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BUTTERFLIES OF THE UPPER FRIO-SABINAL REGION, CENTRAL TEXAS, AND DISTRIBUTION OF FAUNAL ELEMENTS ACROSS THE EDWARDS PLATEAU

DAVID E. GASKIN[1]

Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

ABSTRACT. A survey of the butterfly fauna (1988–96) of the upper Frio-Sabinal region of the southern Edwards Plateau, Texas, is presented. Butterflies were observed along transects at five study sites and during repeated opportunistic transects at 12 secondary localities. A total of 28,035 specimens, comprising 100 species was recorded. Another 51 species were reported by other lepidopterists working 15–25 km south of this region during the same period; most were collected from the vicinity of Concan, in north-central Uvalde Co. Twenty-seven species recorded in the upper Frio-Sabinal region were represented by 1–5 specimens only. Simple approximation models were used to estimate the proportion of the theoretical total species collected to date at the upper Frio-Sabinal site. No statistically significant differences were found between the geographical components at the Frio-Upper Sabinal site and two other well-worked sites; Barton Creek (Travis Co.) and Concan (N. Uvalde Co.). Composition and distribution patterns of the butterfly fauna across the Edwards Plateau were examined by analyzing data from 16 reasonably well-collected counties. Geographically, the butterfly fauna across the Edwards Plateau has a strong W/SW trans-Pecos component in Brewster and neighboring counties, which is only weakly represented in the north and east. A S/SE element is significant only along the Balcones fault region from Uvalde to Travis counties, while a NE/E element is numerically important but decreases sharply west of Real and Uvalde counties. Both are associated with the riparian corridors of the southeast. A N/NW element is widespread, but only weakly represented in all counties. Disturbed habitats were dominated by Pieridae (64%). Intergrading dry, subtropical habitats, dry montane woodland areas, coastal woodlands and southern tropical woodlands were dominated by Hesperiidae (45–75%). Richest ecological zones were the south tropical woodlands (49 species), dry subtropical forest and scrub (32 species) and Great Plains savanna habitats (16 species). Other ecological zones were characterized by 12 species or less. The Hesperiidae was the best represented family (97 species) and the Pyrginae the most abundant subfamily (53 species). There is little endemism in the butterfly fauna of Edwards Plateau. The relative species richness (227, with 35 more in Brewster Co. only) can be attributed largely to its strategic geographical position. It is difficult to specify any one element on the Plateau which could truly be said to be characteristic of the butterfly fauna, because so many of these species reach a range limit at some point on the Plateau.

Additional key words: Papilionioidea, Hesperioidea.

[1]Deceased

Texas has a diverse butterfly fauna commensurate with its size, wide latitudinal range, topographic variety and complex vegetational zones. The southernmost counties of Texas in particular attract entomologists seeking Neotropical species rarely encountered elsewhere in North America (Opler 1993). Information on the butterflies of Texas is scattered throughout books (e.g., Holland 1930, Klots 1951, Howe 1975, Pyle 1981, Opler & Krizek 1984, Scott 1986, Opler & Malikul 1992, Stanford & Opler 1993, Neck 1996), journal articles (e.g., Freeman 1951, Kendall 1964, 1976, Durden 1982, McGuire 1982, McGuire & Rickard 1974), and annual summary reports of the Lepidopterists' Society. However, only the survey by Durden (1982) treats the south-central region in detail. His decade-long survey concentrated on the butterflies found in the ten counties surrounding Austin, with particular focus on Barton Creek Canyon, a locality at the eastern boundary of the Balcones Fault Zone, and in the transition area of the Edwards Plateau and South Central Vegetational Zones (*sensu* Gould 1969, Ajilvsgi 1984, Amos & Gehlbach 1988, Enquist 1987).

The present paper describes and quantifies the butterfly fauna of the upper Frio-Sabinal region, which encompasses the confluence of the East and West Frio Rivers, in the area where Real, Bandera and Uvalde counties meet. Results are compared with data from two other intensively worked sites, Concan (E. Knudsen 1996, *in litt.*) in central Uvalde Co., 15–25 km south of my Frio-Sabinal sites, and Barton Creek Canyon in the Austin region, 160 km to the northeast (Durden 1982).

Relative distributions of the butterfly fauna across 16 counties of the Edwards Plateau are analyzed by geographic components (5), taxonomic groups (15), habitat types (18) and range position or limit (12), the last two following designations by Durden (1982). Comparisons of species-richness in the counties across the plateau are made with caution. While these can reveal real differences attributable to habitat diversity or differences in magnitude of unit area, they can also be a function of unequal sampling effort. Two approximation models were used to identify under-collecting, and assess the probable level of completeness of the total species counts, for 16 counties across the Edwards Plateau for which reasonable data are available.

MATERIALS AND METHODS

Thirteen expeditions were made to the upper Frio-Sabinal Rivers area of the Edwards Plateau, popularly known as "The Hill Country", between March 1988 and April 1996. The study covered localities in adjacent parts of Real, Bandera and Uvalde counties bounded by 29°25–55′N and 99°20–50′W. Observations were made over 224 h during 160 days at five main study sites (Fig. 1), from 243 linear transects on 15

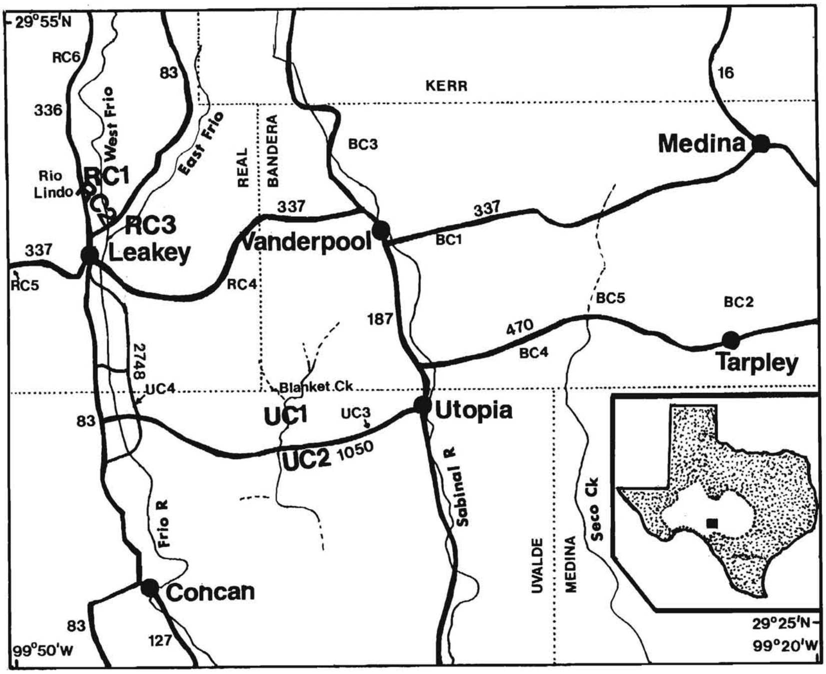

FIG. 1. The upper Frio and Sabinal River region on the south-central Edwards Plateau, Texas. Dotted lines show county boundaries; solid lines state roads (with numbers) and county roads. Study sites have a county abbreviation. The five primary transect sites are in bold.

measured track lines, totaling some 285 km, and an additional 60 h of opportunistic transects at 12 secondary sites (Fig. 1). In both cases, transects were designed, based on initial surveys, to sample all major habitats at each site. Most quantitative observations were collected at sites **RC1-3** near the town of Leakey and **UC1-2** on the Blanket Creek west of Utopia (see below). Transect methodology followed Pollard (1977, 1991), Pollard and Yates (1993), Thomas (1983) and Warren et al. (1984), with minor modifications appropriate to local circumstances.

To facilitate data comparisons, particularly with Durden's detailed butterfly records from Barton Creek, I used species rather than subspecies. Although Durden (1969) argued that "the subspecies is the primary occupant of the niche", the value and definability of either concept is debatable (e.g., Collins 1991, Ehrlich & Murphy 1981a, 1981b, 1982, Hammond 1985, 1990, Kudrna 1986, Miller & Brown 1981, Shapiro 1982), and some of the subspecies listed by Durden have either undergone status changes or are no longer recognized.

Relative abundance of each species was assessed by four categories similar to those used by Durden (1982): **A,** *abundant*—a series of five to ten specimens can be taken in an hour or so; **C,** *common*—such a series can be taken in a day's collecting; **U,** *uncommon*—takes several seasons to collect such a series; **S,** *scarce*—only one to five specimens encountered during the entire study. Durden's category **A** incorporates both my categories **A** and **C.** In my modification, category **A** is reserved only for the handful of species for which well over 1000 specimens were recorded during the survey.

Unlike Durden's semi-quantitative records, results from the time and distance-based transects used in the Frio-Sabinal survey also permit data to be expressed in other ways, such as the logarithmic scaling of numbers per unit search time (see Results), as proposed by Clench (1979).

Butterflies were observed during the following periods: 1988: 16–23 Mar.; 1989: 11–16 May; 1990: 16–21 Sept.; 1991: 6–10 Jul.; 1992: 5–28 May; 5–12 Oct.; 1993: 4–19 May; 1994: 14–24 May; 6–16 Jun.; 8–24 Sep.; 1–7 Nov.; 1995: 12–24 Apr.; 1996: 10–24 Apr. Butterflies were flying on all the days indicated, although in small numbers on two days in March 1988 and two in May 1994.

Several study sites within each of three counties were surveyed (Fig. 1).

NORTHERN UVALDE COUNTY: **UC1.** 547 m. Blanket Creek, on the Indian Blanket Ranch (primary study site subject to periodic minor flooding once or twice each year); **UC2.** 550–580 m. Adjacent section of Ranch Road (RR) 1050 verges (subject to periodic minor flooding); **UC3.** 663 m. Edge of escarpment on RR 1050 about 6 km from Utopia; **UC4.** 540 m. Section of RR 2748, about 1 km from RR 1050 junction.

WESTERN & CENTRAL BANDERA COUNTY: **BC1.** 450 m. Verges of RR 337 about 2 km from junction with HW 187; **BC2.** 520 m. Gun Mountain Ranch near Tarpley; **BC3.** 470 m. Canyon Creek region of Lost Maples State Park (primary study site); **BC4.** 510 m. Verges of RR 470 about 3 km from junction with HW 187; **BC5.** 430 m. On RR 470 about 7 km from Highway (HW) 187.

EASTERN REAL COUNTY: **RC1.** 493 m. "Rio Lindo" property about 3 km N of Leakey, on RR 336 (primary study site subjected to one major flood episode in Dec. 1990); **RC2.** 487 m. West bank of the Rio Frio just E of Rio Lindo (primary study site subject to two major flood episodes, Dec. 1990 & Apr. 1994); **RC3.** 472 m. Twin Forks Estate, about 3 km E of Leakey on RR 337 (primary study site subject to two major flood episodes, Dec. 1990 & Apr. 1994); **RC4.** 450 m. Verges of RR 337 about 5 km E of Leakey; **RC5.** 550 m. Verges of 337 about 5 km W of Leakey on RR 337, towards Camp Wood; **RC6.** 527 m. Verges of RR 336 each side of crossing with Cedar Creek, about 7 km N Leakey (primary study site subject to periodic minor flooding).

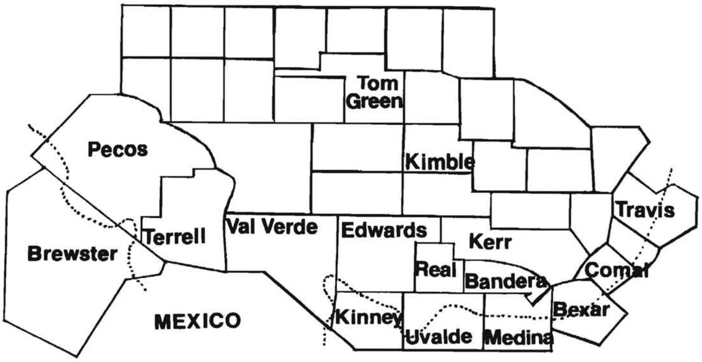

FIG. 2. Schematic map of the southern and central greater Edwards Plateau (after Amos & Gehlbach 1988), showing the 16 counties analyzed. Dotted lines indicate escarpments along the southern edge of the Plateau.

In addition to transect data, records of butterfly species from the 16 counties of Edwards Plateau which have been reasonably well-collected (Fig. 2), were assembled from data points of the maps of Stanford and Opler (1993), their unpublished supplements for 1994 and 1995, annual summaries of the Lepidopterists' Society and unpublished data kindly provided by Mr. E. Knudson, the Zone 6 coordinator for the Society. The data from these two sources showed 227 butterfly species recorded from this area. Each species was categorized by taxon, geographic element, ecological habitat and range limit. Thirty-seven more species were not recorded east of Brewster Co. and are included in comparative totals and calculations only when appropriate.

To compare the species composition of different geographic areas, I used cluster analysis (a program adapted by Dr. Gao Anli of the University Guelph) to calculate dissimilarity coefficients (D) for each pair of taxa. Dissimilarity coefficients (D) are calculated based on the formula $D = 1 - n/N$, where n is the number of areas in which both species occur and N those where either or both occur (Holloway & Jardine 1968, Holloway 1977, 1979). Relationships between all pairs can be displayed as a dendrogram, or in this case, as a compact area dendrogram summarizing average linkage between area groups.

I also assessed the relative completeness of these county species inventories. In such inventories it is important to distinguish real differences among regional faunas from artifacts of unequal collecting effort. Amos and Rowell (1988) faced a similar difficulty during assessments of relatively common species of plants in this region. Three approximation methods were applied to assess the scale of the problem:

1. Records were compared for the 27–33 species of cosmopolitan butterflies with wide ranges through the central and southern United States, most of which should be present in all the 16 counties being assessed on the Edwards Plateau. If less than 24–25 of these had been recorded, then the county was considered as significantly under-collected (see Results).

2. The theoretical maximum number of species of a fauna in a region of known size can be estimated by fitting appropriate field data to one or more asymptotic models. Early examples were given by Fisher et al. (1943), Preston (1948, 1962) and Simpson (1994). Preston (1962) suggested that the numbers of species was an approximate function of the square root of the area in comparable ecological situations. Later models were applied to regional fauna and flora, especially on islands, in various regions of the world by MacArthur (1965, 1972), MacArthur and Wilson (1967), Raven (1967), Robinson (1975), and Holloway (1977, 1979). Whittaker (1972), Poole (1974) and Pielou (1975) provided useful reviews of these techniques.

Preston (1962) and Robinson (1975) demonstrated a linear relationship between plots of log. numbers against log. surface area, for birds of the West Indies, and the Lepidoptera of several South Pacific islands, respectively. This method is applied to the 16 sample counties of the Edwards Plateau in this study (see Results).

3. Clench (1979) found that the number of butterfly species recorded over a period of years at a study site in Pennsylvania followed an asymptotic curve when plotted arithmetically against hours (×100) spent collecting/observing. He used sequential fits of the constant in the logistic equation to predict the asymptotic value. A similar relationship is shown when the logarithm of species number is plotted against the logarithm of the number of individuals in large samples (Holloway 1979). Frio-Sabinal data were assessed using both these methods (see Results).

RESULTS

Species recorded in the Frio-Sabinal region, measurements of abundance, and new county records. A total of 28,035 specimens representing 100 species was recorded and identified in the upper Frio-Sabinal region during 1988–96 (Table 1). These included eight new records for Bandera County, 10 for Uvalde County and 47 for Real County (indicated by bold initials B, R or U in Table 1). In this context "new county record" is defined as a species not listed for Real, Bandera or Uvalde Counties by Stanford and Opler (1993), or in the 1994 Supplement and Addenda appended to that volume.

Records of 51 more species were accumulated by other lepidopterists during the same period (Table 2). Almost all were from the vicinity of

Concan (387 m) on the south-central edge of the canyon zone of the Plateau, in north-central Uvalde County, about 20 km south of the sites in the present study. Twenty-six of these species have been plotted by Stanford and Opler (1993). The other 25, indicated by bold initials in Table 2, are from annual summaries of the Lepidopterists' Society News (1988–95) and unpublished data (Mr. E. C. Knudson, *in litt.*). A few of these were also briefly noted by Stanford and Opler in the unpublished 1994 supplemental list to their 1993 Atlas.

Species totals for the three upper Frio-Sabinal counties are now: Bandera 86 (77), Real 98 (49) and Uvalde 145 (109). The parentheses show counts given by Stanford and Opler (1993). Numbers for Real and Uvalde also significantly exceed those projected (70 and 110 respectively) by Stanford and Opler in their unpublished 1995 supplemental list to the 1993 Atlas.

Relative abundance and absences in the upper Frio-Sabinal region, 1988–96. The five most abundant butterflies at Frio-Sabinal were *Nathalis iole* Bdv. (7613; 27.15%), *Battus philenor* (L.) (6397; 22.82%), *Colias eurytheme* Bdv. (1654; 5.90%), *Eurema nicippe* (Cram.) (1516; 5.41%) and *Strymon melinus* Hbn. (1062; 3.79%). At the other extreme, 29 species were represented by only 1–5 specimens. A plot of the abundance of each species for the Frio-Sabinal fauna shows a typical monotonically decreasing profile (Fig. 3a), exaggerated by the large proportion comprised of *N. iole* and *B. philenor*. Figure 3b illustrates the profile of the abundance curve when the exaggerated influence of those two species is removed.

A number of species expected for this region were never encountered, despite careful examination of sightings and samples of superficially similar taxa. These include:

1. *Heraclides thoas* (L.). I examined the valvae of 43 males netted and released in April–June and September to November. All were *H. cresphontes* Cram. and of these, 15 had the forewing markings similar to those often cited as diagnostic of *thoas*; spot shape seems to be an unreliable criterion for *cresphontes* in this region. The absence of this species in the southern Hill Country is supported by E. K. Knudson (*in litt.*) who had never encountered it during intensive searches and collecting in Uvalde County.

2. Despite the large numbers of small yellows examined, no *Eurema nise* (Cramer) or *E. daira* (Godart) were found, only *E. lisa* in various forms and sizes and the seasonal forms of *N. iole.*

3. The presence of the widespread *Phycioides tharos* (Drury) was anticipated, but not recorded; only *P. phaon* (Edw.) and *P. vesta* (Edw.) were moderately common.

4. *Pieris rapae* (L.) was absent from all sites in all years, despite

TABLE 1. Table 1. Butterfly records from the Frio-Sabinal region of the Edwards Plateau, March 1988 to April 1996. Codes largely follow Durden, 1982 (see text for elaboration): A = abundant, C = common, U = uncommon, S = scarce. Bold letters after species represent new county records: **B**—Bandera; **R**—Real, **U**—Uvalde. Asterisks for *Pyrgus* indicate approximate values based on percent of male genitalia examined in each period. Percentages do not add to 100 due to rounding.

Years / Species	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.	1996 Apr.	All yrs species totals	All yrs percent composition of total
Hesperioidea															
Hesperiidae															
1. *Chiodes zilpa* (Butler) **R**	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
2. *Achalarus toxeus* (Plötz) **R**	—	—	—	—	—	—	—	—	—	S	—	—	—	2	<0.01
3. *Thorybes bathyllus* (Smith) **U**	—	—	—	—	—	—	—	—	—	S	—	C	—	1	<0.01
4. *Thorybes pylades* (Scd.) **B**	—	—	—	S	—	—	—	—	—	C	—	—	U	49	0.17
5. *Gorgythion begga* (Kby) **R**	—	—	—	—	—	—	—	—	—	—	S	—	—	1	<0.01
6. *Systasea pulverulenta* (Fld.) **R**	—	—	—	—	—	—	—	—	—	—	—	S	—	1	<0.01
7. *Gesta gesta* Evans **R**	—	—	—	—	—	—	—	—	—	—	S	—	—	1	<0.01
8. *Erynnis juvenalis* (F.)	S	—	—	—	—	—	—	—	—	—	—	—	—	1	<0.01
9. *Erynnis horatius* (Scd. & Bg.)	U	C	U	C	A	—	U	C	U	C	—	—	—	723	2.58
10. *Erynnis funeralis* (Scd. & Bg.) **R**	—	C	—	—	U	—	U	U	U	U	—	—	—	41	0.15
11. *Pyrgus communis* (Grote)	U	C	C	U	A	C	U	U	C	U	U	U	U	*206	0.73
12. *Pyrgus albescens* (Plötz)	—	—	C	—	C	C	—	C	C	C	U	—	S	*242	0.86
13. *Pyrgus philetas* Edw.	—	—	—	—	—	—	—	—	C	—	S	—	—	13	0.05
14. *Celotes nessus* (Edw.)	—	—	—	—	—	—	—	—	—	—	—	S	—	1	<0.01
15. *Pholisora catullus* (F.)	—	—	—	—	—	—	—	—	—	S	—	—	—	1	<0.01
16. *Nastra julia* (Freeman)	—	—	—	—	—	—	—	—	—	—	S	—	—	5	0.02
17. *Lerema accius* (Smith) **R**	S	—	—	—	U	S	—	—	U	U	S	—	S	18	0.06
18. *Copaeodes aurantiacus* (Hew.)	—	S	C	C	C	U	—	—	—	—	S	S	—	41	0.15
19. *Copaeodes minimus* (Edw.)	—	—	—	C	U	S	—	—	—	U	U	—	S	31	0.11
20. *Hylephila phyleus* (Drury)	U	C	—	U	U	U	U	U	C	C	S	C	—	53	0.20
21. *Hesperia viridis* (Edw.)	—	C	—	U	—	U	—	U	S	U	—	S	S	33	0.12
22. *Wallengrenia otho* (Smith)	—	C	—	U	U	—	U	U	—	A	—	S	—	108	0.38
23. *Atalopedes campestris* (Bdv.) **B**	—	—	U	—	U	A	S	S	U	—	—	C	U	472	1.68

TABLE 1. Continued.

Years / Species	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.	1996 Apr.	All yrs species totals	All yrs percent composition of total
24. *Anatrytone logan* (Edw.) **R**	—	—	—	—	S	—	S	—	S	—	—	—	—	8	0.03
25. *Euphyes vestris* (Bdv.) **R**	—	C	U	C	—	U	U	U	U	A	S	C	U	271	0.97
26. *Amblyscirtes nysa* Edw.	—	S	—	—	S	S	S	—	—	—	—	—	S	9	0.03
27. *Amblyscirtes celia* Skin. **R**	—	—	—	S	—	S	—	—	—	S	—	—	S	6	0.01
28. *Panoquina ocola* (Edw.) **R**	—	—	U	C	U	A	C	U	U	U	C	—	—	29	0.11
29. *Lerodea eufala* (Edw.)	—	—	—	—	—	U	—	—	—	C	—	—	—	109	0.39
Papilionoidea															
Papilionidae															
30. *Battus philenor* (L.)	C	A	A	C	A	C	C	C	C	A	U	C	U	6397	22.82
31. *Battus polydamas* (L.) **U**	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
32. *Papilio polyxenes* F. **R**	—	—	—	U	C	U	—	U	U	U	—	U	S	82	0.29
33. *Heraclides cresphontes* Cram.	—	C	C	—	U	U	U	U	U	C	U	U	S	103	0.37
34. *Heraclides ornythion* Bdv. **U**	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
35. *Pterourus glaucus* L. **B,R,U**	S	S	—	—	—	—	—	U	—	—	—	—	S	10	0.03
36. *Pterourus multicaudatus* Kby.	—	—	—	—	—	—	—	—	—	U	—	—	—	7	0.03
37. *Pterourus troilus* L. **R**	—	S	—	—	—	—	—	—	U	—	—	—	—	5	0.02
38. *Appias drusilla* (Cram.) **R,U**	—	—	—	—	U	—	—	—	—	—	—	S	—	21	0.08
39. *Pontia protodice* (Bdv. & Lct.) **U**	—	C	—	—	C	U	S	S	U	—	S	U	S	118	0.42
40. *Ascia monuste* (L.) **R**	—	—	—	—	—	S	—	—	—	—	—	—	—	1	<0.01
41. *Colias eurytheme* Bdv. **R**	U	C	U	U	A	C	C	C	U	S	C	A	S	1654	5.90
42. *Colias philodice* Godt. **R**	—	—	—	—	—	—	—	—	—	—	S	S	—	5	0.02
43. *Zerene cesonia* (Stoll.) **R**	U	A	C	—	C	U	C	U	U	U	C	U	S	243	0.87
44. *Pheobis sennae* (L.) **R**	—	U	C	—	S	S	U	U	S	U	S	S	—	47	0.17
45. *Phoebis philea* (Johansn.) **R**	—	U	U	—	S	—	S	S	—	S	—	—	—	8	0.03
46. *Phoebis agarithe* (Bdv.) **R**	—	—	U	U	—	—	—	S	—	A	S	—	—	61	0.22
47. *Kricogonia lyside* (Godt.) **R**	—	A	U	U	A	—	C	C	U	A	—	—	S	704	2.51
48. *Eurema lisa* Bdv. & Lct.	—	C	C	C	C	C	—!	U	U	C	C	—	S	348	1.24
49. *Eurema nicippe* (Cram.)	—	A	A	C	A	C	C	C	C	C	A	C	U	1516	5.41
50. *Eurema mexicanum* (Bdv.) **R**	—	—	S	—	—	—	—	—	—	—	—	S	—	3	0.01

TABLE 1. Continued.

Years / Species	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.	1996 Apr.	All yrs species totals	All yrs percent composition of total
51. *Nathalis iole* Bdv.	—	C	A!	U	A	C	U	A	A	U	C	A!	C	7613	27.15
Lycaenidae															
52. *Atlides halesus* (Cram.) **B**	—	—	—	—	S	—	U	U	U	—	—	S	—	20	0.07
53. *Phaeostrymon alcestis* (Edw.) **R**	—	—	—	—	—	—	S	—	—	—	—	—	—	1	<0.01
54. *Satyrium calanus* (Hbn.) **R,U**	—	—	—	—	U	—	C	S	—	—	—	—	—	25	0.09
55. *Calycopis isobeon* (Btl. & Drc.)	—	—	—	—	C	—	U	—	—	C	U	S	—	70	0.25
56. *Mitoura grynea* (Hbn.)	U	U	—	U	C	—	U	—	—	U	—	U	S	86	0.31
57. *Fixsenia favonius* (Smith) **R**	—	—	—	—	C	—	C	S	—	—	—	—	S	109	0.39
58. *Strymon melinus* Hbn.	—	C	C	U	A	U	C	C	C	C	S	U	S	1062	3.79
59. *Brephidium exile* (Bdv.)	—	—	—	—	—	S	S	—	—	—	—	—	—	3	0.01
60. *Leptotes marina* (Reak.) **B**	—	—	—	—	—	—	—	—	S	U	—	—	—	6	0.02
61. *Hemiargus ceraunus* (F.) **R**	—	—	—	—	—	U	—	—	—	S	—	—	—	5	0.02
62. *Hemiargus isola* (Reak.)	—	A	C	C	C	U	C	C	C	U	U	C	U	820	2.92
63. *Everes comyntas* (Godt.) **B,R**	—	—	—	—	—	U	—	—	—	—	S	—	—	6	0.02
Riodinidae															
64. *Calephilis nemesis* (Edw.)	—	S	—	—	—	—	—	—	—	S	S	—	—	4	0.02
65. *Calephilis rawsoni* McAlp.	—	—	—	—	—	S	—	—	—	—	—	—	—	1	<0.01
Libytheidae															
66. *Libytheana carinenta* (Cram.)	—	C	—	—	U	—	U	—	—	U	S	U	—	39	0.14
Nymphalidae															
67. *Agraulis vanillae* (L.).	U	C	C	C	C	C	U	C	C	U	C	U	U	433	1.54
68. *Dryas julia* (F.) **U**	—	—	—	S	—	—	—	—	—	—	—	—	—	2	0.01
69. *Heliconius charitonius* (L.).	—	—	—	S	—	—	—	—	—	—	—	—	—	2	0.01
70. *Polygonia interrogationis* (F.) **R**	—	S	U	—	—	—	—	U	—	—	—	—	—	8	0.03
71. *Polygonia comma* (Harr.) **R,U**	—	—	S	—	—	—	—	—	—	—	—	—	—	2	<0.01
72. *Nymphalis antiopa* (L.) **B,R**	—	S	—	—	S	—	S	S	—	—	—	—	—	6	0.02
73. *Vanessa virginiensis* (Dry)	U	C	—	—	C	U	C	C	U	U	S	C	—	368	1.31
74. *Vanessa cardui* (L.) **R**	—	U	U	—	U	U	S	—	—	—	—	C	—	65	0.23

TABLE 1. Continued.

Years / Species	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.	1996 Apr.	All yrs species totals	All yrs percent composition of total
75. *Vanessa atalanta* (L.)	U	C	C	—	C	U	U	C	U	U	U	C	S	324	1.15
76. *Junonia coenia* (Hbn.) **B,R**	—	—	C	U	C	C	U	C	C	U	U	U	S	193	0.691
77. *Junonia nigrosuffusa* B. & MD. **R**	—	—	—	—	S	—	—	S	S	—	—	S	—	4	0.02
78. *Euptoieta claudia* (Cram.) **R**	U	A	C	U	A	C	C	C	A	S	S	C	S	705	2.51
79. *Anthanassa texana* (Edw.) **R**	S	A	—	—	C	U	U	C	U	—	U	C	S	143	0.51
80. *Phyciodes phaon* (Edw.)	—	C	U	U	A	U	S	C	U	C	U	—	U	321	1.14
81. *Phyciodes vesta* (Edw.)	—	A	C	—	C	U	—!	C	U	—	S	C	U	213	0.76
82. *Charidryas nycteis* (Dbld.) **R**	—	—	—	—	—	—	—	—	C	—	U	C	S	48	0.17
83. *Chlosyne lacinia* (Gey.)	—	C	C	—	U	C	—!	S	U	—	U	C	—	116	0.41
84. *Chlosyne janais* (Drury) **R**	—	—	—	—	S	S	—	U	U	S	—	—	—	13	0.05
85. *Thessalia theona* (Mén.)	—	—	—	—	U	—	—	—	S	—	—	—	—	8	0.03
86. *Texola elada* (Hew.) **R**	—	—	—	—	—	S	—	—	S	S	C	S	—	8	0.03
87. *Basilarchia archippus* (Crm.) **R**	—	—	—	—	—	—	—	—	—	—	—	S	—	2	0.01
88. *Basilarchia astynax* (F.)	—	—	—	—	—	—	S	—	S	—	—	—	—	2	0.01
89. *Adelpha bredowii* (Gey.)	—	—	—	—	—	U	U	U	S	U	—	S	S	35	0.12
90. *Mestra amymone* (Mén)	—	—	—	—	—	C	—	—	—	C	C	—	—	97	0.35
91. *Anaea andria* Scd. **R**	—	—	C	—	—	U	S	S	U	S	—	U	S	58	0.21
92. *Asterocampa celtis* (Bd. & Lt.) **R**	—	S	C	—	S	U	U	—	U	S	—	S	—	25	0.89
93. *Asterocampa leila* (Edw.) **R**	—	—	—	—	—	—	—	—	—	U	—	—	—	3	0.11
94. *Asterocampa clyton* (Bd. & Lt.) **R**	—	—	—	—	—	U	—	—	—	—	—	—	—	6	0.02
Satyridae															
95. *Megisto cymela* (Cram.) **R, U**	—	—	—	—	C	—	C	U	—	—	U	U	—	197	0.70
96. *Megisto rubricata* (Edw.)	—	C	C	U	C	—	C	C	S	U	—	C	S	76	0.27
97. *Cercyonis pegala* (F.) **R**	—	C	A	C	C	C	S	C	C	C	—	—	—	339	1.21
98. *Hermeuptychia hermes* (F.) **U**	—	—	—	—	—	—	—	—	—	S	S	—	—	2	0.01
Danaidae															
99. *Danaus plexippus* (L.)	—	U	U	—	C	C	U	U	S	A	U	U	S	327	1.17
100. *Danaus gilippus* (Cram.)	—	C	C	U	C	C	C	C	U	C	C	U	S	201	0.72
														28035	*100.00

TABLE 2. Records of butterfly species in the Frio-Sabinal region from sources other than the present survey. Bold initials indicate new county records since 1993, following Table 1. Abbreviations: CB: Charles Bordelon, Jr.; ECK: Ed Knudson; JD: Joseph F. Doyle III; JR: Joann Karges.

Species no.	Family & species	County	Reference
Hesperiidae			
101.	*Epargyreus clarus* (Cram.) **U**	Uvalde.	ECK, *in litt.* 1996.
102.	*Chioides albofasciatus* (Hew.)	Uvalde.	Stanford & Opler (1993). CB, Lep. Soc. Summ. 1993.
103.	*Urbanus proteus* (L.) **U**	Uvalde.	ECK, *in litt.* 1996.
104.	*Urbanus dorantes* (Stoll.) **U**	Uvalde.	ECK, *in litt.* 1996.
105.	*Achalarus jalapus* (Plötz) **U**	Uvalde.	CB, Lep. Soc. Summ. 1994.
106.	*Astraptes fulgerator* (Walch) **U**	Uvalde.	CB, Lep. Soc. Summ. 1993.
107.	*Cogia hippalus* (Edw.)	Uvalde.	ECK, *in litt.* 1996.
108.	*Cogia outis* (Skin.)	Uvalde.	Stanford & Opler (1993, p. 21).
109.	*Staphylus mazans* (Reak.)	Uvalde.	Stanford & Opler (1993, p. 27).
110.	*Staphylus hayhurstii* (Edw.)	Bandera.	Stanford & Opler (1993, p. 28).
111.	*Achlyodes thraso* (Hbn.) **U**	Uvalde.	ECK, *in litt.* 1996 (*mithridates*).
112.	*Grais stigmatica* (Mab.)	Uvalde.	Stanford & Opler (1993, p. 36).
113.	*Chiomara asychis* (Stoll.) **U**	Uvalde.	ECK, *in litt.* 1996.
114.	*Erynnis tristis* (Bdv.) **U**	Uvalde.	CB, Lep. Soc. Summ. 1993. Listed in Stanford & Opler 1994 unpubl. suppl.
115.	*Pyrgus oileus* (L.)	Uvalde.	ECK, *in litt.* 1996. Listed in Stanford & Opler (1993).
116.	*Heliopetes macaira* (Reak.) **U**	Uvalde.	JR, Lep. Soc. Summ. 1995.
117.	*Heliopetes lavianus* (Hewitson) **U**	Uvalde.	JD, Lep. Soc. Summ. 1995.
118.	*Ancyloxypha numitor* (F.)	Real, Bandera.	Stanford & Opler (1993, p. 65).
119.	*Ancyloxypha arene* (Edw.)	Uvalde Co.	Stanford & Opler (1993, p. 65).
120.	*Polites vibex* (Gey.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 75).
121.	*Ambylscirtes aenus* Edw. **U**	Bandera, Uvalde.	Stanford & Opler (1993, p. 87). ECK, *in litt.* 1996.
122.	*Ambylscirtes oslari* (Skin.)	Bandera, Uvalde.	Stanford & Opler 1993, p. 87. ECK, *in litt.* 1996.

TABLE 2. Continued.

Species no.	Family & species	County	Reference
123.	*Ambylscirtes eos* (Edw.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 89). ECK, *in litt.* 1996.
124.	*Calpodes ethlius* (Stoll.) **U**	Uvalde Co. Concan.	ECK, *in litt.* 1996.
125.	*Megathymus yuccae* (Bdv. & Lct.)	Bander, Real, Uvalde.	Stanford & Opler (1993, p. 101). ECK, *in litt.* 1996.
Pieridae			
126.	*Paramidea midea* (Hbn.)	Uvalde.	Stanford & Opler (1993, p. 121). ECK, *in litt.* 1996.
127.	*Anteos clorinde* (Godt.) **U**	Uvalde.	ECK, *in litt.* 1996.
128.	*Anteos maerula* (F.) **U**	Uvalde.	ECK, *in litt.* 1996.
129.	*Eurema proterpia* (F.) **U**	Uvalde.	ECK, *in litt.* 1996.
Lycaenidae			
130.	*Chlorostrymon simaethis* (Drury) **U**	Uvalde.	ECK, *in litt.* 1996.
131.	*Ministrymon clytie* (Edwards) **U**	Uvalde.	CB, Lep. Soc. Summ. 1994. Stanford & Opler 1994, unpubl. supp.
132.	*Ministrymon azia* (Hew.) **R, U**	Real, Uvalde.	Stanford & Opler 1994, unpubl. supp. ECK, *in litt.* 1996.
133.	*Xamia xami* (Reak.) **U**	Uvalde.	ECK, *in litt.* 1996.
134.	*Incisalia henrici* (G. & R.)	Bandera, Real, Uvalde.	Stanford & Opler (1993, p. 158). ECK, *in litt.* 1996.
135.	*Parrhasius m-album* (Bdv. & Lct.) **U**	Uvalde.	CB, JD, ECK. Lep. Soc. Summ. 1993. Stanford & Opler 1994, unpubl. supp.
136.	*Strymon alea* (Godm. & Salv.) **U**	Uvalde.	CB,ECK, Lep. Soc. Summ. 1995.
137.	*Strymon columella* (F.)	Uvalde.	Stanford & Opler 1993, p. 164. ECK, *in litt.* 1996.

TABLE 2. Continued.

Species no.	Family & species	County	Reference
138.	*Zizula cyna* (Edw.)	Uvalde.	Stanford & Opler 1993, p. 170. ECK, *in litt.* 1996.
Riodinidae			
139.	*Calephelis perditalis* B & McD. **U**	Uvalde.	ECK, *in litt.* 1996.
140.	*Caria ino* (Godm. & Salv.) **U**	Uvalde.	ECK, *in litt.* 1996.
Nymphalidae			
141.	*Dione moneta* Hbn. **U**	Uvalde.	ECK, *in litt.* 1996.
142.	*Euptoieta hegesia* (Cram.) **U**	Uvalde.	ECK, *in litt.* 1996.
143.	*Phycoides tharos* (Drury) **U**	Bandera, Real, Uvalde.	Stanford & Opler (1993, p. 211). ECK, *in litt.* 1996.
144.	*Phyciodes tulcis* (Bates) **U**	Uvalde Co.	Stanford & Opler (1994 unpubl. supp.).
145.	*Anartia jatrophae* (Johansn.)	Uvalde Co.	Stanford & Opler (1993, p. 221).
146.	*Siproeta stelenes* (L.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 222). ECK, *in litt.* 1996.
147.	*Eunica monima* (Stoll.) **U**	Uvalde.	ECK, *in litt.* 1996.
148.	*Dynamine dyonis* Gey. **U**	Uvalde.	NR, JR, CN, ECK, CB, JD, Lep. Soc. Summ. 1995
149.	*Biblis hyperia* (Cram.) **U**	Uvalde.	ECK, *in litt.* 1996.
150.	*Anaea aidea* (Guer.-Mén.) **U**	Uvalde.	ECK, *in litt.* 1996.
Danaidae			
151.	*Danaus eresimus* (Cram.)	Uvalde.	Stanford & Opler (1993, p. 257). ECK, *in litt.* 1996.

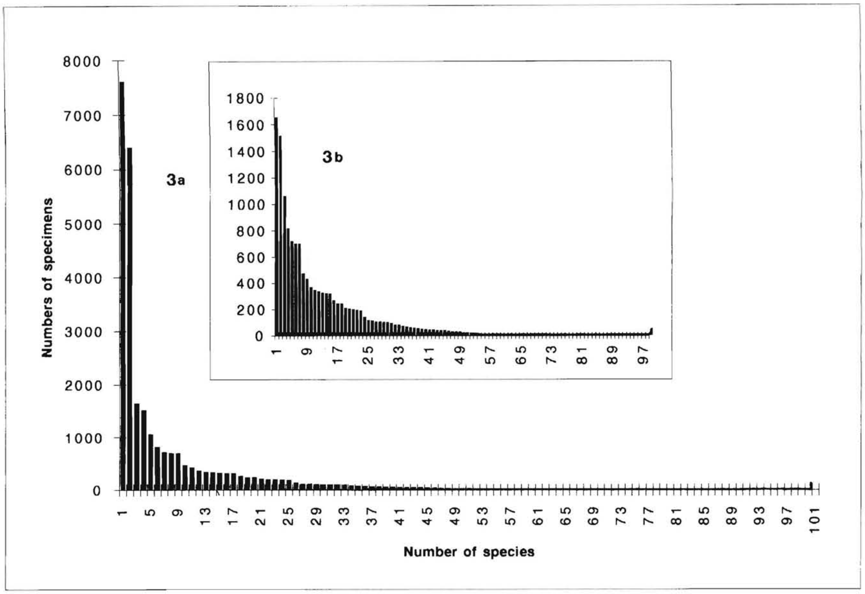

FIG. 3. Abundance versus species of butterflies recorded on transects from the upper Frio-Sabinal region 1988–1996, showing a typical monotonically decreasing profile (3a). 3b (inset) shows the profile with the two commonest species, *N. iole* and *b. philenor* removed.

scrutiny of all white butterflies netted or observed at each locality, even in the cultivated areas around Utopia and Leakey townships.

5. Among the Hesperioidea, specimens of *Erynnis* Shrank and *Pyrgus* Hbn. were netted and examined whenever possible to minimize the chance of overlooking similar species. *P. philetas* Edw. was found to occur in the hotter, later part of the year at some sites, but all *Erynnis* examined proved to be *E. horatius* (Scudd. and Burg.) or *E. funeralis* (Scudd. and Burg.), with the exception of a single *E. juvenalis* (F.) taken at the Blanket Creek in March 1988.

6. The apparent absence of *Polites vibex* (Gey.) was also noteworthy because it has been recorded previously in Bandera and Uvalde counties, as well as Kerr and Medina (Stanford and Opler 1993). Occasionally, males may have been confused with *Hylephila phyleus* (Drury) on transects, or females overlooked among clusters of the more common *Atalopedes campestris* (Bdv.), even though we were actively looking for *P. vibex*.

Assessment of relative completeness of county inventories. Records of butterfly species for counties on the Edwards Plateau range from 170 in Bexar, to only two in Midland (Stanford and Opler 1995 un-

TABLE 3. Counts of butterfly species from well-collected counties of the Edwards Plateau, by geographical range. See text for methods of assigning butterfly species to a particular range. *"Tom Green" is a conglomerate based on records of the moderately worked nearby counties (providing a provisional estimate for the central northern region of the Plateau).

Geogr. element	Brewst.	Pecos	Terrell	V. Verde	Edwards	Kinney	Real	Uvalde	*"Tom Green"	Kimble	Kerr	Bandera	Medina	Bexar	Comal	Travis	MEANS
N/NW	15	3	5	6	8	4	14	15	12	8	21	14	5	19	14	19	11.4
NE/E	18	7	9	18	7	12	28	36	20	16	44	28	18	47	40	50	24.8
S	20	4	7	11	5	11	12	43	6	5	29	8	10	49	29	43	18.3
W/SW	77	13	19	16	10	19	15	20	11	10	22	7	12	24	16	21	19.5
COSM.	31	25	28	29	17	27	29	31	36	23	31	29	33	31	30	31	28.8
TOTALS	**161**	**52**	**68**	**80**	**47**	**73**	**98**	**145**	**85**	**62**	**147**	**86**	**78**	**170**	**129**	**164**	—

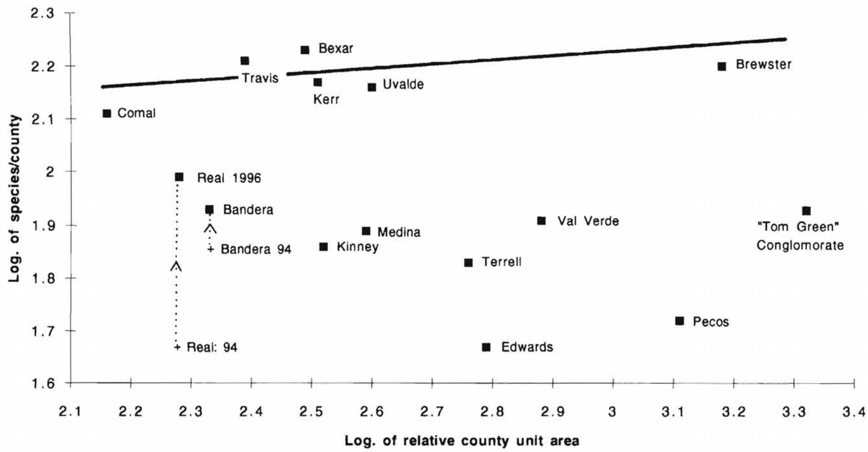

FIG. 4. Log-log relationship between total species recorded in each county versus area in square kilometers, assuming similar ecological parameters (after Preston 1962). Values on or near the line are presumed to be close to the "maximum". Counties falling below the line are probably under-collected, but may have less diverse habitat.

publ. supp.). Of course Midland is an extreme case, but unequal collecting effort may still be an important, but overlooked, factor when relatively high species totals are being compared. The cosmopolitan butterfly species were summed for each of the 16 sampled counties of the Edwards Plateau. Thirteen had records of 27–33 such species and three had 17–25, with a mean of 28.8 (Table 3). In the case of Real Co., 49 species in total had been recorded by 1993, of which 23 were cosmopolitan. These might seem to be appropriate numbers, because Real is one of the smallest counties on the Plateau, but Stanford and Opler's (1993) data base showed *Vanessa cardui*, *V. virginiensis*, *J. coenia*, *A. texana*, *F. favonius* and *E. vestris* still unrecorded, so Real was obviously under-collected. During the present survey, the species total for Real has risen to 98, with a cosmopolitan element of 29.

When the data on number of species per county from the Edwards Plateau counties are log-transformed and plotted against log(county area) (Fig. 4), the well-collected counties such as Bexar, Brewster, Comal, Kerr, Travis and Uvalde fall close to the line, while most of the others counties fall well below it. The recent data from the Frio-Sabinal surveys have shifted the values for Bandera and more markedly, Real Co., closer to the line in Fig. 4. This data indicate that the theoretical "maximum" species total for both these counties could be 160–165 species, *if* ecological parameters and migratory patterns are approximately comparable across the Plateau (see Discussion).

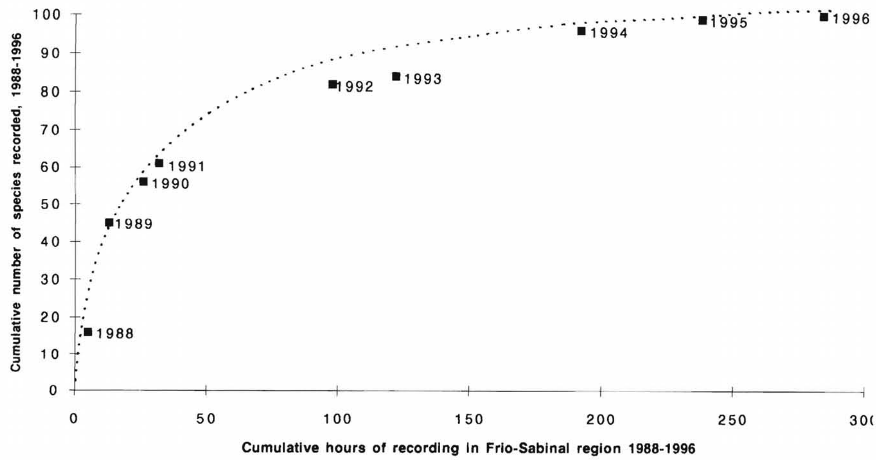

FIG. 5. Clench (1979) extimated "maximum" number of species for a by plotting cumulative number of species against cumulative sampling time. The curve for Frio-Sabinal seems asymptotic after 8–9 years of recording.

When the Edwards Plateau data are plotted following the models of Clench (Fig. 5), and Holloway (Fig. 6) however, the asymptotic curves indicate that the "maximum" number of species in Bandera and Real counties might be only 110–120, not 160–165.

Linkages across the Edwards plateau. Species totals for Edwards (47 species), Pecos (52), Terrell (68), Kinney (73) and Kimble counties

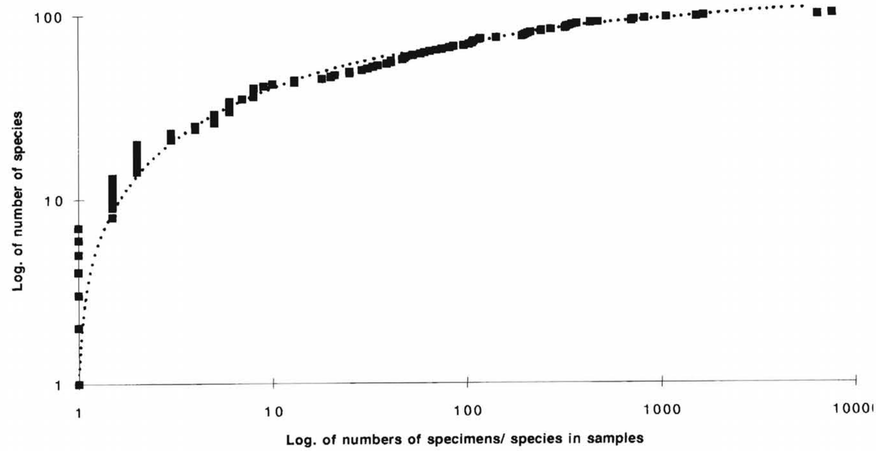

FIG. 6. Holloway (1979) plotted log species number against log number of specimens in large samples. The asympototic curve produced from the Frio-Sabinal data is similar to Fig. 5.

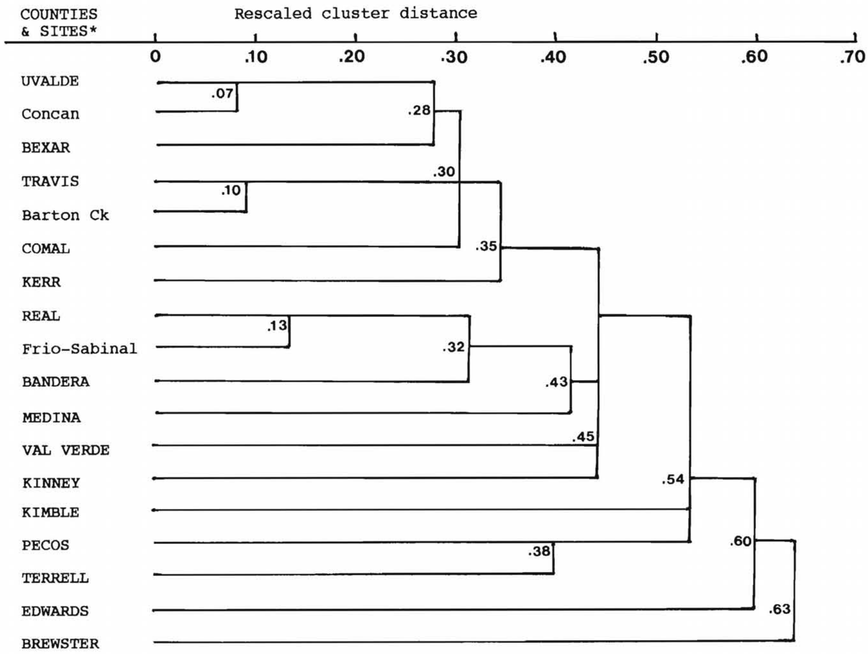

FIG. 7. Dendrogram showing provisional interrelationships of the butterflies of the Edwards Plateau. Dissimilarity coefficients were calculated for each pair of taxa of the total species sample. The butterfly fauna in the southeastern cluster of counties is more cohesive than those in the west. The relative isolation of Brewster County was anticipated, but that of Edwards may be a function of under-collecting.

(62), are likely to be too low, although all but the last range from relatively dry to arid (Riskind and Diamond 1988). The estimate for Tom Green county (85) is a composite (see Table 3 caption) and should be interpreted with special caution. Totals for other counties (78 to 170 species), i.e., Bandera, Bexar, Brewster, Comal, Kerr, Real, Travis, and Uvalde counties are not likely to change by more than 5–20% in the near future. Projecting totals by weighted averages is risky without good information.

The dendrogram (Fig. 7) shows the dissimilarity coefficients for pairs of counties or groups of counties. Lower numbers (a lower dissimilarity coefficient) indicate a greater degree of overlap in the butterfly fauna of those regions. This dendrogram demonstrates the relative distinctiveness of Brewster Co., even from Pecos and Terrell counties, despite their having some faunal components in common. Edwards appears almost as isolated as Brewster. The general faunal cohesion of the southeastern block of counties, Travis, Comal, Bexar, Kerr and Uvalde is confirmed, as is the anticipated similarity of Real and Bandera counties. The

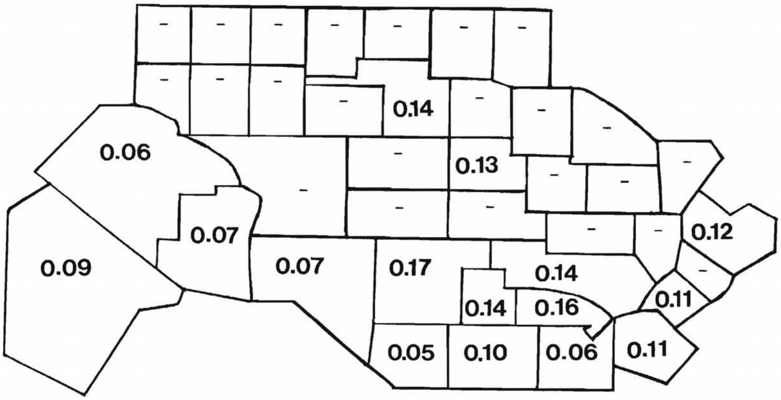

FIG. 8. N-NW species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

Barton Creek site is shown to be usefully representative of the fauna of Travis, as are Concan of Uvalde Co., and Frio-Sabinal of Bandera and Real counties. Remaining counties also appear relatively isolated but interpretation is best reserved until more information is available.

A frequency count revealed that only 37 species were known to occur in all but one to three of the counties, while 114 of the 261 had been recorded in only one to three counties. Among families, restricted distribution was most apparent in the Hesperiidae; 54% and 57% of all Pyrginae and Hesperiinae, respectively, were restricted to three or fewer of the sample counties, generally in the western sector of the Plateau.

Comparative distributions of butterfly species on the Edwards plateau. The data matrix was used to show all species classified by: A) Geographical components by counties (Table 3), B) Species in ecological habitats by counties (Table 4) and taxon (subfamilies) (Table 5); C) Relative position by county with respect to overall range (Table 6). All data are given as numbers, not percentages.

Comparison of geographical components. Butterfly species were allocated to one of five groups based on their geographical distribution relative to the Edwards Plateau (Table 3): 1) N/NW-species which have predominantly California–Rockies–Great Plains distributions (Fig. 8); 2) NE/E–prairie–eastern coastal woodlands (Fig. 9); 3) S-tropical coastal forest (Fig. 10); 4) SW/W (Sonoran–Coahuilan) (Fig. 11), and 5) COSM-cosmopolitan species, or ranging at least through Mexico– Texas–central Gulf states (not figured). Most attributions are from Durden (1982); species not recorded by him are by my allocation. Data were extracted from Stanford and Opler (1993), and their unpublished supplements of 1994, 1995. Accounts by Howe (1975), Pyle (1981), Scott (1986), Opler

TABLE 4. Numbers of butterfly species from 16 selected counties across the Edwards Plateau, classified by habitat zones following Durden (1982). Parenthetical values for Brewster County include 37 species not yet recorded east of this county.

Habitat v. county	Brewst.	Pecos	Terrell	V. Verde	Edwards	Kinney	Real	Uvalde	Tom Green	Kimble	Kerr	Bandera	Medina	Bexar	Comal	Travis
A. Disturbed sites	9(10)	6	8	8	4	7	9	8	9	6	99	8	8	9	7	11
B. Great Plains flora	10(11)	6	8	8	5	5	12	10	12	7	15	11	6	14	14	16
C. Dry warm temp. —subtropical	24(25)	14	17	15	9	14	14	17	14	13	17	14	13	20	19	21
D. Subtropical thorn forest	8(11)	4	5	6	5	8	5	9	5	3	6	5	4	12	6	7
E. Subtrop. thorn scrub/desert	8(12)	3	5	5	6	6	5	8	5	4	6	1	3	8	4	4
F. Oak/Jun. Sonor. grass/woodland	3(24)	1	1	2	2	1	2	3	1	1	2	1	1	3	1	2
G. Broad temp.— trop. woodland	5(6)	0	1	2	1	2	3	4	1	1	5	2	1	3	3	3
H. Eastern mixed forest	1	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1
I. Gulf Coast trop. woodland	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
J. Subtropical & Gt. Plain brush	3(4)	3	3	4	0	3	5	6	5	2	7	4	5	6	7	5
K. Subtrop. mont. woodland	7(9)	1	3	0	1	2	2	5	2	1	8	3	2	4	2	6
L. Eastern decid. woodland	10	4	6	11	6	5	15	17	11	11	19	17	13	19	18	19
M. Appalach.-Miss. Basin woodland	4	1	1	1	2	2	4	5	3	3	9	3	3	8	6	10
N. Southern coast woodland	2	1	1	1	0	2	2	4	2	0	4	3	3	10	5	6
O. Western decid. woodland	6	1	3	3	2	2	5	6	4	2	6	5	1	7	7	6
P. Endemics of S. Madre/Balcones	0	0	0	2	0	0	0	2	0	0	1	0	1	2	2	3
Q. Endemics of C. Texas/Coahuila	3	2	1	4	2	3	5	5	3	3	5	5	3	5	5	5
R. South tropical woodland	21(23)	5	5	8	2	11	9	35	7	5	26	3	11	37	22	38
TOTALS	**124(161)**	**52**	**68**	**80**	**47**	**73**	**98**	**145**	**85**	**62**	**147**	**86**	**78**	**170**	**129**	**164**

TABLE 5. Numbers of butterfly subfamilies from 16 selected counties across the Edwards Plateau classified by habitat zones following Durden (1982). The 37 species recorded from Brewster or counties further west are excluded (see Table 4).

Habitat vs. taxon	Pyrg.	Hesp.	Megath.	Papil.	Pierid.	Liphyr.	Thecl.	Polyom.	Riod.	Libyth.	Helico.	Arg/Ml.	Nymph.	Satyr.	Danaid.	Totals
A. Disturbed sites	0	0	0	0	7	0	0	0	0	0	0	0	3	0	1	**11**
B. Great Plains flora	1	5	0	1	0	0	1	1	0	0	0	1	2	4	0	**16**
C. Dry warm temp. —subtropical	10	6	1	1	3	0	2	1	2	0	0	4	0	0	1	**32**
D. Subtropical thorn forest	2	3	3	0	1	0	2	2	1	0	0	0	1	0	0	**15**
E. Subtrop. thorn scrub/desert	4	1	0	0	0	0	3	0	0	0	0	4	0	0	0	**12**
F. Oak/Jun. Sonor. grass/woodland	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	**3**
G. Broad temp.— trop. woodland	2	1	0	1	1	0	0	0	0	0	0	1	0	0	0	**7**
H. Eastern forest	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
I. Gulf Coast trop. woodland	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
J. Subtropical & Gt. Plain brush	0	0	1	0	1	0	2	0	0	0	0	4	0	0	0	**9**
K. Subtrop. mont. woodland	4	5	0	1	0	0	1	0	0	0	0	0	1	0	0	**12**
L. Eastern decid. woodland	3	9	0	1	0	0	2	0	0	1	0	2	2	0	0	**20**
M. Appalach.-Miss. Basin woodland	4	0	0	0	1	1	1	1	0	0	0	1	1	0	0	**10**
N. Southern coast woodland	3	5	0	1	1	0	0	0	0	0	0	0	1	1	0	**12**
O. Western decid. woodland	2	0	0	1	2	0	0	0	0	0	0	1	2	0	0	**8**
P. Endemics of S. Madre/Balcones	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	**3**
Q. Endemics of C. Texas/Coahuila	0	1	1	0	0	0	1	0	2	0	0	0	0	0	0	**5**
R. South tropical woodland	16	1	0	4	8	0	1	2	0	0	5	1	10	0	1	**49**
TOTALS	**53**	**38**	**6**	**12**	**25**	**1**	**18**	**8**	**7**	**1**	**5**	**19**	**25**	**5**	**3**	**226**

TABLE 6. Numbers of butterfly species in 16 selected counties across the Edwards Plateau, classified by ranges and range limits following Durden (1982).

Range vs. county	Pecos	Terrell	V. Verde	Brewstr.	Edwards	Kinney	Real	Uvalde	Tom Gr.	Kimble	Kerr	Bandera	Medina	Bexar	Comal	Travis
A. At eastern limit of range	6	8	8	56	4	7	9	8	9	6	99	8	8	9	7	11
B. In eastern part of range	6	8	8	10	5	5	12	10	12	7	15	11	6	14	14	16
C. In middle part of range	14	17	15	24	9	14	14	17	14	13	17	14	13	20	19	21
D. At northeast limit of range	4	5	6	8	5	8	5	9	5	3	6	5	4	12	6	7
E. At northwest limit of range	3	5	5	8	6	6	5	8	5	4	6	1	3	8	4	4
F. At northern limit of range	1	1	2	3	2	1	2	3	1	1	2	1	1	3	1	2
G. In northern part of range	0	1	2	5	1	2	3	4	1	1	5	2	1	3	3	3
H. At southeast limit of range	0	0	0	1	0	0	1	1	1	0	1	1	0	1	1	1
I. At southwest limit of range	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
J. At southern limit of range	3	3	4	3	0	3	5	6	5	2	7	4	5	6	7	5
K. In southern part of range	1	3	0	7	1	2	2	5	2	1	8	3	2	4	2	6
L. At western limit of range	4	6	11	1	6	5	15	17	11	11	19	17	13	19	18	19
TOTALS	**52**	**68**	**80**	**161**	**47**	**73**	**98**	**145**	**85**	**62**	**147**	**86**	**78**	**170**	**129**	**164**

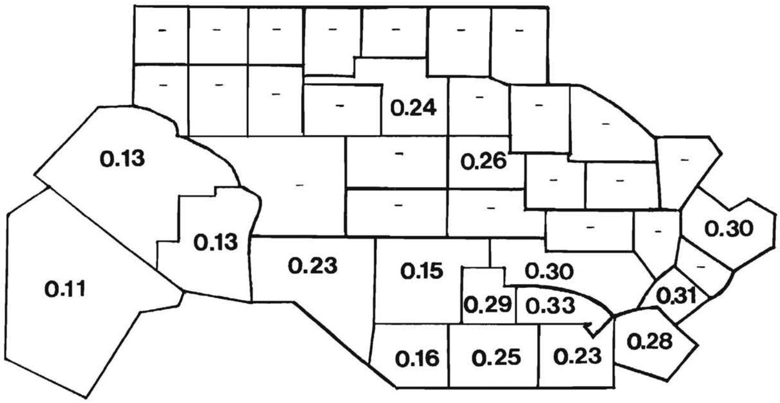

FIG. 9. N-NE species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

and Krizek (1984), Opler and Malikul (1992) and Neck (1996) were consulted for clarification of habitat and eastward range, when necessary.

The distribution of each regional geographical component is presented as the proportion of total species recorded for each county. Paired *t*-tests indicated that the variances of samples were not significantly different from those corrected for relative area ($p = 0.37–0.51$). Significant differences between the geographical groups were confirmed by ANOVA ($p < 0.01$). The N/NW element (0.06–0.17) is uniformly weak across the Plateau (Fig. 8). NE/E species account for 0.25–0.33 of each total in most of the eastern and central region, falling to 0.11–0.13

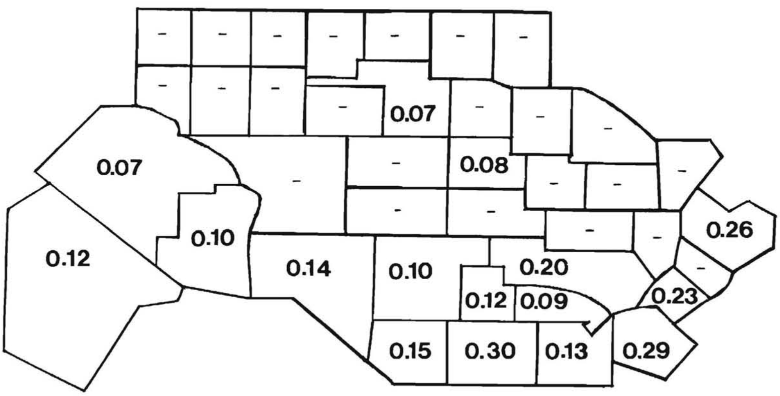

FIG. 10. S species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

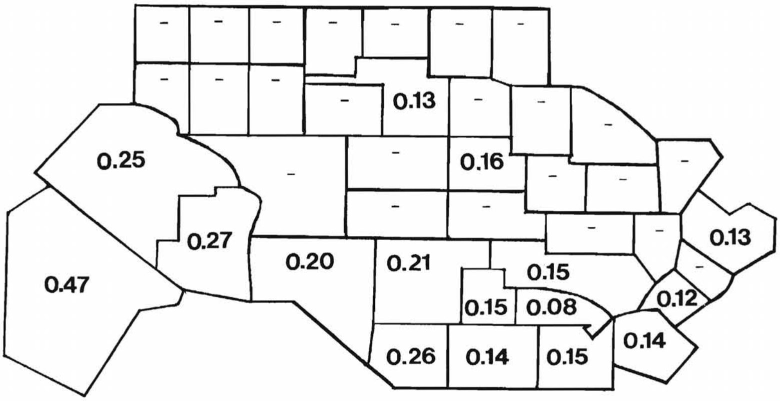

FIG. 11. W-SW species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

in the west (Fig. 9). The S (tropical) element is strongly represented only in the southeast region of the Plateau (Fig. 10), while the W/SW (Sonoran–Coahuilan) element (Fig. 11) is predominant (0.21–0.47) in the western and southwestern counties, but 0.16 or less in the central and eastern regions.

Comparison by habitat zones. Butterfly data from the 16 counties were tabulated by subfamily against 17 habitat types designated by Durden (1982) by county (Table 4) and by taxon (Table 5). Some interesting patterns were noted, which do not require statistical analysis.

Type A: *Disturbed habitats* were typified by 11 species but dominated by Pieridae (7 species–64%).

Type B: *Great Plains grassland habitat* supported 16 species on the Plateau; Hesperiinae (5) and Satyrinae (4), together comprising 56% of the total.

Types C–E: The intergrading dry, warm subtropical habitats, *Arid woodland* (C), *Thorn forest* (D) and *Thorn scrub* (E) together accounted for 58 of the total species, dominated by Hesperiidae (29), comprised of Pyrginae (16), Hesperiinae (10) and Megathyminae (3). Together with Theclinae (7) and Melitaeinae (8), these taxa accounted for 75% of the total.

Type J: In the subtropical *Great Plains brush habitat* nine species were recorded; four (44%) were Melitaeinae.

Type K: In *Subtropical montane woodlands* 12 species were represented, Hesperiidae; (9, 75%), Pyrginae (4) and Hesperiinae (5).

Type L: *Eastern deciduous woodland habitat* accommodated 20 species of the total; (9, 45%) were Hesperiinae.

Type M: *Basin woodlands* were characterized by 10 species of which four (40%) were Pyrginae.

Type N: *Southern coast woodlands fauna* comprised 12 species, again dominated by Hesperiidae (67%–Pyrginae 3, Hesperiinae 5).

Type R: The largest faunal group of butterflies was that associated with *South tropical woodlands*, 49 species, mostly sporadic in their appearance in any given county, and dominated by Pyrginae (16, 33%), subtropical Pieridae (8, 16%) and subtropical Nymphalinae, Apaturinae and Heliconiinae (10, 20%).

Types F–I and O–Q (see Table 5 and Durden 1982): the remaining seven habitat types were sparsely characterized by 1–8 species (mean 5.7) scattered across the range of families and subfamilies.

Overall, the Hesperiidae was the best represented family in the 16 counties, (97, 43% of the total), while the Pyrginae was the most abundant subfamily (53, 23.5%).

Comparisons of range limits. The diversity of the butterfly fauna of the Edwards Plateau is largely a function of its strategic position (see above); but despite a respectable total of 227 species for the 16 counties, even excluding those found only in Brewster or westward, it is surprisingly difficult to point to any one category, other than the Eastern deciduous woodland group which could truly be said to be characteristic of the geographic unit.

Of the 11 cosmopolitan species associated with disturbed habitats (Durden's Category A), only one (9%), the northern straggler *Colias philodice*, reaches its southern limit of range limit on the Plateau (Table 6). Of the 15 species of the Great Plains fauna (B), five (33.3%) are at their southern or eastern limit, while only five (25%) of the Eastern deciduous woodland species (L) are at their S or SW limit (Table 6).

However, the number of species which reach a range limit on the Plateau comprise more than 50% in all remaining ecological habitat groups (Table 6); C (50%), D and E (73%), F (66.6%), G (86%), H and I (100%), J (55%), K (83%), M (80%), N (91.5%), O (62.5%), P (100%), Q (60%) and R (57%). The implication is that a moderate change in one or more climatic factors could have a significant effect on present species composition. Given the altitude of much of the region (300 m+), an extended period of cooler climate might eliminate many of the southern components, upwards of 60–100 species. Warming trends might seem more likely at present, but the effect would perhaps be more variable, depending whether seasonal and annual rainfall decreased or not.

DISCUSSION

Location and environment. Much of the Edwards Plateau is a southward extension of the Great Plains Physiographic Province (Hunt

1974), and the southern extremities of the Rocky Mountains are only some 200 km from its northwestern margin. Altitudes ranges from about 900 m in northern counties such as Tom Green, to 300 m at Concan in north-central Uvalde Co. on the southern extremity of the Balcones Escarpment. The western section of the Plateau blends into the arid, subtropical Trans-Pecos region. The major rivers and associated riparian systems generally run northwest to southeast; their ecological influence is widespread and particularly significant in the southeast and less so in the southwest. The counties of the Edwards Plateau are on hard, porous limestone (Gould 1969, Ajilvsgi 1984), except where the central, basaltic Llano Uplift breaks through. In contrast, on the eastern margin of the Plateau, counties such as Bastrop, Lee, Fayette and most of Caldwell have sandstone and shale soils, with podsols, peat bogs, and Neogene sands and clays covered with coastal-type prairie (Durden 1982).

Isohyets over western and central Texas have a consistent general north-south orientation (Riskin & Diamond 1988), with a marked clinal decrease in annual rainfall from east to west. As a consequence, Brewster, Pecos and Terrell counties have annual rainfalls of only 20–35 cm. Eastern and northeastern counties receive more than twice that (ca. 90 cm). Significant differences in rainfall occur even across the south-central region of the Plateau and along the complex southern margin of the exposed limestone scarp of the Balcones Fault. The upper Frio-Sabinal area receives about 30% less rain annually (60 cm) than Austin (85 cm).

Floristic patterns on the plateau. The geography, physical environment and climatic characteristics of the Plateau have all played roles in colonization and establishment of distribution patterns of the historical and extant flora and fauna. Amos and Rowell (1988) applied principal component analysis (PCA) to a large database of woody and endemic vascular plant records, to try to determine the ecological relationships, floristic patterns, and perhaps origins of the regional components. The analysis identified two major floristic zones across the Plateau: a numerous and diverse eastern component and a less rich and less widespread western one. Val Verde County was identified as the major transitional zone. A third, southern element of Neotropical origin was important only in the counties along the southern rim of the Plateau. Simple regional characterizations are complicated by the existence of parallel ecological habitats within each floristic zone (Gehlbach 1988). For example, the woody taxa of the Plateau tend to form tight geographical clusters (Amos and Rowell 1988), while in contrast, the vascular endemics, are clustered in a relatively few eastern counties without any such detectable associations.

Flora in adjacent zones at the same latitude across the Plateau can be surprisingly dissimilar. Using data of Ajilvsgi (1984) and Enquist (1987), I examined a sample of 313 vascular plants from about 70 families (not just endemics), and compared the composition of the south-central Edwards Plateau (Real, Bandera, Uvalde and Kerr counties) with that of the South Central Vegetation Zone, the westerly section of which takes in parts of Travis, Hayes, Comal and Bexar counties on the curved margin of the Balcones Fault between San Antonio and the Austin region. Although 148 species were common to both regions, 52.7% of the flora was not shared; 73 species in South Central are not known from the Edwards Plateau and 92 found on the Plateau are not recorded from South Central.

North-south differences in flora can be quite marked over relatively small distances as well. The upper Frio-Sabinal vegetation consists predominantly of Juniper-Oak savanna (Amos and Gehlbach 1988). The northern, eastern and western margins do not include any transitional areas, but intergrade with Mesquite Savanna in the north-central parts of Uvalde and Medina counties along the southern margin of the Balcones Fault (Simpson 1994).

The eastern counties have much more complex vegetation patterns. Llano County and the western part of Burent lie in the Central Texas Mesquite-Oak Savanna; Hays, Travis and Williamson straddle the southern tongue of the Blackland Prairie; while the eastern counties of Lee, Bastrop, Caldwell and Fayette are in the Post Oak Savanna zone (Simpson 1994).

The origin of the small but widespread eastern deciduous element on the Plateau remains an enigma. Amos and Rowell (1988) conclude that the following explanation remains the most likely; i.e., that it represents an isolated remnant of an earlier cool climate forest which extended into and through the Gulf states. The distributions of groups of endemic plants, often taxonomically related within each cluster, seems to imply that the Plateau had several long periods of climatic and ecological stability during the Tertiary.

These clusters of floristic endemics are not matched by corresponding distribution patterns among butterfly taxa, which show little endemism in the region (see Durden 1982). As a general rule, winged insects would seem to have greater potential for mobility and rapid colonization than most plants with distributions restricted to certain ecological regimes.

On the other hand, there is marked correspondence between components in the butterfly fauna and large-scale geographical groupings in the regional floras. In the butterflies, a western-southwestern element is strong in Brewster, Pecos and Terrell and Kinney counties, but declines by nearly 50% to the north and east (Fig. 11). This equates with the Far West vegetation zone of Gould (1969) and Ajilvsgi (1984). The subtropical south-southeastern element makes up 25–30% of the butterfly species in some southeastern counties (Fig. 10), but is almost insignificant in the northern counties of higher altitude and in the western counties, most of which have limited riparian habitat. This component parallels the mixed South Central and Coastal Texas vegetation zones. The northeast-eastern butterfly component contributes about 25–33% to the total species in the eastern and northern counties (Fig. 9), and can be equated to the South Central vegetational zone. Finally, the butterfly element of largely northwestern distribution, relatively weak in all sampled counties (6–17% of total species, Fig. 8), is not just equivalent to the Panhandle vegetation zone of Gould (1969) and Ajilvsgi (1984) but has its origins beyond the Plateau, as part of the large western Woodlands and Chaparral zone. Amos and Rowell (1988) also stressed that the NW region of the Edwards Plateau was floristically allied with the High Plains, not the rest of the Plateau.

For much of the year, central Texas is usually hot and dry, conditions to which many Hesperiidae are well adapted, but not so many other butterfly taxa. The relative species richness of the south-central and eastern Edwards Plateau is supported by the extensive rivers that flow south and southeast from the high country to South Texas, and the variable riparian habitat associated with them. The importance of healthy riparian systems to butterfly diversity and conservation in two other semi-arid warm temperate regions has been previously noted by Yela (1992: Central Spain) and Gaskin (1996: Greece). This important habitat also facilitates the frequent penetration of southern tropical and subtropical species of Lepidoptera into the relatively northern and eastern counties of the Plateau (Fig. 12), even when wind directions are not particularly favorable.

Geographical range, climatic zone and general adaptation to a particular ecological regime are useful characteristics by which we can classify faunal components such as butterflies. In most cases, however, a significant fraction of any county record consists of a long "tail" of occasional visitors, non-resident species, and the updated Frio-Sabinal list is no exception (Tables 1, 2). There is a natural tendency to focus on the new and unusual, but this can divert attention from the species which are important, consistent components of local ecosystems. Each individual species, sub-species and often, population, needs a suite of natural resources to survive; a favorable temperature range, suitable food plants for oviposition, nutrition for larvae and adults, relatively safe perches for adults at night, and sites for pupation and whichever instar over-winters. Each stage of the life history is vulnerable to a range of density dependent and independent events over which individuals have relatively little control.

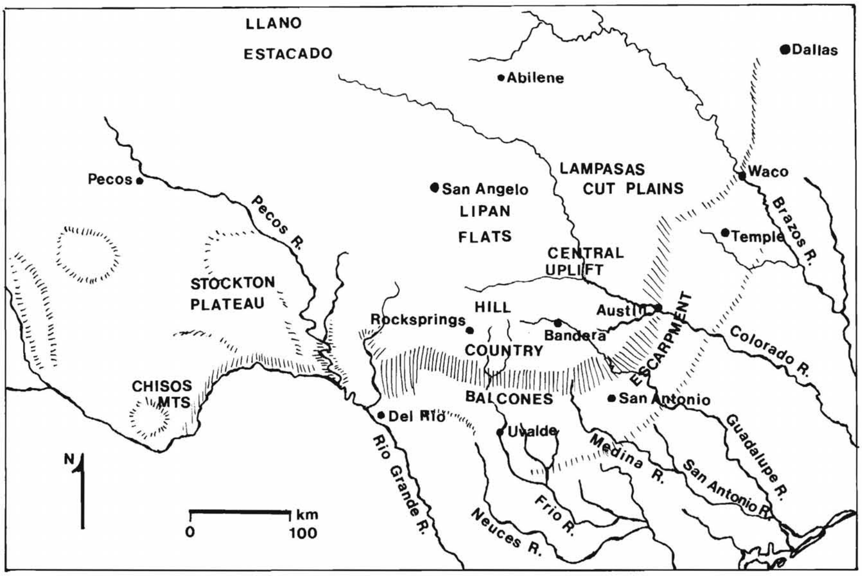

FIG. 12. Major landform features of the greater Edwards Plateau (*sensu* Gould 1969) and associated structures in the trans-Pecos region. Decline in altitude to the S and SE, together with the relative abundance of rivers and riparian habitat in that region probably facilitates butterfly dispersal and seasonal migration northwards.

We need to understand the potential importance of rather subtle factors. Durden (1982) for example, noted that the tropical elements of the butterfly fauna of south Texas and northern Mexico are most commonly encountered in the Austin region when the daily photoperiod is shortest. Not all his rarities found around Austin were dated, but at least 11 unique or scarce records of southern species were reported between late September and November (Durden 1982).

Consistent differences in local climatic conditions can exert effects important over relatively short distances. For example, there is a general similarity between the three intensively worked sites in this article; Barton Creek, Concan and upper Frio-Sabinal. Yet altitude in most of the Frio-Sabinal region exceeds that of the Austin Barton Creek site studied by Durden (1982) by about 100–300 m, providing somewhat cooler, windier weather for part of the year, especially at night. Concan, in north-central Uvalde is right on the southern edge of the escarpment, and about 150 m lower in altitude than my sites, with corresponding higher humidity and somewhat different soils and drainage. The relative frequency of dispersive weather systems over the three sites may also vary because of the different isohyet regimes and topographies.

Such variation can have important effects on microhabitats and conservation of semi-isolated butterfly populations. For example, spacing of trees and amount of understory can differ in subtle ways that do not easily yield to simple measurement. At one site in central Europe, for example, Kudrna (1993) discovered that a population of a *Parnassius* species was in serious decline because the degree of shading of the food plant in the understory had slowly increased to a point where the thermal regime was too cool for the larvae to complete their metamorphosis within the available growing season.

Even when resources for adult and larval butterfly species visibly occur throughout a region, spacing and density of these host plants can differ from one site to another. Such variation may be apparent to searching butterflies, but not necessarily to entomologists. There are many more mysteries on the Edwards Plateau still waiting to be solved.

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