

PHENOLOGY AND DIVERSITY OF A BUTTERFLY POPULATION IN SOUTHERN ARIZONA

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ABSTRACT. Butterfly populations were examined on the Santa Rita Experimental Range in southern Arizona in 1970-71. Thirty-nine species were recorded of which 14 were considered common and typical of the desert grassland community. Butterfly activity was noted in all months except November 1970 and January and February 1971. Peak species number and abundance were after the summer rains. Reduced abundance in spring 1971 was attributed to the dryness of the previous winter. Season lengths for the two years were similar. Univoltinism was 33% of the fauna in 1970 and 46% in 1971 and was a rainy season phenomenon. Species diversity (H') closely paralleled species counts.

It is widely recognized that flight periods of butterfly species in most areas are seasonal depending on several factors including emigration, voltinism, competition and tolerances of the component species to various environmental extremes. Differences in interspecific dates of emergence and lengths of flight periods and intraspecific synchrony result in changes in diversity throughout the total favorable season. Detailed studies of phenology and seasonal changes in diversity of butterfly populations in limited areas are nearly lacking (e.g., Emmel and Emmel 1962, 1963a, Shapiro 1975). I made observations on relative abundance and phenology of the butterflies in a small area in southern Arizona from May 1970 to November 1971, incidental to my studies of bird populations in the same area. In this paper I examine seasonal patterns of abundance and diversity of the butterflies and relate these, as possible, to environmental variables.

Study Area

All observations reported here were made on an area of approximately 50 ha. on the Santa Rita Experimental Range, elev. 1150 m, ca. 10 km SE of Sahuarita, Pima Co., Arizona. The study area, on the western slope of the Santa Rita Mountains, sloped slightly to the northwest and was dissected by several washes. This resulted in a heterogeneous habitat, typical of the surrounding area, with the larger trees and shrubs tending to be concentrated along water courses. The community including the study area was described as a desert-grassland biotic community (Lowe 1964) invaded by woody growth due mainly to protection from fire (Humphrey 1968). The dominant vegetation included mesquite (*Prosopis juliflora*), paloverde (*Cercidium microphyllum*), hackberry (*Celtis pallida*) and

TABLE 1. Temperature and rainfall at the Santa Rita Experimental Range weather station during the study period (rainfall data for May through August of both years are measurements made on the study area itself).

Mean monthly temperature (°C)												
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean	8.6	9.9	12.7	16.9	21.1	26.1	26.6	25.0	24.2	19.6	13.4	10.1
1970	—	—	10.4	14.0	22.3	26.6	27.2	24.8	21.8	16.3	*	*
1971	9.9	10.1	14.2	15.7	19.2	25.1	26.9	23.2	22.6	15.6	—	—

Monthly rainfall (cm)												
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean	4.3	4.2	2.9	1.5	0.4	1.9	10.1	11.9	4.8	2.3	2.6	3.5
1970	—	—	5.9	0.7	0.0	2.5	9.5	2.4	9.6	1.2	0.1	0.3
1971	0.0	4.4	0.0	2.3	0.1	0.1	6.9	12.1	10.9	6.8	—	—

* data not available.

cholla cacti (*Opuntia fulgida* and *O. spinosior*) with an understory of several grass species, some small woody bushes (especially *Acacia greggii*), succulents and herbs.

Rainfall and temperature for the study period are given in Table 1. Temperatures averaged near normal during the study. Rainfall was near normal through July 1970; August was drier than average and September wetter. The winter (October–March) of 1970–71 was one of the driest on record with rainfall for the period 13.8 cm below average. Thereafter, 1971 rainfall was about average.

Prosopis and *Acacia* began leafing and blooming in April. *Celtis* put out a few leaves at this time and a few grasses and annuals appeared. The summer rainy season initiated the annual growth of many grasses and herbs. *Celtis* and *Cercidium* came into full leaf at this time and additional leaf growth and flowering was seen on *Prosopis* and *Acacia*.

METHODS

Observations were made by counting all butterflies seen within 5 m of me as I walked through the area. Most actual counts were made over a 3–4 hour period between 0700 and 1300 on clear, windless days. Each of these days was considered as a standard observation day and relative abundance was expressed as number observed per day by 10 or 11 day periods. I made observations on other days of species composition which occasionally added to the species list for that time period. Specimens of most species observed were obtained from or near the study area.

RESULTS

Species Composition

A total of 39 species (32 in both 1970 and 1971) were recorded during this study (Table 2). Thirteen species were represented by no more than 2 observations in each of the two years. Nine additional species (*D. plexippus*, *E. claudia*, *S. melinus*, *H. isola*, *C. eurytheme*, *N. iole*, *P. protodice*, *P. communis*, *S. ceos*) were seen 2 or less times in one of the two years. Of the latter, all except *H. isola* and *P. protodice* were recorded in considerably greater numbers in the alternate year. Three species (*M. leda*, *E. amyntula*, *C. hippalus*) recorded several times in 1970 were absent in 1971. This leaves 14 species which I consider as typical and relatively common in this plant association. Nine of these (*A. leilia*, *D. chara*, *L. bachmanii*, *A. palmeri*, *L. marina*, *H. ceraunus*, *E. nicippee*, *P. catullus*, *E. funeralis*) are definitely resident in the area; the others (*D. gilippus*, *V. cardui*, *C. cesonia*, *P. sennae*, *B. philenor*) are

TABLE 2. (Continued)

		April			May			June			July			Aug.			Sept.			Oct.			Nov.			
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
<i>Nathalis iole</i>	1970	--	--	--	--	--	0	0	0	0.3	0	0.5	0.2	0.8	2.2	1.0	0.3	0	0	0	0	0	0	0	0	0
Boisduval	1971	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0
<i>Pyrgus communis</i>	1970	--	--	--	--	--	0	0	0	0	0	0.7	X	0.3	0.4	0.2	0	0	0	0	0	0	0	0	0	0
(Grote)	1971	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	X	0	0	0	--	--	--	0
<i>Staphylus ceos</i>	1970	--	--	--	--	--	0	0	0	0	0	1.0	0	0	0.2	0	0	0.3	0	0	0	0	0	0	0	0
(Edwards)	1971	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	--	--	--	0
<i>Cogia hippalus</i>	1970	--	--	--	--	--	0	0	0	0	1.5	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(Edwards)																										
OTHER SPECIES ¹	1970	--	--	--	--	--	0	0.5	0	0.6	0.9	2.8	0.4	0.7	0	0	0	0.3	0	0	0	0	0	0	0	0
	1971	0	0	0	0	0	0	0.5	0	0	0	0	0	0	2.0	1.1	1.6	0	0.3	0	0	0	--	--	--	0
TOTAL SPECIES	1970	--	--	--	--	--	9	8	8	8	10	20	18	22	17	14	12	9	4	0	4	0	0	0	0	0
	1971	0	2	2	3	2	4	4	4	1	2	1	9	8	17	19	22	10	11	2	--	--	--	--	5	--
NUMBER OF DAYS	1970	--	--	--	--	3	2	3	4	4	6	6	6	5	5	3	3	3	2	1	2	2	2	2	2	2
	1971	2	2	2	4	2	3	2	1	1	3	1	5	6	8	10	6	2	3	1	--	--	--	2	--	
NUMBER OF INDIVIDUALS/DAY	1970	--	--	--	--	67.3	103.0	39.9	9.5	10.1	54.2	57.7	50.7	55.8	41.4	46.5	78.2	7.3	0	5.0	0	0	0	0	0	0
	1971	0	2.5	2.0	3.1	3.0	8.3	11.0	13.0	1.0	2.3	2.0	11.0	27.9	29.5	44.5	59.1	73.5	45.2	2.0	--	--	--	6.0	--	

¹ *Danaus plexippus* (Linnaeus), 1970: July, Sept., 1971: Aug., Sept.; *Anaea aidea* (Guerin-Meneville), 1971: Sept.; *Limenitis astyanax arizonensis* Edwards, 1971: March; *Texola elauda perse* (Edwards), 1971: Sept.; *Chlosyne lacinia crocale* (Edwards), 1970: July; *Euptoieta claudia* (Cramer), 1970: July, Aug.; *Vanessa atalanta* (Linnaeus), 1971: Aug.; *Vanessa annabella* (Field), 1970: Aug.; *Agraulis vanillae incarnata* (Riley), 1970: June, July; *Brephidium exilis* (Boisduval), 1970: June; *Hemiargus isola alce* (Edwards), 1970: July, 1971: June, Aug., Sept.; *Colias eurytheme* Boisduval, 1970: July, Aug., 1971: Aug., Sept.; *Pieris protodice protodice* Boisduval and Leconte, 1970: June, July, 1971: Sept.; *Papilio polyxenes asterius* Stoll, 1970: July, 1971: Sept.; *Papilio cressphontes* Cramer, 1971: Aug.; *Lerodea eufala* (Edwards), 1971: Aug., Sept.; *Hylephila phyleus* (Drury), 1971: Aug.; *Copacodes aurantiaca* (Hewitson), 1970: Sept., 1971: Aug.

² March (1971, 2, 2 days): no butterflies; March (1971, 3, 2 days): *Leptotes marina* 1.0, *Battus philenor* 2.5, other species 0.5; December (1970, 1, 1 day): *Nathalis iole* 3.0; December (1970, 2 and 3, 1 day each): no butterflies.

strong flying and wide ranging species which may or may not have used the area for reproduction.

All species recorded during this study were previously seen by me in other similar habitat and in other vegetation types in southern Arizona. No species not recorded on the study area were seen in adjacent areas. I thus consider the species list relatively complete.

The butterflies of the study area were representative of the Southeastern Arizona desert scrub habitat with considerable influence from the foothill canyon habitat as outlined by Brown (1965). All species seen on the study area were recorded in one or both of the above habitats by Brown (1965) except *V. annabella* and *E. amyntula*.

The Santa Rita Range butterfly fauna belong to 10 families (if Apaturidae and Heliconiidae are separated from Nymphalidae). Nymphalidae and Hesperidae were represented by the most species (8 each) followed by Lycaenidae (7) and Pieridae (6). Overall, the familial composition was more diverse than in many temperate communities (e.g., Emmel and Emmel 1963b) which often lack representatives of families with southern distribution (Heliconiidae) or with restricted larval food habits (Apaturidae and Libytheidae).

Apaturidae was by far the most abundant family in terms of individuals, due to the high abundance and long flight period of *A. leilia*. Lycaenidae and Libytheidae were next in individual abundance followed by Riodinidae and Pieridae. The two families with most species were represented by very few individuals. This distribution of individuals by family contrasts sharply with that in the Sierra Nevada of California where individual and species distribution was similar (Emmel and Emmel 1963b).

Phenology

Activity by adult butterflies was observed in all months except November 1970 and January and February 1971. The general pattern of activity was similar during the two years (Fig. 1). During spring and early summer there was a plateau in number of species which then increased rapidly to a peak in late summer before decreasing to a small number of species in fall. In both years, there were peaks of abundance in both spring and late summer with a period of nearly no activity between (Fig. 1). In 1970, the spring peak was much larger, and the summer peak began earlier and lasted longer than in 1971.

Phenology of the fauna as a whole appeared largely related to rainfall. Precipitation for winter 1969-70 was near average, and the spring population in 1970 was probably typical for the area. The very dry winter of

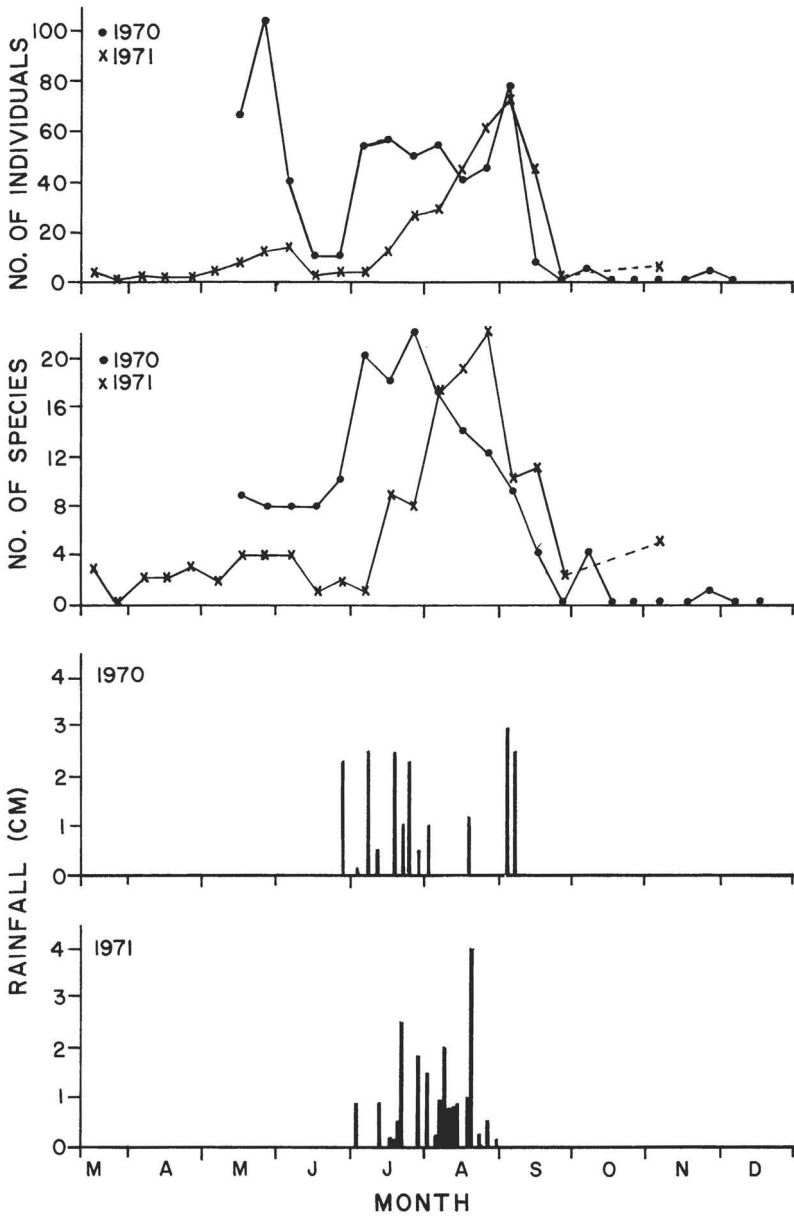


Fig. 1. Rainfall pattern (1 May-5 Sept.) and butterfly activity on the Santa Rita Experimental Range, Arizona, in 1970 and 1971.

1970-71 was probably responsible for the reduced diversity and abundance in spring 1971.

Differences in the overall summer flight period can be directly attributed to differences between the summer rainfall patterns (Fig. 1). The first heavy rain of 1970 was on 29 June and was followed by another similar rain less than a week later. These were sufficient to stimulate the summer growth of vegetation. Butterfly diversity and abundance increased rapidly after these rains but diversity decreased rapidly during the below average dryness of August. Abundance increased in September due mainly to the emergence of a large brood of *L. bachmanii*. Both diversity and abundance decreased rapidly in late September and early October.

The 1971 rainy season began on 2 July with a relatively light rain. The next rain did not occur until 14 July after which there were several additional, closely spaced rains (Fig. 1). The vegetation responded minimally to the first rain but much of the new growth dried considerably between rains. The second and subsequent rains initiated and maintained the usual spectacular summer growth of vegetation. There was no emergence or immigration of butterflies with the first rain. The second rain, however, was followed by a rapid increase in species number and abundance similar to the increase after the first rain of 1970. The timing of the autumn decrease was similar to 1970.

The 3 principal spring species showed a peak in about late May or early June with continued emergence into early fall as noted above. Several patterns were evident among the rainy season species. Certain resident species showed an immediate emergence within a few days of the first rain. These included *A. leilia*, *D. chara*, *P. catullus* and possibly *E. funeralis*. Other species including the immigrant *D. gilippus*, *P. sennae* and possibly *C. caesonina* and the resident *E. nicippee* occurred in peak numbers 2-4 weeks after the beginning of the rains. The second brood of *A. palmeri* was timed similarly. Additional immigrants, *V. cardui* and *B. philenor*, showed peak abundance about 2 months after the beginning of the rains. In both years, however, *L. bachmanii* reached peak abundance in mid-September. In all other instances where sufficient records exist, the summer peak in abundance was later in 1971 than in 1970 similar to the overall pattern for all species combined as discussed above. Nearly all species had greater peak abundance in 1970 than in 1971.

The relationships of the various species within a larval food plant guild are complex. Adults of the principal *Prosopis* feeders, *A. palmeri* and *H. ceraunus*, were spring fliers with the latter flying slightly later than the former although *A. palmeri* had a relatively large brood after the rains in 1970. Another *Prosopis* feeder, *M. leda*, emerged only after the rains

began. Of the two species which feed as larvae on *Cassia*, *E. nicippee* was resident and *P. sennae* was an immigrant. Both showed peak abundance from early August to mid-September. There was almost complete overlap of peak flight activity in 1970 but *P. sennae* showed peak abundance earlier than *E. nicippee* in 1971. The *Celtis* feeding guild, represented by *A. leilia* and *L. bachmanii*, showed overall peak abundance in mid-September. The two years differed with little overlap in peak flight period in 1970 and almost complete overlap in 1971.

The few notes taken on adult resource use indicate use of several flowering species. The spring species were most often seen visiting *Acacia* and *Prosopis* flowers. In summer, flowers of *Mirabilis multiflora* (used principally by *P. catullus*), *Ipomoea coccinea* (*B. philenor*), *Hymenoclea salsola* (*D. gilippus*, *L. bachmanii*) and *Zinnia pumila* (*D. chara*, *E. claudia*) were visited.

Temporal partitioning may be partly responsible for increased diversity of some butterfly populations (Clench 1967). Replacement of one set of species by another within a season allows increased diversity without increasing competition for adult resources. It must be recognized, however, that the observed phenology of adult activity is often closely integrated with the phenology of immature stages which is largely beyond the scope of the present discussion.

The numerical data in Table 2 were analyzed using the methods of MacArthur (1964) and Ricklefs (1966). Season length was calculated using the information-theoretical measure (H') for the combined abundance of all species (total season) and for each species that was observed in 4 or more 10 day periods (specific season). The specific seasons were averaged and divided into the total season resulting in a figure which indicates species turnover through the total flight season. Use of H' places greater weight on periods of abundance and less on periods of rarity and more accurately reflects the length of the flight period than extreme dates.

Total season length was about 11 ten-day periods in both years (11.4 in 1970, 10.7 in 1971) and average specific season was over 5 ten-day periods (5.31 in 1970, 5.26 in 1971). There appeared, therefore, to be two turnovers among the species present. The turnover in 1970 was obvious with the rainy season species clearly replacing the spring species. The 1971 replacement was less clear but apparently involved the replacement of early rainy season species by those of the later parts of rainy season. While this may have had some effect in 1970, it was largely marked by the large spring broods and longer rainy season of that year.

In general, the phenological patterns were similar to those found by

Brown (1965). The major differences were that Brown did not find spring broods of *A. palmeri*, *L. marina* and *H. ceraunus*, although he found *L. bachmanii* and *D. chara* in spring, two species which I did not observe. In southwestern New Mexico, Ferris (1976) also found phenology to be relatively similar to southern Arizona. He noted a spring brood of all of the above 5 species.

Voltinism

Voltinism varied both inter- and intraspecifically (Table 2). Two (*D. chara*, *P. catullus*) of the 9 common residents were univoltine during both years. *E. nicippe* and *E. funeralis* appeared to be so in 1971 but were at least bivoltine in 1970. Eight rare species were encountered frequently enough to determine voltinism. In 1970, *M. leda*, *P. communis* and *C. hippalus* were univoltine whereas *S. melinus*, *E. amyntula* and *N. iole* were bivoltine. In 1971, *L. eufala* was univoltine and *H. isola* was bivoltine. Thus 33% of the resident fauna was univoltine in 1970 and 46% in 1971. Univoltine species, in all cases, appeared in summer after the beginning of the rains. Univoltinism in other long summer faunas is principally a spring and early summer phenomenon (Shapiro 1975). The mid- to late summer univoltinism in southern Arizona is undoubtedly related to the greatly increased suitability of the habitat following the summer rains.

The remainder of the Santa Rita fauna was at least bivoltine. Three species (*A. palmeri*, *L. marina*, *H. ceraunus*) had large spring and smaller summer broods, especially in 1971. The summer populations were represented by scattered individuals observed over a period of 2-3 months. In 1970, *A. palmeri* may have had 4 broods. These 3 species may be spring univoltines in years when the summer rains fail.

Four rare species (*S. melinus*, *E. amyntula* and *E. funeralis* in 1970 and *H. isola* in 1971) had a distinct brood in early June and at least one other of about the same size following the beginning of the rains. *S. melinus* and *H. isola* appeared to have but one post-rain brood; the others possibly 2 or 3. In both years, small numbers of *A. leilia* occurred before the rains. There were 3 distinct peaks possibly indicating 3 additional broods after the rains in 1970, but in 1971 there was but one large peak in mid and late September. Fresh individuals were noted throughout the flight season of both years indicating continued emergence.

Emergence was limited to after the rains in *L. bachmanii*, *E. nicippe* and *N. iole*. *L. bachmanii* had a small brood immediately after the beginning of the rains, a large brood in September and possibly another one or two smaller broods still later in the season. *E. nicippe* appeared

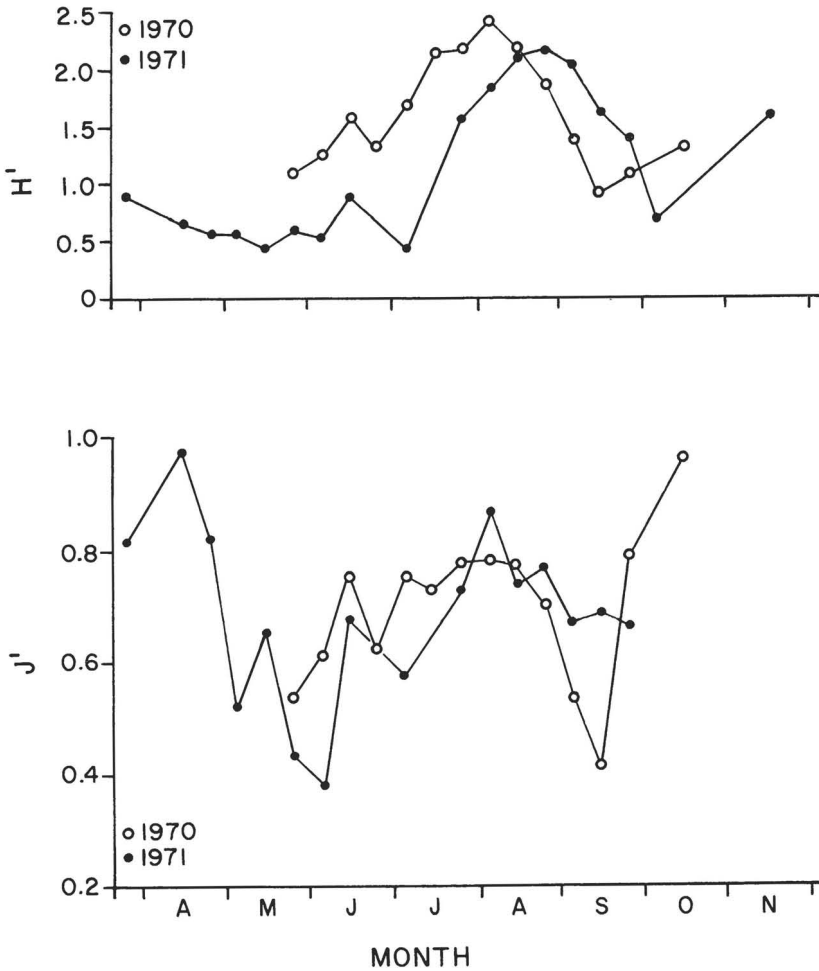


Fig. 2. Seasonal changes in species diversity (H') and equitability (J') of butterflies on the Santa Rita Experimental Range, Arizona.

to have at least 2 broods in 1970 but probably only one in 1971 unless the October records were of an additional brood. *N. iole* had at least 2 broods in 1970 but was all but absent in 1971.

Two immigrant species (*D. gilippus*, *P. philenor*) occurred in small numbers before the rains and reached a definite peak in numbers in late summer. *P. sennae* also showed a peak in abundance after the rains. Other immigrant species occurred irregularly in low numbers after the rains. Unworn individuals of these species occurred throughout the season.

Species Diversity

Diversity of a population can be examined in several ways. The method most often used for butterflies is species counts for each of several seasons. This diversity measure for the Santa Rita fauna was examined previously (Fig. 1). Another measure of diversity based on information theory (H') accounts for both species numbers and relative abundance. This measure has not been widely used for insect populations (Janzen and Schoener 1968) mainly because of the wide range of detectability of the component species (see Shapiro 1975). In this study, I made a concerted effort to obtain accurate counts in a relatively narrow transect and none of the species encountered were particularly secretive. I believe that no species was grossly under- or over-represented in my counts and that the numbers in Table 2 reflect the true relative abundance. Therefore, I used these values to calculate H' for each 10 day period of the two seasons. The ratio of H' to maximum diversity possible if each species were equally abundant is another component of diversity termed equitability (J' , see Pielou, 1966). These were also calculated for each 10 day period.

Diversity, measured by H' , showed a seasonal pattern which closely paralleled species counts (Fig. 2). Linear regression analysis showed that the number of species explained over 80% of the variation in H' ($r = .899$, $N = 31$). In contrast, equitability fluctuated widely, showed no correlation ($r = .005$) with species counts and was most constant during the rainy season (Table 2). Considering each season as a whole, H' and J' were slightly greater (2.34 and 0.67) in 1970 than in 1971 (2.20 and 0.63). The average J' for Santa Rita butterflies of about 0.65 is slightly lower than the average of 0.74 calculated for insect populations containing a larger number of orders and thus greater trophic diversity (see Austin and Tomoff, in press).

CONCLUSIONS

The complexity of the phenology of the southern Arizona butterfly fauna was first indicated by Brown (1965). He noted that most lowland species were rainy season fliers or had a spring brood and additional broods during the rainy season. He further recognized the wide annual fluctuations with populations dependent on the local precipitation.

Several factors seem apparent in the flight patterns of the species present. Strict seasonal phenology with only the magnitude affected by rainfall was exhibited by the 3 principal spring species and by *L. bachmanii* in fall. Spring flight by the *Prosopis* feeders is timed for the larvae to take advantage of the fresh herbage or flower buds and for the adults'

nectar source which appears to be mainly *Prosopis* and *Acacia*. The second brood of *A. palmeri* appears timed to the new herbage growth by *Prosopis* following the summer rains. Flowering by *Prosopis* following the rains is limited and this may account for the very small numbers of *L. marina* and *H. ceraunus* at this season.

The flight seasons of the remaining species are nearly limited to after the beginning of the summer rains. This suggests that rainfall itself and/or the resultant increase in humidity combined with the warm summer temperatures act to break diapause of the resident species. The rapidity of which adults appear after the first rain may relate to the stage of the life cycle at which diapause occurs or to a cumulative effect of successive rains. The enforcement of diapause by heat and aridity in desert regions has been previously noted (Wiltshire, 1956). Non-resident individuals of wide ranging species may be attracted by increased vegetation growth and flowering by many plants. Adults of 12 species of butterflies were observed feeding at the flowers of 2 plant species, *Mirabilis* and *Zinnia*, which flower abundantly and nearly exclusively after the rains begin. The nearly consistent lateness of the 1971 season compared to 1970 (Table 1) is further indication that rainfall is the important ultimate factor in the phenology of many species.

The seasonality of the Santa Rita Range butterfly fauna differs considerably from other temperate zone faunas previously examined. The general trend in most populations is for a rather rapid increase in species number to a mid summer peak and then a decrease into autumn (Shapiro, 1975). Only the tidal marsh in California showed a peak in species numbers in late summer or fall. No temperate butterfly community showed the strict dependence on summer rains. These differences in phenology (and voltinism) can be largely attributed to climatic differences; the areas studied by Shapiro (1975) were largely Mediterranean or Mediterranean-montane in climate. The Arizona community was similar to others, however, in that peak populations corresponded to peak vegetation growth. Seasonal phenology in southern Arizona shows certain similarities to that in the Neotropics where Ebert (1969) found peak activity during the rainy season.

ACKNOWLEDGMENTS

This study was conducted while I was funded to study birds by the US/IBP Desert Biome Program under National Science Foundation Grant GB15886 at the University of Arizona. I thank Donald Thomas and Robert Ricklefs for critical comments on an early draft of the manuscript.

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