

FAMILY Group	Huntington	Present Study
Papilionidae	5 species	6 species
Pieridae	13	10
Danaidae	4	2
Ithomiidae	11	6
Satyridae	16	10
Brassolidae	2	4
Morphidae	2	3
Heliconiidae	12	13
Nymphalidae	27	21
Riodinidae	40	11
Lycaenidae	34	4*
Hesperiidae	99	2*

* = only these species censused; others observed.

and reproductive activities for the permanent forest species.

As just suggested, the influence of rainfall on adult activity may also play an important role in causing seasonal population fluctuations. The total number of hours of sun per day available to the butterflies for flying and reproductive activity was considerably less in the wet season than in the dry season due to afternoon cloudiness and rain. In a long-term or seasonal sense, then, it is selectively advantageous to have a species' main flight period in a time other than the wettest part of the rainy season. The most advantageous time to fly and reproduce during the year would seem to be the period immediately following the close of the wet season, for later in the dry season (when environmental conditions are still excellent for adult activity) the larval foodplants may not be in suitable condition for feeding by newly-hatched larvae. The apparent reality of this supposition is reflected in the following data on changes in faunal organization from the wet season to the dry season.

2. *Seasonal fluctuations in species diversity.*

When the number of species flying in the Clearing and Forest study areas are graphed for each month (Fig. 4), it is clear that (1) diversity in the Forest area increases in the dry season but it is still at a relatively low level compared to that of the Clearing fauna, and (2) diversity in the Clearing fauna, containing clearly the species requiring a higher level of sunlight for activity, reaches a *maximum diversity* during the *Transition Period* immediately following the Wet Season, before the Dry Season conditions fully prevail.

This surprising confirmation of the preceding suppositions (section 1) leads us to propose this as an example of a perhaps more widespread phenomenon in the tropics: a "Seasonal Ecotone." An ecotone, simply defined, is merely "a transition area between two adjcent communities" (Webster's New Collegiate Dictionary). Treating the wet-season butterfly fauna and the dry-season fauna as separate communities, the transition period between the wet and dry seasons may be called a "Seasonal Ecotone," and is simply a temporal analogy of the spatial concept of an ecotone. This seasonal ecotone may be a general phenomenon in influencing tropical species diversity, in that one could find the greatest number of active species (of short-life-cycle animals) between two distinct seasons, merely because both wet and dry season communities may be represented. The broader application of the seasonal-ecotone concept is currently being considered for a number of tropical and

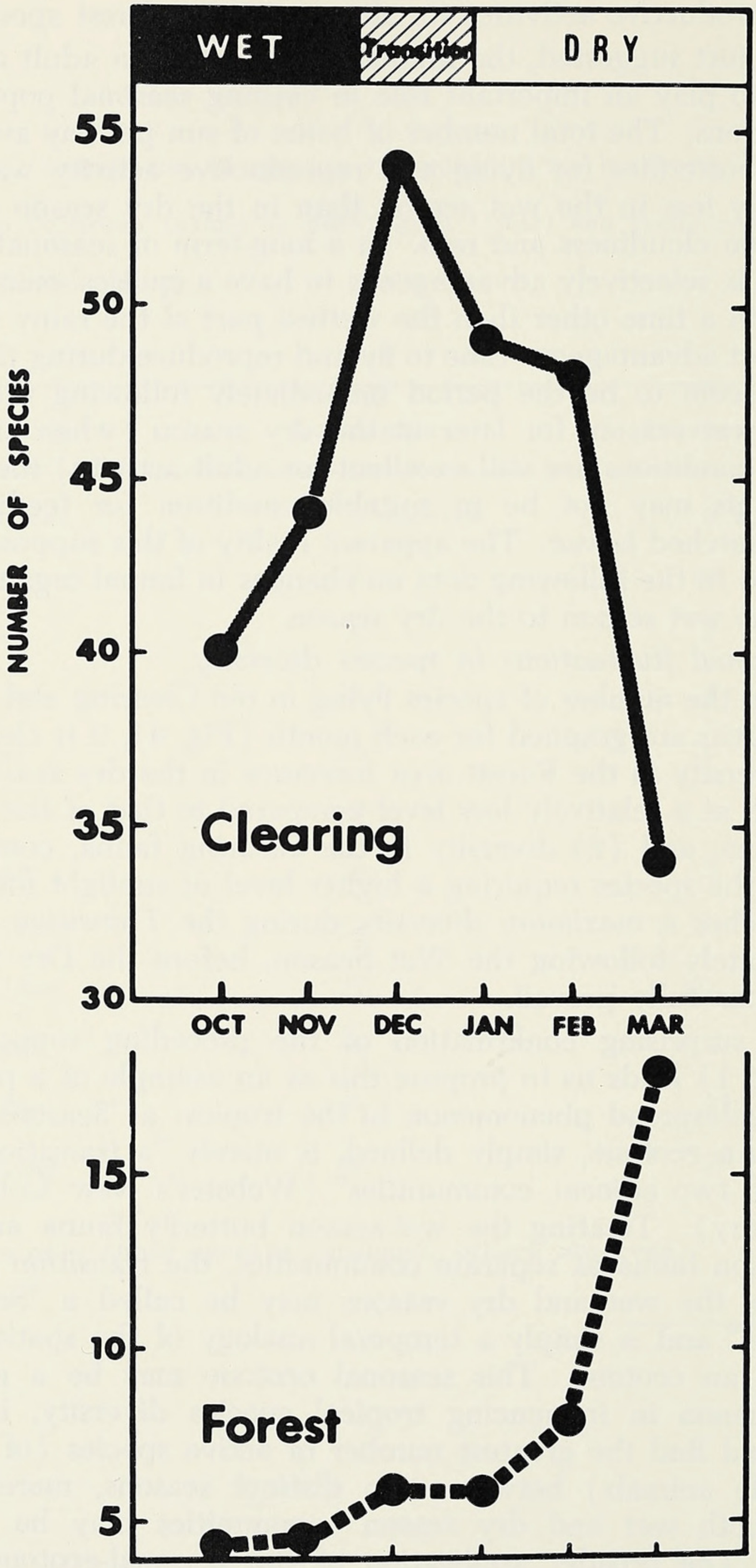

Fig. 4.—Number of butterfly species observed in Clearing (top) and Forest (bottom) study areas per month from wet to dry season, 1968-1969.

temperate animal groups (Emmel, in preparation). However, it is clear with diurnally-active insects such as the butterflies that the most reproductively favorable conditions also may exist at this time and hence the seasonal ecotone fauna does not merely represent an overlapping of communities but one which has responded in an evolutionary sense to the most satisfactory breeding period during the annual cycle (which exists even in a tropical evergreen forest.) Preliminary review of data from Costa Rican sites and elsewhere (Emmel, in preparation) indicates that diversity increases only at the gradual wet season-dry season seasonal ecotone (December in the northern Neotropics), not at the sharp point of dry season-wet season transition (April or May in the northern Neotropics). This presumably is the result of dry-season-species' adult intolerance of the rainy conditions suddenly initiated by the start of the wet season.

SUMMARY

Butterfly faunal censuses were made in a large clearing and in the rain forest on Barro Colorado Island, Panama, during the wet season and dry season, 1968-69. There were significant changes in both population densities and species composition (as represented by flying adults) from month to month and between climatic seasons at this tropical site. These fluctuations are apparently associated with available sunlight for thermoregulation and with condition of larval hosts.

The greatest number of species flies at the transition period between the wet and dry seasons. This "seasonal ecotone" is probably due to both an overlapping of dry- and wet-season faunas and to the favorable junction of environmental factors for adult activity by tropical butterflies at that particular time.

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