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SEASONALITY AND PHENOLOGY OF THE BUTTERFLIES (LEPIDOPTERA: PAPILIONOIDEA AND HESPERIOIDEA) OF MEXICO'S CALAKMUL REGION

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Abstract

The phenology of butterflies was analyzed in the Calakmul Region (CR) in the state of Campeche, México, over the course of 3 years. Altogether, 60,662 individuals were recorded, consisting of 359 species in 207 genera, 18 subfamilies, 5 families, and 2 superfamilies. Greatest species diversity was recorded during Oct and Nov. Monthly fluctuation in diversity was defined by rare species. Hesperiidae (135 species) and Nymphalidae (111 species) were the most diverse families, and showed the greatest variation with respect to distribution of species richness throughout the year. Papilionidae showed the greatest species richness during the dry season. Pieridae, Nymphalidae, and Lycaenidae showed peaks of greatest species richness and relative abundance during the rainy season. Results were compared to faunal studies of the Sierra de Atoyac de Álvarez, in the state of Guerrero, and of the Sierra de Manantlán, in Jalisco and Colima. Important similarities were observed among phenological patterns in the butterfly fauna of the 3 regions, especially between CR and Manantlán. The phenology of species with greater relative abundance was analyzed in relation to wingspan as a parameter of adult size. The small and medium-sized groups, taken together, showed variations in species richness. An analysis of species seasonality was conducted with NMDS, ANOSIM and SIMPER, in the program PRIMER 4.0. Differences among the composition of butterfly communities with respect to the seasons were found.

Key Words: Calakmul Biosphere Reserve, rare species, Yucatán Peninsula

Resumen

La fenología de las mariposas fue analizada en la región de Calakmul (CR), Campeche, México. A lo largo de tres años se registraron 60,662 individuos, de 359 especies en 207 géneros, 18 subfamilias, cinco familias, y dos superfamilias. La mayor diversidad fue registrada durante octubre y noviembre. La fluctuación mensual de la diversidad fue definida por las especies raras. Las familias con mayor diversidad fueron Hesperiidae (135 especies) y Nymphalidae (111 especies) y presentaron la mayor variación con respecto a la distribución de la riqueza de especies a través del año. Papilionidae mostró la riqueza más grande de especies durante la estación seca. Pieridae, Nymphalidae y Lycaenidae presentaron sus máximos de riqueza de especies y abundancia relativa durante la estación lluviosa. Se hizo una comparación entre el presente estudio y los de fauna de Atoyac de Álvarez, en el estado de Guerrero, y de Manantlan, en Jalisco y Colima. Se observaron semejanzas entre la fenología de las tres regiones, especialmente entre CR y Manantlan. La fenología de las especies con mayor abundancia relativa fue analizada en relación a la envergadura alar como un parámetro del tamaño de las especies. Los grupos pequeños y medianos, en conjunto, muestran variaciones en la riqueza de especies. Se realizó un análisis de estacionalidad de especies con las matrices de datos, aplicando NMDS, ANOSIM y SIMPER con el programa PRIMER 4.0. Se encontraron diferencias en la composición de las comunidades de mariposas con respecto a las estaciones.

Translation provided by the authors.

Phenology is the study of the sequence of determined biological events; this type of observation began with the first agrarians of various cultures (Williams-Linera & Meave 2002; Shapiro et al. 2004). With respect to insects, phenology is defined as the process of the appearance of different stages in the life cycle of a taxonomic group over the course of a year, and across several seasons (dry and wet or warm and cold periods). Among butterflies, this phenomenon has generally been described based on the appearance of the adult stage or imago of various species. The presence and activity of each generation has been explained as a function of diverse climatic or vegetation factors, such as temperature, precipitation, seasonality of vegetation, food availability, and food quality. Phenological patterns in butterflies may be determined by fruiting or flowering plants (Tanaka & Tanaka 1982; Young 1982; Scott 1986; Wolda 1987, 1988a), annual humidity distribution (Wolda 1987), cloudiness (Luis & Llorente 1990), photoperiodic changes (Shapiro 1975), substrate availability and palatability of larval food plants (Owen et al. 1972).

As with most other insects, butterfly life cycles are strictly linked to seasonal changes (Owen 1971), such as temperature, day length or photoperiod, and humidity, among others. Species richness is influenced by climatic factors, which determine reproduction and survival conditions, and therefore dictate the number of individuals or biomass documented. Voltinism is defined as the relationship between life cycle, annual climatic behavior, and the number of generations per year. Depending on the number of generations per year, terms such as univoltinism, bivoltinism, trivoltinism and multivoltinism are used to characterize the phenology of a population, species, or taxon (Gullan & Cranston 2000). Flight in adults is fundamental to conducting diverse vital actions such as feeding, reproduction, and oviposition. Given that butterflies are heliothermic organisms, their flight is dependent upon sunlight (Shapiro 1975). Gilbert & Singer (1975) and Shapiro (1975) suggested that interactions with hostplants and climate may explain most of the distributional patterns seen among Lepidoptera. Shapiro (1975) emphasized that this seasonal history tends to be extremely conservative even at the family level; an example is the stage at which diapause takes place (e.g., various Pieridae as pupae and many Lycaenidae as eggs).

The phenology of an insect fauna is summarized by the pattern of species emergence throughout the year, which shows records obtained through several generations during several years. When studying phenology, we can distinguish at least 3 principal components of the insect community. The first component refers to species that are present year after year, regardless of the particular environmental conditions of any given year. The second component consists of species occurring in a given season, generally univoltine species. The third component consists of species whose abundance is too low to determine their seasonality.

Describing insect phenology is a complex endeavor. Species behavior, relative abundance, and the sampling methods are usually biased towards certain taxonomic groups. Often, information obtained on relative abundance does not correspond with reality. For example, greater efforts are generally employed in collecting rare or very localized species, and less effort is usually made to collect abundant or common, vagile, and widely distributed species (eurytopics) (Pozo et al. 2005).

The objective of this paper is to describe seasonal and phenological patterns of the butterfly community (Papilionoidea and Hesperioidea) in the tropical forest of the Calakmul region, based on 2 different methodologies, with data collected during 26 months over the course of 3 years.

MATERIALS AND METHODS

Study Area

The Municipality of Calakmul is located in southeastern Campeche State, Mexico, in the center of the Yucatan Peninsula. With an area of 16,806 km^2, Mpio. Calakmul borders the State of Quintana Roo to the east and the Department of El Petén, Guatemala, to the south. Almost half of the municipality was placed under protection by decree of the Calakmul Biosphere Reserve (CR) in 1989 (Fig. 1). The reserve includes an area of 7,232 km^2, with an altitude 100 to 300 m above sea level. The Reserve has a semi-humid, warm climate. Annual precipitation ranges from 600-1200 mm, and annual average temperature is 24.6°C (Fig. 2) (INEGI 1996). The dry season extends from Feb to May, followed by the rainy season from Jun to Sep, which in turn is followed by the "nortes" (or cold) season, from Oct to Jan. "Nortes" refer to frequent fronts of cold winds that cross the Gulf of Mexico and carry humidity from a NE to SW direction (Williams-Linera & Meave 2002).

In the CR, 7 vegetation types are found: tall tropical evergreen forest, medium height tropical semi-evergreen forest, medium height tropical semi-deciduous forest, savanna, low tropical semi-evergreen forest, low tropical semi-deciduous forest and, low tropical semi-deciduous seasonally flooded forest. The medium height tropical semi-evergreen forest and low tropical semi-deciduous forest dominate the landscape within the CR (Martínez & Galindo-Leal 2002).

Sampling

The butterfly fauna of CR was surveyed during 266 d distributed over 26 months, across 3 years (Mar 1997-Dec 1999), representing approximately 5562 person-h and 8840 trap-h (Table 1). Sampling was conducted at sites dominated by the most representative vegetation types of the region, medium height tropical semi-evergreen forest (selva mediana, or Upland Standard Forest *sensu* Schulze 1992) and low tropical semi-decid-

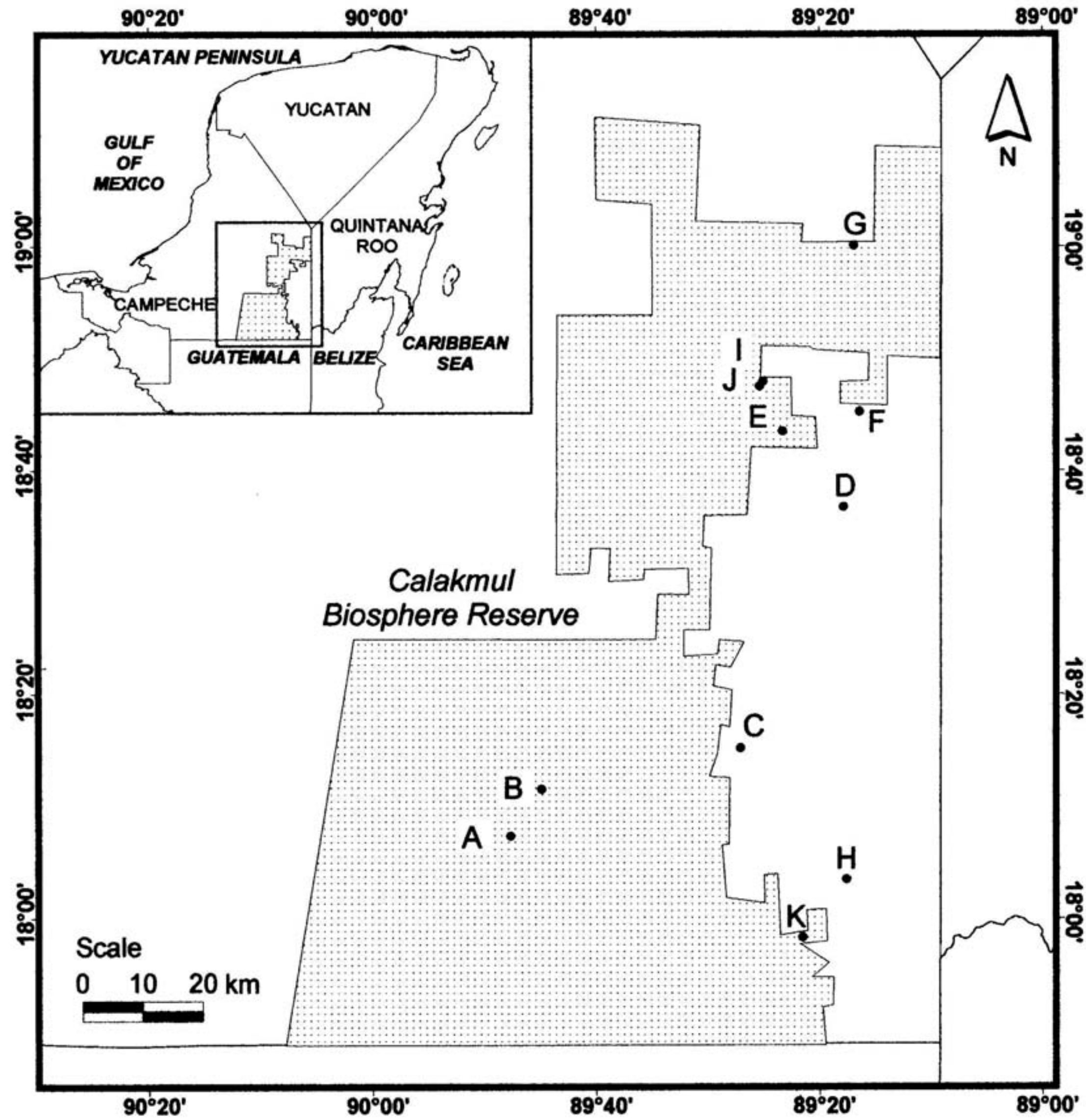

Fig. 1. Location of the 11 study sites within and near the Calakmul Biosphere Reserve: A = Calakmul Archeological Zone; B = road to Calakmul Archeological Zone; C = Narciso Mendoza Ejido; D = Nuevo Becal Ejido; E = entrance to El Papagayo; F = path to Flores Magón; G = north of Mancolona; H = Plan de Ayala Ejido; I = west of El Refugio Ejido, with medium tropical semi-evergreen forest; J = west of El Refugio Ejido, with low tropical semi-deciduous forest. Ejido = communal property.

uous forest (selva baja or Low Forest *sensu* Rzedowski 1983), as determined by botanist Esteban Martínez. Within each forest type, transects of 500 m were established within habitat types of different successional stages, including primary forest, forest disturbed more than 10 years ago, and forest disturbed within the past 10 years. In each habitat type, replicate transects were sampled (separated by at least 300 m), for a total of 18 transects in the first year, and 12 transects during the second and third years (Table 2), at a total of 11 localities. Six localities are within or near the northern portion of the CR, and 5 are within or near the southern part of the CR (Fig. 1).

The first year, sampling was conducted 4 tines each season at each locality. The second year, sampling was conducted only during the months of greatest butterfly abundance, from Jun to Nov. The third year, all localities were sampled monthly. Two sampling methods were utilized, di-

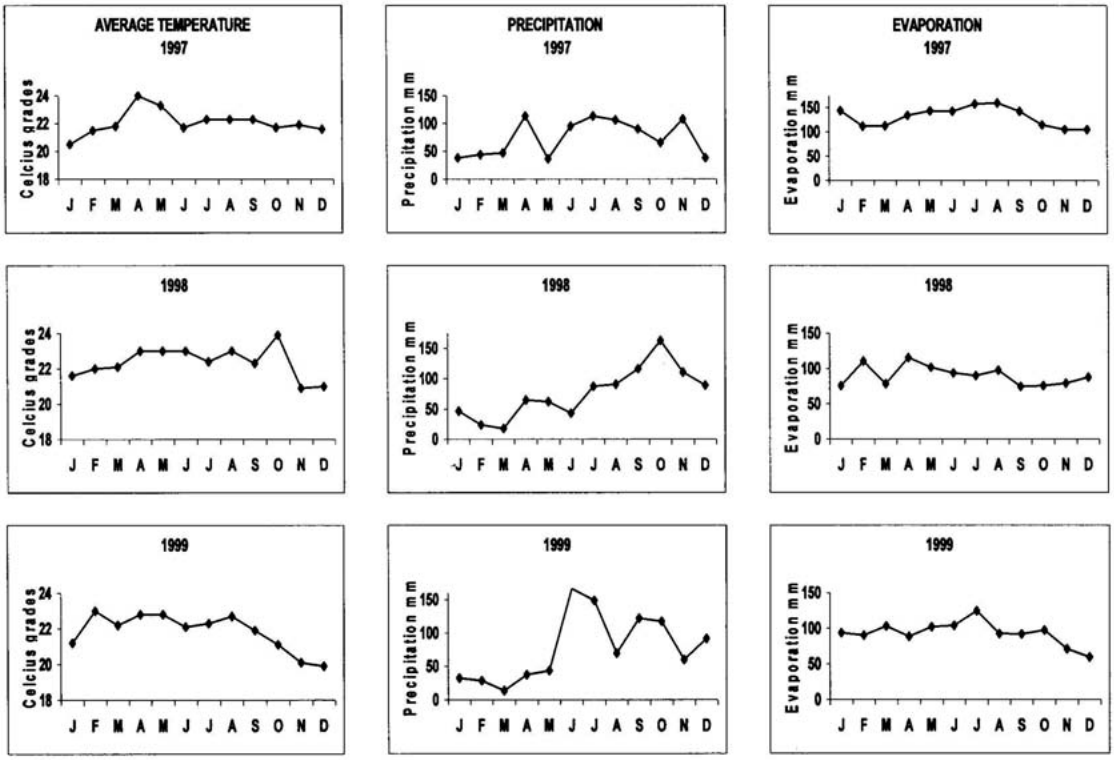

Fig. 2. Annual evaporation levels, precipitation and temperature recorded for 1997, 1998, and 1999 at the Zoh-Laguna Research Station in the Calakmul region.

rect search (DS) and transects (T). For each method, 2 sampling techniques were employed: traps with bait (t) and entomological nets (n). Transects (T) were established through the forest by clearing a small path of 500 m length, with a machete, and wide enough to permit the passage of the observer without altering the canopy. In each transect, 10 Van Someren-Rydon traps (Rydon 1964) baited with banana, pineapple, and beer, were hung (from 0700 to 1800 h) at 50 m intervals, on alternate sides of the path. Fresh bait was added each morning. Two surveyors spent 120 to 150 min in each transect. Surveyors walked each transect, spending 10 min at each trap to record trap contents (on a pre-prepared form) and sample nearby individuals with entomological nets. Direct Search surveys (DS) were more opportunistic. These were conducted by walking along roads (2 observers for approximately 8 h per d) in search of sites where butterflies were concentrated (sunny gaps, nectar sources, damp ground, etc.), sampling butterflies as opportunities were encountered. In addition, 10 traps baited with fermenting fruit (as above) were placed in "optimal" localities along the roadsides and checked periodically.

Upon determination to species-level, trapped butterflies were usually released. In cases where the identity of a trapped butterfly was uncertain or unknown, it was collected for determination at,

TABLE 1. NUMBER OF DAYS PER MONTH SAMPLING WAS CONDUCTED, INCLUDING ANNUAL TRAP-HOURS AND MAN-HOURS, FOR 1997, 1998, AND 1999.

	J	F	M	A	M	J	J	A	S	O	N	D	Total	Trap-hours	Man-hours
1997	—	—	12	12	—	12	—	12	—	14	12	12	86	3440	2322
1998	13	—	—	—	—	—	13	11	14	9	9	8	77	2310	1386
1999	3	9	9	10	7	7	8	10	11	9	12	8	103	3090	1854
Total													266	8840	5562

TABLE 2. TRANSECTS IN EACH HABITAT TYPE SURVEYED IN 1997, 1998, AND 1999.

Vegetation type	Primary			Disturbance >10 years			Disturbance <10 years		
	1997	1998	1999	1997	1998	1999	1997	1998	1999
MT[a]	3	2	2	3	2	2	3	2	2
LT[b]	3	2	2	3	2	2	3	2	2
Total	6	4	4	6	4	4	6	4	4

[a]Medium tropical semi-evergreen forest.
[b]Low tropical semi-deciduous forest.

and integration into the Zoology Museum at El Colegio de la Frontera Sur, Chetumal, Mexico (duplicate specimens are deposited at the Zoology Museum of the Universidad Nacional Autónoma de Mexico, Mexico City). To determine the extent to which released butterflies may be re-trapped and re-counted, all individuals released for a 3-month period were marked before release, and recapture data was collected. Recapture data confirmed that once released from a trap, individuals did not usually return to traps (Hughes et al. 1998). However, only long-lived and phylopatric species, or those with a small "home range" could cause a bias in the data through recaptures, and few such species were encountered in the CR.

Data from fieldwork were entered into the database of the Lepidoptera collection at the Zoology Museum at ECOSUR, representing a total of 60,662 records of 359 species, in 207 genera, from 18 subfamilies, 5 families and 2 superfamilies (nomenclature follows Llorente et al. 2006; A. Warren 2000, except that for the analyses we considered the families Riodinidae and Lycaenidae together).

Analysis

Monthly species abundance (phenology) and seasonal distribution (seasonality) data were analyzed. In order to describe phenological patterns, analyses were divided into 2 parts. First, the total number of individuals and species recorded was considered, and a family-level analysis was conducted (Shapiro 1975). Second, the phenology of the most abundant species was analyzed (species with 100 or more records during the 3 years of sampling. The abundant species were divided into 3 size categories (Young 1982; Vargas-Fernández et al. 1999). Because of the great diversity of butterfly species within the CR, adult size showed great variability (e.g., *Pyrisitia nise nelphe*) (R. Felder 1869), (forewing length = 17 mm ± 0.9 mm) and *Leptotes cassius cassidula* (Boisduval 1870), (12.7 mm ± 1.1 mm) *vs. Archaeoprepona demophon centralis* (Fruhstorfer 1905), (54 mm ± 4.4) and *Morpho achilles montezuma* Guenée 1859 (67 mm ± 4.0 mm). Wingspan intervals were used as a proxy of body size (Vargas-Fernández et al. 1999). The 3 arbitrary wingspan size categories were: small (≤30 mm), medium (31-50 mm), and large (≥51 mm).

Seasonality

For each year, a data matrix was constructed, which recorded the species and their abundance in each season (dry, rainy, and cold or "nortes"). An NMDS analysis was applied to each matrix. Data was log-transformed according to the Box and Cox test (Legendre & Legendre 1998). For these analyses we used PRIMER 4.0 software (Carr 1996), and results were graphed with SigmaPlot Version 7.1, Systat. In order to statistically evaluate differences among groups in each season, an ANOSIM test (ANalyis Of SIMilarities) was applied, and subsequently, a SIMPER (SIMilarity PERcentages) analysis was applied to detect species that contributed to group formation, and those species which acted as discriminants among groups (Herrando-Pérez 2002).

RESULTS

Phenology

In general, the phenological patterns found in this study are similar to those described by de la Maza and de la Maza (1985a, b) and Austin et al. (1996), with peak butterfly diversity at the end of the dry season and another peak during the rainy season. Reduced species diversity was observed from the end of the rainy season to the middle of the dry season (Fig. 3). Nine percent of the Calakmul butterfly species have been recorded in every month; similarly, Austin et al. (1996) reported 10% of the butterfly fauna from the Tikal area, Guatemala (about 100 km S of Calakmul), from all months.

The month with the greatest species richness was Oct 1997, with 231 species, and the month with the greatest relative abundance was Aug 1998, with 17,324 individuals (more than the 1997 annual total of 16,257 records). Maximum species diversity was observed during Oct and Nov, in agreement with previous studies in México (Vargas-Fernández et al. 1992, 1999). This pe-

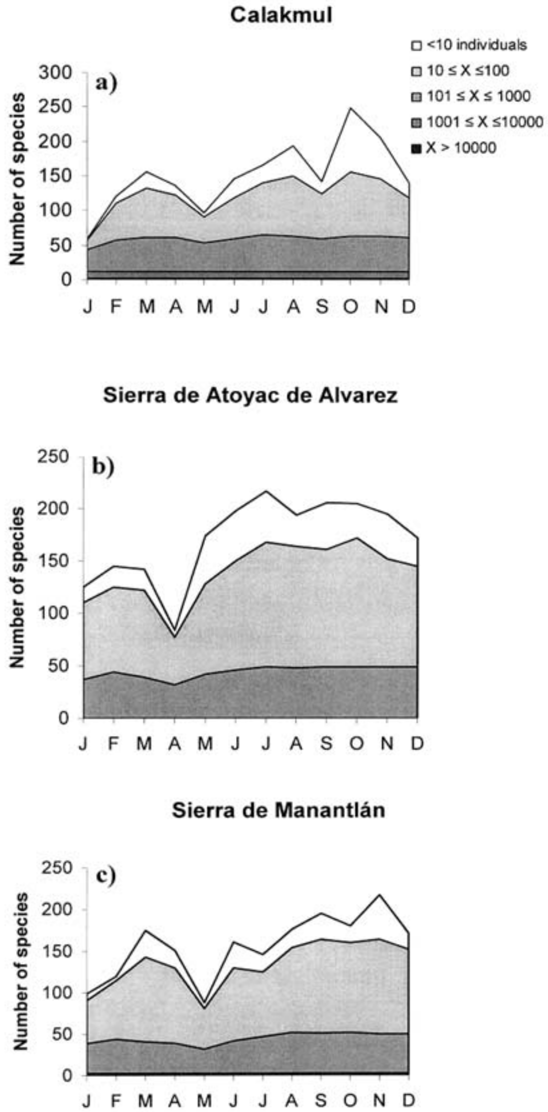

Fig. 3. a) Phenological pattern of the butterfly fauna of the Calakmul region, showing species abundance throughout the year; b) phenological pattern of the butterfly fauna of the Sierra de Manantlán, Jalisco-Colima; c) phenological pattern of the butterfly fauna of the Sierra de Atoyac de Álvarez, Guerrero.

riod coincides with the end of the rainy season. The year with the greatest species richness was 1997, with 265 species recorded (74% of the total species number), although a similar diversity was observed in 1998 (261 species). During 1999, species richness decreased to just 58% of the total species diversity recorded in this study.

Large numbers of records for any given month do not necessarily indicate great species diversity. The greatest number of records obtained during any month of the study was 17,324 records in Aug 1998, representing 28.56% of the total records obtained during this study. However, these individuals represented only 108 species (Table 3), and 3 migratory species comprised 86.5% of the sample: *Memphis pithyusa* (R. Felder, 1869), *Anaea troglodyta aidea* (Guérin-Ménéville, 1844) and *Eunica tatila tatila* (Herrich-Schäffer, 1855). *Memphis pithyusa* was the most frequently recorded species in this study, with 12,848 records (Table 6).

Table 4 shows that 90.8% of the species recorded during this study were represented by only 19.7% of the recorded individuals. Species which were present from 9 to 12 months equaled 28.4% of total species recorded, and 95.4% of the total number of records. There were 140 species present during 6 or more months of the year (98.1% of all records), while 178 species were recorded only during 3 or fewer months, representing half of the fauna studied (49.58% of species and 1.31% of records). Among species surveyed in this study, 183 are represented by 10 or fewer records (60 of which were only recorded once). These are the "rare" species and represent 0.001% of the total number of records.

Butterflies were divided into 5 groups according to their relative abundance (Fig. 3). The first group contains species represented by 10 or fewer records (183 species), the second group by 11 to 100 records (110 species), the third by 101 to 1000 records (55 species), the fourth by 1001 to 10,000 records (10 species) and the fifth by more than 10,000 records. This last group only included one species (*M. p. pithyusa*). Monthly variation in species richness is clearly defined by the first 2 groups, represented by 293 species (81.6% of total species richness and 7.5% of total relative abundance), 96 of which were recorded during only 1 month (of those, 35 in Oct), and 60 of these represented by only 1 individual (21 in Oct) (Fig. 3). Table 4 shows species frequency by month, from those present all year (33 species), to those recorded only during 1 month. It is remarkable that half of the fauna (178 species) was recorded during 3 or fewer months, whereas 84 species were present during 10 or more months. Thus, half of the species are strongly seasonal (49.6%).

The 2 peaks in species richness coincide with the greatest relative abundance (Fig. 3a and Table 3). The largest peak was observed from Jun to Dec, which corresponds with the rainy season, although there were markedly fewer species during Sep. The smaller peak was observed from Feb to Apr. We estimated that a minimum of 110 species should fly each month, if we consider that 28-35% of species in this study were found during the entire year, and every year.

Family Level Phenology

The most diverse families in the study area are those showing the largest variation in species

TABLE 3. SPECIES DIVERSITY AND ABUNDANCE OF THE BUTTERFLY FAUNA OF THE CR.

Year	J	F	M	A	M	J	J	A	S	O	N	D	Total
Species													
1997			102	95		112		152		231	187	122	265
1998	50						103	108	137	101	74	60	261
1999	35	121	131	119	98	94	142	90	74	73	72	53	208
1997-1999	59	121	157	138	98	147	168	196	144	250	207	143	359
Individuals													
1997			800	1985		1414		2325		4277	3739	1717	16257
1998	1075						4002	17324	4621	2984	1403	680	32089
1999	320	1712	2232	1308	524	482	1906	1408	571	527	832	494	12316
1997-1999	1395	1712	3032	3293	524	1896	5908	21057	5192	7788	5974	2891	60662

richness throughout the year (Hesperiidae = 135 species, Nymphalidae = 111 species; Fig. 4). In contrast to other families, peak diversity of Papilionidae was observed during the late dry season into the early rainy season, as reported by Austin et al. (1996) for the Tikal area. Relative abundance of Papilionidae was distributed irregularly throughout the year, but the greatest number of individuals (27.5%) was recorded in Apr (Table 5); the greatest species richness was in Jul (13 species), Apr (11 species) and Aug (11 species). Diversity and relative abundance of Pieridae species remained more or less constant throughout the year, showing a slight increase during the rainy months of Aug to Nov; Oct was the peak month for species richness (with 21 species) as well as relative abundance. Hesperiidae, Lycaenidae, and Nymphalidae showed 2 periods of increased species richness: the first (and lesser) occurred during the dry season, while the second (and greater) occurred during the rainy season; these two periods are separated by the dry month of May when a decreased species diversity was observed. Specifically, the greatest species diversity for Lycaenidae was Oct (44 species; a second peak in Mar with 25 species), with the greatest relative abundance in Aug; the lowest species diversity and relative abundance among Lycaenidae was observed in Jan. The greatest species diversity for Nymphalidae was observed in Oct (with a smaller peak in Mar), while the greatest relative abundance was in Aug (with a smaller peak in April). The difference in abundance of Nymphalidae between dry and rainy seasons was greatly accentuated: 90% between the months of highest and lowest abundance (Table 5). Similarly, over 2 times as many species of Lycaenidae, and over 3 times as many species of Hesperiidae were recorded in the rainy season than in the dry season (Table 5).

Phenology of Abundant Species Related to Size

Sixty-eight species were considered abundant (Table 6), and 75% of these were recorded from all months. These species are distributed among 5 families, but most (51 species) are nymphalids.

TABLE 4. NUMBER OF MONTHS IN WHICH A NUMBER OF SPECIES AND INDIVIDUALS WERE DETECTED. FOR EXAMPLE, 19 SPECIES WERE DETECTED DURING 7 MONTHS OF THE YEAR.

Number of months	Number of species	Percentage	Cummulative percentage	Number of individuals	Percentage	Cummulative percentage
1	96	26.74	26.74	231	0.38	0.38
2	60	16.71	43.45	363	0.60	0.98
3	22	6.13	49.58	203	0.33	1.31
4	20	5.57	55.15	260	0.43	1.74
5	21	5.85	61.00	378	0.62	2.37
6	11	3.06	64.07	442	0.73	3.09
7	19	5.29	69.36	556	0.92	4.01
8	8	2.23	71.59	348	0.57	4.58
9	18	5.01	76.60	1557	2.57	7.15
10	21	5.85	82.45	2770	4.57	11.72
11	30	8.36	90.81	4846	7.99	19.71
12	33	9.19	100.00	48708	80.29	100.00
Total	359	100.00		60662	100.00	

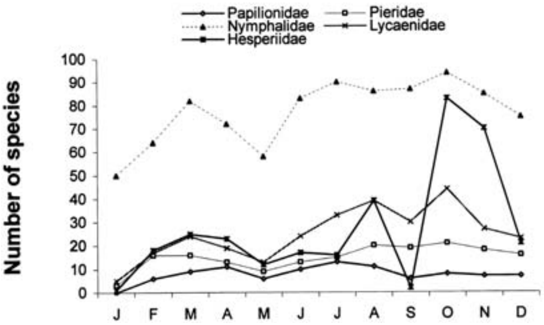

Fig. 4. Phenological patterns displayed by butterfly families present in the Calakmul region (for this figure, Riodinidae is included within Lycaenidae).

These 68 species represent 91.6% of the records obtained in this study, but represent only 18.9% of the total species richness. Out of the 3 groups formed according to size categories, 25 species are small, 32 are medium, and 11 are large.

Some variation exists with respect to seasonal trends in species richness of the 3 size categories (Fig. 5). For the small-sized group, a difference of 40% exists between the months of greatest and least species richness. For medium-sized butterflies, this difference is 31.25%, and for large butterflies, a 36% difference exists. Figure 5b shows the largest relative abundance for the 3 categories from Jun to Dec, with a strong decrease during Sep.

Seasonality

Butterfly diversity was found to be significantly variable among dry, rainy, and cold seasons (Fig. 6 and Fig. 7) during each year of the study (1997: stress = 0.15; 1998: stress = 0.05; 1999: stress = 0.18). Of the 359 species used for this analysis, 9% (32 species) provided more than 80% of the effective data when grouping the communities in each of the 3 seasons (Table 7), 50% of differentiation among communities of each season was determined by the relative abundance of 31 species (8.6% of the total). Of the 32 species comprising the communities in each season, 2 did not contribute to the distinction among communities (*Myscelia cyaniris cyaniris* Doubleday (1848) and *Siderone galanthis* (Cramer 1775)), and 1 did not contribute to the formation of groups (*Marpesia chiron marius* (Cramer 1779)), although it did when groups were analyzed separately. Of these 32 species, only 3 did not belong to Nymphalidae: *Kricogonia lyside* (Godart 1819), *Glutophrissa drusilla tenuis* (Lamas 1981) and *Polygonus savigny savigny* (Latreille, (1824)) (Table 7).

When species richness by family in each season is considered (Fig. 7a), it is clear that Hesperiidae differed in phenological behavior from the other families. This family had the greatest species richness in the cold season, with values more than double of those observed during the rainy and dry seasons. Nymphalidae and Lycaenidae showed maximum species richness during the rainy season, with a slight decrease in the cold season, while Pieridae and Papilionidae showed minimal variations. Pieridae showed a slight increase during the rainy season, at a time when diversity of Papilionidae decreased to values lower than those of the dry season.

Relative abundance by season was strongly influenced by Nymphalidae (Fig. 7b). Seasonal differences among the other families were not detected on this scale, due to the abundance of nymphalid species. Nevertheless, abundance of Hesperiidae showed an increase in the cold season (Table 5).

Discussion

Phenology Considering the Relative Abundance of Species

Wolda (1988b) concluded that there are differences in phenological patterns among insect faunas typical of temperate and tropical zones. Under the assumption that seasonal changes are minimal in the tropics, adults of the majority of species should be present throughout the year (Owen 1971), whereas in temperate zones adults are restricted to the most favorable seasons (usually spring and summer). Nevertheless, upon examining climatic variations for each year of our

Table 5. Temporal distribution of the relative abundance of butterflies in the CR. Underlined numbers indicate maximum values.

Taxon	J	F	M	A	M	J	J	A	S	O	N	D	Total
Papilionidae	0	9	73	168	69	43	83	54	22	31	26	32	610
Pieridae	9	125	256	303	38	73	235	414	264	460	347	198	2722
Nymphalidae	1363	1384	2408	2599	333	1609	5248	20127	4698	6409	5239	2508	53922
Lycaenidae	22	108	171	135	56	122	214	372	173	280	163	100	1916
Hesperiidae	1	86	127	88	28	49	128	90	35	608	199	53	1492
Total	1395	1712	3032	3293	524	1896	5908	21057	5192	7788	5974	2891	60662

TABLE 6. NUMBER OF INDIVIDUALS BY MONTH AND YEAR OF THE MOST ABUNDANT SPECIES (68 SPECIES) THAT WERE USED TO ANALYZE THE PHENOLOGY CONSIDERING THE SIZE OF THE SPECIES.

Taxon	J	F	M	A	M	J	J	A	S	O	N	D	1997	1998	1999	Total
Small																
Eunica tatila tatila (Herrich-Schäffer [1855])	120	456	1111	199	76	159	1640	3722	242	472	449	341	344	5261	3382	8987
Pareuptychia metaleuca metaleuca (Boisduval 1870)	109	5	8	40	3	2	28	79	24	41	131	43	328	39	146	513
Pyrisitia nise nelphe (R. Felder 1869)	2	24	37	10	5	8	47	105	53	81	96	32	308	83	109	500
Hermeuptychia hermes (Fabricius 1775)	22	40	73	51	2	31	30	11	13	75	104	34	315	23	148	486
Cissia pseudoconfusa Singer, DeVries & Ehrlich 1983	33	6	31	43	11	28	25	34	16	83	120	38	239	49	180	468
Kricogonia lyside (Godart 1819)		2	79	198	19	7	36	36	50	5	12	1	20	98	327	445
Mestra dorcas amymone (Ménétriés 1857)		11	16	13	4	12	19	35	16	94	22	36	169	20	89	278
Cissia pompilia (C.Felder & R. Felder 1867)	1	10	19	11	1	2	26	31	13	57	38	20	135	29	65	229
Eumaeus toxea (Godart [1824])	13	19	23	29	8	20	27	39	4	6	20	7	88	26	101	215
Juditha molpe molpe (Hübner [1808])		3	8	21	14	22	59	45	9	16	8	4	54	70	85	209
Cepheuptychia glaucina (H.W. Bates 1864)	6	15	27	25	13	3	6	6	7	12	21	66	51	73	83	207
Cissia similes (Butler 1867)	16	8	11	64	5	10	2	4	4	18	40	5	125	22	40	187
Nica flavilla bachiana (R.G. Maza & J. Maza 1985)	39	6	8	36	2		11	13	5	3	33	11	107	3	57	167
Cissia confuse (Staudinger 1887)	6		16	20		12	8	3		68	23	8	156	8		164
Pareuptychia ocirrhoe ssp. n.	9	26	8	22		3	26		3	9	31	18	65	3	87	155
Yphtimoides renata (Stoll 1780)	2	5	12	18	1	9	8	15	10	10	25	37	61	43	48	152
Thessalia theona theona (Ménétriés 1855)		10	13	4	3	9	11	36	8	20	25	8	59	15	73	147
Tegosa frisia tulcis (H.W. Bates 1864)	1	34	22	4	1	1	5	3	6	29	9	10	56	10	59	125
Leptotes cassius cassidula (Boisduval 1870)		7	29	32	11	8	12	4	7	5			48	26	41	115
Pteronymia cotytto cotytto (Guérin-Ménéville [1844])			34			1	19	1	1	17	38	3	49	3	62	114
Dynamine dyonis Geyer 1837		6	2			3	3	12	4	39	30	13	88	13	11	112
Pyrgus oileus (Linnaeus 1767)		18	21	12	6	3	14	8		19	9		42	2	66	110
Mesosemia tetrica Stichel 1910	4	10	5	3			1	14	16	29	13	12	34	46	27	107
Pyrisitia dina westwoodi (Boisduval 1836)		4	7	1	2	2	14	9	21	13	16	9	27	29	42	98
Heliopetes alana (Reakirt 1868)		4	15	8	4	2	6	5		31	7	8	60	1	29	90
Medium																
Memphis pithyusa pithyusa (R. Felder 1869)	204	99	76	144	5	242	707	6757	2154	1750	538	172	1737	10398	713	12848
Anaea troglodyta aidea (Guérin-Ménéville [1844])	4	19	8	18	1	231	742	5332	911	157	36	11	218	6873	379	7470
Memphis forreri (Godman & Salvin 1884)	139	23	40	144	16	117	296	353	30	735	249	68	1408	468	334	2210
Opsiphanes cassina fabricii (Boisduval 1870)	35	9	4	23	1	5	69	595	172	375	137	16	863	471	107	1441
Myscelia ethusa ethusa (Doyère [1840])	3	116	72	85	24	17	125	333	70	19	462	1	42	996	289	1327
Memphis moruus boisduvali W.P. Comstock 1961	89	123	46	60	27	12	44	298	51	173	174	95	300	287	605	1192
Taygetis virgilia (Cramer 1776)	139	4	13	144	6	65	28	172	41	171	220	50	776	189	88	1053
Hamadryas februa ferentina (Godart [1824])	22	21	36	89	16	78	45	47	164	80	57	36	225	301	165	691

TABLE 6. (CONTINUED) NUMBER OF INDIVIDUALS BY MONTH AND YEAR OF THE MOST ABUNDANT SPECIES (68 SPECIES) THAT WERE USED TO ANALYZE THE PHENOLOGY CONSIDERING THE SIZE OF THE SPECIES.

Taxon	J	F	M	A	M	J	J	A	S	O	N	D	1997	1998	1999	Total
Heliconius erato petiverana Doubleday 1847	6	50	28	168	6	8	35	67	35	101	127	51	401	82	199	682
Glutophrissa drusilla tenuis (Lamas 1981)	3	30	20	27	1	14	33	149	33	103	60	20	179	168	146	493
Hamadryas guatemalena guatemalena (H.W. Bates 1864)	4	11	3	22	3	24	15	146	31	64	92	68	150	288	45	483
Hamadryas julitta (Fruhstorfer 1914)	9	55	83	126	9	48	35	49	11	15	8	6	90	41	323	454
Polygonus manueli manueli Bell & W. P. Comstock 1948		22	28	9	4	6	82	3	34	184	21	11	52	265	87	404
Heliconius charithonia vazquezae Comstock & Brown 1950		26	28	23	3	2	14	47	30	89	60	35	190	34	133	357
Temenis laothoe hondurensis Fruhstorfer 1907	29	5	26	72	3	31	8	46	53	43	22	11	197	74	78	349
Dryas iulia moderata (Riley 1926)	2	12	9	15	1	6	10	45	47	110	44	27	157	86	85	328
Colobura dirce dirce (Linnaeus 1758)	78	7	4	20	2	7	8	13	7	21	111	41	237	28	54	319
Anartia amathea fatima (Fabricius 1793)		19	87	10	5	3	12	11	14	56	64	28	214	10	85	309
Fountainea eurypyle confusa (Staudinger 1887)	78	32	20	135	19	90	95	228	65	209	74	137	156	8	135	299
Marpesia chiron marius (Cramer 1779)			6	6		8	33	52	67	53	9	2	76	107	53	236
Biblis hyperia aganisa Boisduval 1836		12	17	7	2	5	6	15	10	65	48	16	98	33	72	203
Phoebis agarithe agarithe (Boisduval 1836)		6	16	12		6	31	11	6	80	27	7	133	40	29	202
Protographium philolaus philolaus (Boisduval 1836)			35	75	53	11	6	4					68	10	106	184
Pieriballia viardi viardi (Boisduval 1836)	4	10	15	1			2	11	16	38	51	28	124	11	41	176
Adelpha paraena massilia (Felder & Felder 1867)	1	6	13	1		4	10	31	26	66	6	5	58	92	19	169
Opsiphanes quiteria quirinus Godman & Salvin 1881	18		11	17		5	5	30		42	20	20	156	9	3	168
Consul electra electra (Westwood 1850)	18	14	26	36	1		11	18	3	8	13	14	75	21	66	162
Asterocampa idyja argus (H.W. Bates 1864)	3	4		4			7	10	46	44	8	5	23	95	13	131
Ganyra josephina josepha (Salvin & Godman 1868)			9		1	6	2	22	3	40	15	31	69	28	32	129
Myscelia cyaniris cyaniris Doubleday [1848]	1	4	4	9	1	40	27	20		2	1	7	57	42	17	116
Danaus gilippus thersippus (H.W. Bates 1863)		3	12	5	9	12	10	13	9	18	16	2	29	17	63	109
Anartia jatrophae luteipicta Fruhstorfer 1907		2	12	5	3	5	9	7	13	26	15	4	44	12	45	101
Large																
Archaeoprepona demophon centralis (Fruhstorfer 1905)	29	23	62	198	6	25	535	338	10	258	387	217	931	949	208	2088
Archaeoprepona demophoon gulina (Fruhstorfer 1904)	23	13	71	101	6	39	148	267	31	120	508	309	984	415	237	1636
Morpho achilles montezuma Guenée 1859	18			36	3	22	6	116	42	26	283	235	410	108	269	787
Historis acheronta acheronta (Fabricius 1775)		1		124	7	16	45	307	4	3	5	5	96	344	77	517
Historis odius dious Lamas 1995	9	1	8	62	1	22	45	72	13	56	38	9	198	100	38	336
Prepona laertes octavia Fruhstorfer 1905		2	10	24	3	3	70	64	3	52	51	8	147	106	37	290
Anteos maerula (Fabricius 1775)		24	24	22	2	13	26	25	10	20	25	16	67	26	114	207
Siderone galanthis ssp. n.	4	10	5	37	2	4	19	27	10	26	16	1	74	63	24	161
Siproeta stelenes biplagiata (Fruhstorfer 1907)	2	3	2	7	2		15	26	17	48	22	13	38	50	69	157
Phoebis philea philea (Linnaeus 1763)		3	10	6	5	9	14	8	8	25	10	24	68	16	38	122
Prepona pylene philetas Fruhstorfer 1904	1	4	12	24	2	1	9	30	4	8	4	1	37	31	32	100

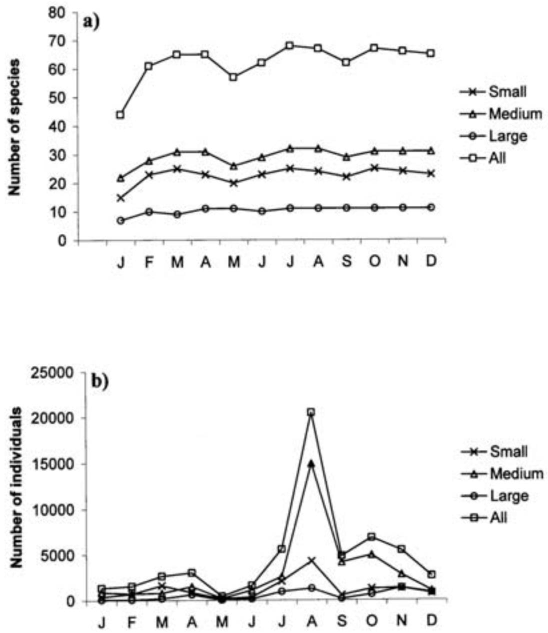

Fig. 5. Analysis of phenological patterns and relative abundance according to adult size. a) Phenology represented by size groups: small (<30 mm wingspan); medium (31 to 50 mm); large (>51 mm); and combined. b) Relative abundance of individual butterflies by size group.

study, the expected uniformity in phenological patterns of butterfly species at our tropical study sites does not exist. During the 3 years of our study, there were important differences in precipitation levels, and to a lesser degree, in temperature, which caused levels of evaporation to differ between years. Our results indicate a species turnover of more than 30% (as represented by adults), from the dry to rainy season. This helps explain seasonal variation in butterfly species richness, as only 33 species (9%) fly year-round, either as 1 long-lived generation, multiple superimposed generations, or several non-superimposed generations. The greatest species richness was observed during 1997, the year with the largest evaporation levels.

In the CR, biotic and abiotic factors are not homogeneously distributed, generally due to soil characteristics of the region, which in turn determine the existence of a heterogeneous mosaic of vegetation types. This mosaic is so intertwined that it is difficult to define vegetation types, and even more so to distinguish them (Galindo-Leal 2001; García-Gil et al. 2001; Martínez & Galindo-Leal 2002). This in turn produces a differential spatial and temporal distribution of the lepidopteran fauna. It is possible that the phenology of each species is more closely related to these factors, in response to the different micro-habitats where they live.

In order to investigate this relationship, our results were compared with phenological data on the butterflies of the Sierra de Atoyac de Álvarez, Guerrero (Vargas-Fernández et al. 1992), and the Sierra de Manantlán, Jalisco-Colima (Vargas-Fernánez et al. 1999). Both areas cover altitudinal transects; the former from 300 to 2500 m, and the latter from 250 to 1750 m. The sampling protocols used in these studies are equivalent to that of the present study, thus we believe that comparisons can be made among phenological data obtained for each of the 3 areas. However, the 2 Sierras (mountain ranges) present biotic and abiotic conditions that differ from those found in the CR, and have different biogeographical histories. While the Sierra de Atoyac de Álvarez and the Sierra de Manantlán are situated along Mexico's Pacific watershed, they differ in latitude, average precipitation levels, and average temperature.

Species richness of Papilionoidea is very similar across the 3 areas (although Hesperiidae were not surveyed by Vargas-Fernández et al. 1992, 1999). In Atoyac de Álvarez, 337 species were recorded, with the greatest species richness in Jul (216 species), whereas in Manantlán, 315 species were recorded, with a maximum diversity of 216 in November. In the CR, 359 species were recorded (250 in Oct), representing an average difference in overall diversity among the sites of about 12%.

Unique environmental attributes of each region should cause phenological patterns among the butterfly fauna to vary among them. Some reviews of butterfly phenology suggest that climate is the main factor controlling the activity of these organisms (Brakefield & Shreeve 1992; Warren 1992; Gutiérrez & Menéndez 1998). However, climatic factors may be influenced by differences between habitats or years, correlated with microclimatic changes at local or regional levels. In this study, phenological similarities were found with respect to species richness trends throughout the year. Two periods of maximum species richness were distinguished: the period of greatest diversity during the rainy season, and the other peak during the dry season. This indicates that phenological patterns among tropical butterfly faunas are much more complex than some authors have recognized.

Several authors have suggested that tropical faunas may be characterized by a large number of species with very low densities (Lamas et al. 1991; Owen 1971; Owen et al. 1972), which form the group of "rare" species. This group is an important part of the species diversity of each region and is the modulating factor of phenological changes, as demonstrated in this study. Upon examining those species represented by fewer than 10 records for each of the 3 regions we compared, it is evident that they represent a significant proportion of total species richness, and that they

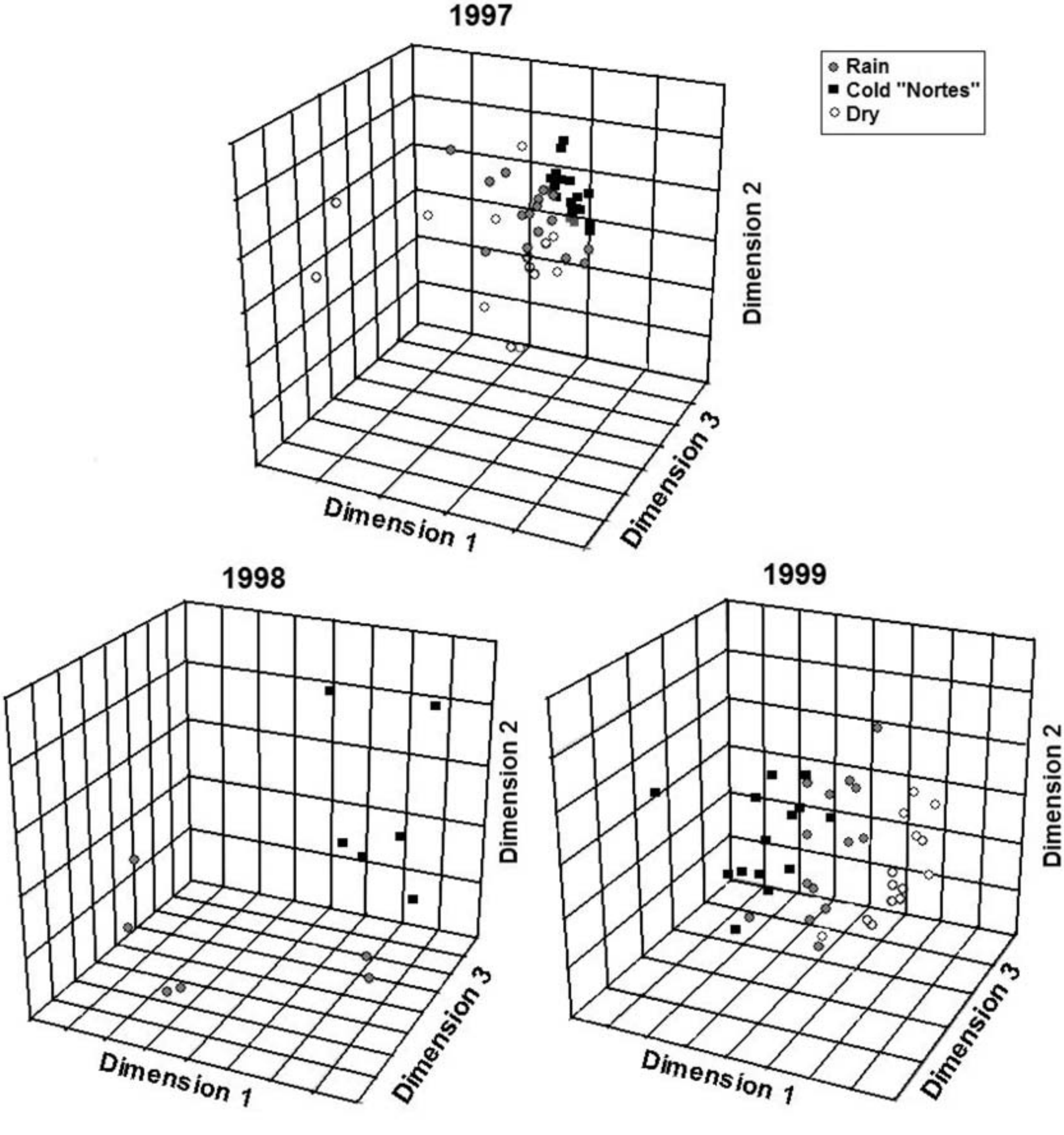

Fig. 6. Plots of the 3 axes obtained by NMDS for data from 1997, 1998 and 1999. Transformed data Log (y + 1). 1997: stress = 0.15, 1998: stress = 0.05 and 1999: stress = 0.18.

have a large impact on the overall phenological patterns observed in each region. The group of rare species from Manantlán is comprised of 117 species (37.1% of the total fauna), from Átoyac de Alvarez 144 species (42.7%), and from the CR 183 species (51%). The group of rare species may change from year to year due to seasonal and environmental variables, which have been poorly studied. Therefore, details on the specific mechanisms that lead to seasonal variation in the composition of rare species are needed to fully understand phenological patterns in any area.

If we consider precipitation and temperature (causes of available humidity) as principal factors in determining the phenological patterns of vegetational communities, and therefore of butterflies, the timing and severity of the dry season is likely to be one of the most consequential factors in determining regional phenological patterns. In Atoyac de Álvarez, the difference in humidity between the two seasons is lower than that of Manantlán, which minimizes the effects of the dry season and leads to an earlier peak in species richness. Furthermore, the average number of

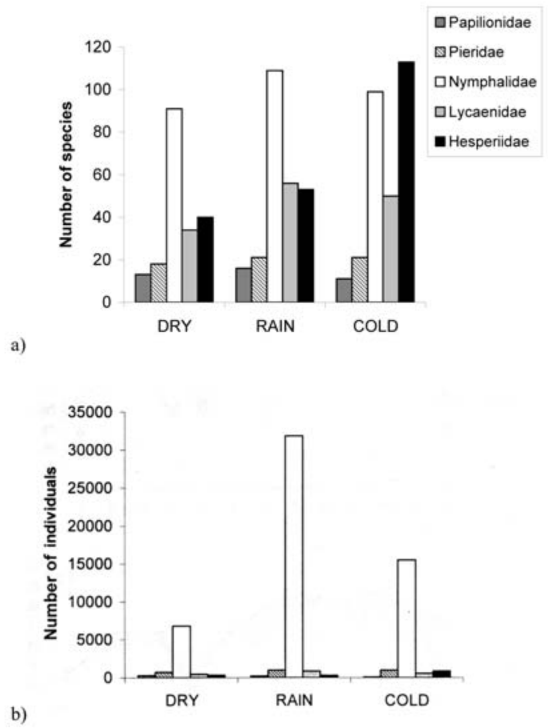

Fig. 7. a) Diversity of Papilionidae, Pieridae, Nymphalidae, Lycaenidae (including Riodinidae) and Hesperiidae across the 3 seasons (dry, rain, cold) of the Calakmul region. b) Relative abundance of adults of all families combined for each season.

TABLE 7. SPECIES LIST THAT CONTRIBUTED TO DISTINGUISH THE COMMUNITY OF BUTTERFLY FOR EACH SEASON IN THE CALAKMUL AREA.

Pieridae
Kricogonia lyside (Godart, 1819)
Glutophrissa drusilla tenuis (Lamas, 1981)
Nymphalidae
Heliconius erato petiveranus Doubleday, 1847
Historis odius dious Lamas, 1995
Historis acheronta acheronta (Fabricius, 1775)
Colobura dirce dirce (Linnaeus, 1758)
**Myscelia cyaniris cyaniris* Doubleday, [1848]
Myscelia ethusa ethusa (Doyère, [1840])
Eunica tatila tatila (Herrich-Schäffer, [1855])
Hamadryas februa ferentina (Godart, [1824])
Hamadryas guatemalena guatemalena (H.W. Bates, 1864)
Hamadryas julitta (Fruhstorfer, 1914)
Temenis laothoe hondurensis Fruhstorfer, 1907
Nica flavilla bachiana (R.G. Maza y J. Maza, 1985)
***Marpesia chiron marius* (Cramer, 1779)
Archaeoprepona demophon centralis (Fruhstorfer, 1905)
Archaeoprepona demophoon gulina (Fruhstorfer, 1904)
Prepona laertes octavia Fruhstorfer, 1905
**Siderone galanthis* ssp. nov.
Anaea troglodyta aidea (Guérin-Méneville, [1844])
Consul electra electra (Westwood, 1850)
Fountainea eurypyle confusa (A. Hall, 1929)
Memphis forreri (Godman & Salvin, 1884)
Memphis phila boisduvali W.P. Comstock, 1961
Memphis pithyusa (R. Felder, 1869)
Morpho achilles montezuma Guenée, 1859
Opsiphanes invirae fabricii (Boisduval, 1870)
Cepheuptychia glaucina (H.W. Bates, 1864)
Cissia pseudoconfusa Singer, DeVries & Ehrlich, 1983
Pareuptychia binocula metaleuca (Boisduval, 1870)
Pareuptychia ocirrhoe ssp. nov.
Taygetis virgilia (Cramer, 1776)
Hesperiidae
Polygonus manueli manueli Bell & W. P. Comstock, 1948

*Species that contributed to form groups.
**Species that contributed to separate the groups.

species present per month is greater in Atoyac de Álvarez than in the other 2 regions. On the other hand, in Manantlán, the process of species accumulation to the point of maximum diversity is slower, possibly because deciduous or semi-deciduous vegetation (drier forests than those of Atoyac de Álvarez) is present at almost all localities below 1800 m. The same phenomenon is also be observed in the CR, where the dry season is very pronounced, particularly due to the soil type characterized by calcareous rock, which causes rapid drainage. As a consequence of this, a greater similarity exists between the phenological patterns of the butterfly fauna of Manantlán and CR, than between CR and Atoyac de Álvarez.

While the "rare" species of a region comprise an important component of overall species diversity (as for CR, Fig. 8a), they do not allow for a straightforward phenological analysis, since the composition of rare species may change monthly and yearly. Thus, in order to study seasonal and annual phenological patterns, we excluded rare species to standardize comparisons (Fig. 8b). With rare species excluded, overall phenological patterns in Manantlán and CR show great similarity, while those of Atoyac de Álvarez are discordant. This may be due to the shorter and less severe dry season of Atoyac de Álvarez, as compared to the other 2 regions. However, if we displace the data from Atoyac de Álvarez 1 month forward (Fig. 8c), phenological patterns of the 3 regions are all remarkably similar. The months with the greatest species richness are Oct for CR (157 species) and Atoyac de Álvarez (172) and Nov for Manantlán (164). In contrast, the months of lowest diversity are May for CR (93) and Manantlán (81), and Apr for Atoyac de Álvarez (77). This pattern is well known to many experienced collectors in Mexico,

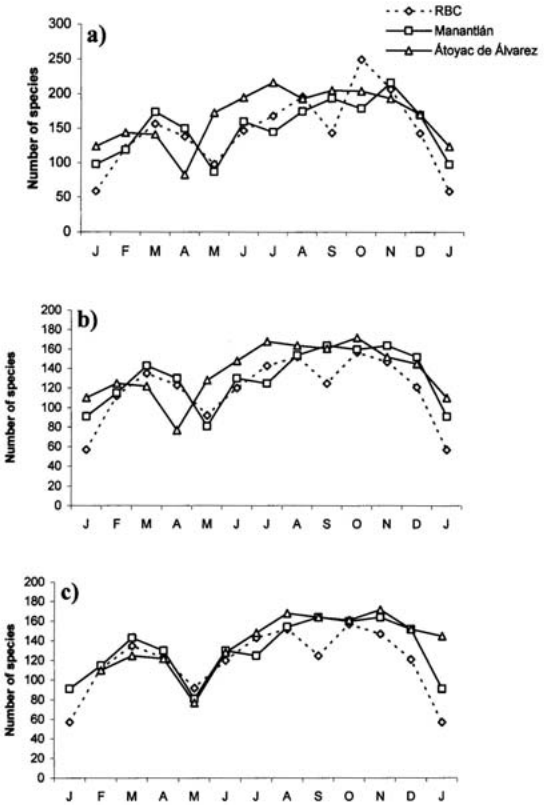

Fig. 8. Phenological patterns of the butterfly fauna of 3 regions in Mexico. RBC = Calakmul Region, Yucatan; Manantlán = Sierra de Manantlán, Jalisco-Colima; Atoyac de Álvarez = Sierra de Atoyac de Álvarez, Guerrero. a) Phenological patterns of the 3 regions considering all species; b) phenological patterns excluding rare species; c) phenological patterns with a 1-month (forward) displacement for the Sierra de Atoyac de Álvarez.

yet this is the first time this pattern has been quantified with data from various regions.

Family Level Phenology

Papilionidae is composed of few species, most of which are large-bodied, often with small population sizes. Longer survivorship due to their large adult size may allow this family to maintain relatively constant levels of species richness throughout the year. Larger butterflies are good at maintaining their water balance (Janzen & Schoener 1968), the greatest problem confronted by insects during the dry season. The effect of humidity is important with respect to insect body size, and those organisms with small bodies desiccate more easily than those with medium to large bodies (Young 1982). In addition, the relatively consistent diversity of Papilionidae across the seasons could be related to phenological patterns of larval foodplants or the availability of adult nectar or mineral resources. For species with long reproductive lives (e.g., Heliconiinae), availability of nectar resources may be especially important in determining phenological patterns (Gilbert & Singer 1975).

In contrast, the Lycaenidae and Riodinidae are characterized mostly by small-sized species, many of which center their reproductive activities (and therefore adult voltinism) around the flowering periods of larval foodplants (New 1993); in the CR this is most often from Mar to Oct. Only 2 medium-sized lycaenids (*Eumaeus toxea* (Godart, 1824) and *Juditha molpe molpe* (Hübner, 1808)) are found throughout the year in the CR. The remaining species of Lycaenidae and Riodinidae are seasonal, and appear only during favorable conditions for reproduction.

Phenology of the Most Abundant Species with Respect to Size

In the CR, we found that small and medium sized species show monthly fluctuations in species richness, contrasting with the patterns seen in Manantlán (Vargas-Fernández et al. 1999). These fluctuations are not greatly pronounced, but taken together they can help explain seasonal variation. Small and medium-sized species show the greatest species turnover across seasons, and many of them are univoltine. As also found by Young (1982), small-sized organisms tend to have their largest populations during the most humid season of the year.

Seasonality

This study shows that in the tropical CR, seasonal variation in the abundance and diversity of the butterfly fauna is small. However, through a careful analysis, seasonal differences in the fauna can be identified and compared to those of other regions. We found that in the CR, variations in phenological patterns are largely due to "rare" species represented by fewer than 10 records, whereas the seasonality of the butterfly community is described by the most abundant species, which define the faunas of the rainy, dry and cold seasons. Of the 33 most abundant species in the CR, the 11 most common are represented by 1000 to 10,000 records, while the remaining 22 species are represented by 100 to 1000 records per taxon. Of these, 15 species are present year-round.

Faunal studies on Lepidoptera of tropical regions based on systematic sampling methods conducted during all months of the year are scarce. Likewise, few studies have investigated seasonality in tropical lepidopteran faunas. The information presented herein explains phenological and seasonal patterns of butterfly abundance and diversity, and should be useful in future studies on the phenology of this immensely diverse group.

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REFERENCES CITED

AUSTIN, G. T., N. M. HADDAD, C. MÉNDEZ, T. D. SISK, D. D. MURPHY, A. E. LAUNER, AND P. R. EHRLICH. 1996. Annotated checklist of the butterflies of the Tikal National Park Area of Guatemala. Trop. Lep. 7: 21-37.

BRAKEFIELD, P. M., AND T. G. SHREEVE. 1992. Diversity within populations, pp. 178-196 *In* R. L. H. Dennis [ed.], The Ecology of Butterflies in Britain. Oxford University Press, Oxford.

CARR, M. R. 1996. PRIMER, Plymouth Routines in Multivariate Ecological Research (user manual). Plymouth Marine Laboratory, UK.

DE LA MAZA, J., AND R. G. DE LA MAZA. 1985a. La fauna de mariposas de Boca de Chajul, Chiapas, México (Rhopalocera). Parte I. Rev. Soc. Mex. Lep. 9: 23-44.

DE LA MAZA, J., AND R. G. DE LA MAZA. 1985b. La fauna de mariposas de Boca de Chajul, Chiapas, México (Rhopalocera). Parte II. Rev. Soc. Mex. Lep. 10: 1-24.

GALINDO-LEAL, C. 2001. Calakmul: Seeing the forest through the trees. Wildflower 17: 28-31.

GARCÍA-GIL, G., M. I. MARCH, AND M. A. CASTILLO-SANTIAGO. 2001. Transformación de la vegetación por cambio de uso del suelo en la Reserva de la Biosfera Calakmul, Campeche. Investigaciones Geográficas, Bol. Inst. Geogr. UNAM: 45-57.

GILBERT, L. E., AND M. C. SINGER. 1975. Butterfly ecology. Annu Rev. Ecol. Syst. 6: 365-397.

GULLAN, P. J., AND P. S. CRANSTON. 2000. The Insects: An Outline of Entomology, Second Edition. Blackwell Science, Ltd., Oxford.

GUTIÉRREZ, D., AND R. MENÉNDEZ. 1998. Phenology of butterflies along an altitudinal gradient in northern Spain. J. Zool. (Lond.) 244: 249-264.

HERRANDO-PERÉZ, S. 2002. Manual de Ecología Matemática. PCA, CLUSTER, MDS. Torbellino Press, Onda.

HUGHES, J. B., G. C. DAILY, AND P. R. EHRLICH. 1998. Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). Rev. Biol. Trop. 46: 697-704.

INEGI (INSTITUTO NACIONAL DE GEOGRAFIA Y ESTADISTICA). 1996. Anuario Estadistico del Estado de Campeche. INEGI, Gobierno del Estado de Campeche, Aguascalientes, Aguascalientes.

JANSEN, D. H., AND T. W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecol. 49: 96-110.

LAMAS, G., R. K. ROBBINS, AND D. J. HARVEY. 1991. A preliminary survey of the butterfly fauna of Pakitza, Parque Nacional del Manú, Perú, with an estimate of its species richness. Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos 40: 1-19.

LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical Ecology. English 2nd ed., Elsevier, Amsterdam.

LLORENTE-BOUSQUETS, J., A. LUIS-MARTÍNEZ, AND I. VARGAS-FERNÁNDEZ. 2006. Apéndice general de Papilionoidea: Lista sistemática, distribución estatal y provincias biogeográficas, pp. 945-1009 *In* J. J. Morrone and J. Llorente-Bousquets [eds.], Componentes Bióticosprincipales de la Entomofauna Mexicana, Las prensas de Ciencias, UNAM, México, DF. 1025 pp.

LUIS-MARTÍNEZ, M. A., AND J. LLORENTE-BOUSQUETS. 1990. Mariposas en el Valle de México: Introducción e historia I. Distribución local y estacional de los Papilionoidea de la Cañada de los Dínamos, Magdalena Contreras, D. F. México. Folia Entomol. Mex. 78: 95-198.

MARTÍNEZ, E., AND C. GALINDO-LEAL. 2002. La vegetación de Calakmul, Campeche, México: Clasificación, descripción y distribución. Bol. Soc. Bot. Mex. 71: 7-32.

NEW, T. R. 1993. Conservation Biology of Lycaenidae (Butterflies). Occasional Papers of the IUCN Species Survival Commission 8: 1-173.

OWEN, D. F. 1971. Tropical Butterflies. Oxford University Press, London.

OWEN, D. F., J. OWEN, AND D. O. CHANTER. 1972. Seasonal changes in relative abundance and estimates of species diversity in a family of tropical butterflies. Oikos 23: 200-205.

POZO, C., J. LLORENTE-BOUSQUETS, A. LUIS-MARTÍNEZ, I. VARGAS-FERNÁNDEZ, AND N. SALAS. 2005. Reflexiones acerca de los métodos de muestreo para mariposas en las comparaciones biogeográficas, pp. 203-215 *In* J. Llorente-Bousquets and J. J. Morrone [eds.], Regionalización Biogeográfica en Iberoamérica y Tópicos Afines: Primeras Jornadas Biogeográficas de la Red Iberoaméricana de Biogeografía y Entomología Sistemática (RIBES XII.I-CYTED). UNAM, México. 577 pp.

RYDON, A. 1964. Notes on the use of butterfly traps in East Africa. J. Lep. Soc. 18: 51-58.

SHAPIRO, A. M. 1975. The temporal component of butterflies species diversity, pp. 181-195 *In* M. L. Cody AND J. M. Diamond [eds.], Ecology and Evolution of Communities. The Belknap Press of Harvard University, London. 545 pp.

SHAPIRO, A. M., R. VANBUSKIRK, G. KAREOFELAS, AND W. D. PATTERSON. 2004. Phenofaunistics: seasonality as a property of butterfly faunas, pp. 111-147 *In* C. L. Boggs, W. B. Watt, and P. R. Ehrlich [eds.], Butterflies. Ecology and Evolution Taking Flight. The University of Chicago Press, Chicago and London. 739 pp.

SCOTT, J. A. 1986. The Butterflies of North America. A Natural History and Field Guide. Stanford University Press, Stanford, CA.

TANAKA, L. K., AND S. K. TANAKA. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. Biotropica 14: 114-123.

VARGAS-FERNÁNDEZ, I., J. LLORENTE-BOUSQUETS, AND A. LUIS-MARTÍNEZ. 1992. Listado lepidopterofaunístico de la Sierra de Atoyac de Álvarez en el estado de Guerrero: Notas acerca de su distribución local y estacional (Rhopalocera: Papilionoidea). Folia Entomol. Mex. 86: 41-178.

VARGAS-FERNÁNDEZ, I., J. LLORENTE-BOUSQUETS, AND A. LUIS-MARTÍNEZ. 1999. Distribución de los Papilionoidea (Lepidoptera: Rhopalocera) de la Sierra de Manantlán (250-1650 m) en los estados de Jalisco y Colima. Publ. Espec. Mus. Zool. UNAM 11: 1-153.

WARREN, A. D. 2000. Hesperioidea (Lepidoptera), pp. 535-580 *In* J. E. Llorente-Bousquets, E. González Soriano, and N. Papavero [eds.], Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento. Volumen II. Universidad Nacional Autónoma de México, Mexico City. xvi + 676 pp.

WARREN, M. S. 1992. Butterfly populations, pp. 73-92 *In* R. L. H. Dennis [ed.], The Ecology of Butterflies in Britain. Oxford University Press, Oxford. 368 pp.

WILLIAMS-LINERA, G., AND J. MEAVE. 2002. Patrones fenológicos, pp. 407-431 *In* M. R. Guariguata and G. H. Kattan [eds.], Ecología y Conservación de Bosques Neotropicales. Editorial Libro Universitario Regional, Cartago, Costa Rica. 691 pp.

WOLDA, H. 1987. Altitude, habitat and tropical insect diversity. Biol. J. Linn. Soc. 30: 313-323.

WOLDA, H. 1988a. Insect seasonality: Why? Annu. Rev. Ecol. Syst. 19: 1-18.

WOLDA, H. 1988b. Seasonality and the community. pp. 69-75 *In* J. H. R. Gee and P. S. Giller [eds.], Organization of Comunities, Past and Present. British Ecological Society, Oxford. 588 pp.

YOUNG, A. M. 1982. Errata: over-exploitation of larval host plants by *Heliconius* butterflies. J. New York Entomol. Soc. 90: 117-118.