L.E. Gilbert. 1985. Ecological factors which influence migratory behavior in two butterflies of the semi-arid shrublands of South Texas. In: Migration: Mechanisms and Adaptive Significance. ed. M.A. Rankin. Contributions in Marine Science, Suppl. Vol 27. Marine Science Institute, Univ. of Texas at Austin, Port Aransas. pp. 724-747.

ECOLOGICAL FACTORS WHICH INFLUENCE MIGRATORY BEHAVIOR IN TWO BUTTERFLIES OF THE SEMI-ARID SHRUBLANDS OF SOUTH TEXAS

L. E. Gilbert

Department of Zoology and Brackenridge Field Laboratory
The University of Texas
Austin, Texas 78712, U.S.A.

ABSTRACT

Temporal and spatial patterns of drought and rainfall influence patterns of host leaf production and extent of parasitoid-induced mortality in south Texas Lepidoptera. These factors can in turn interact to induce population outbreak and migratory flight in *Libytheana* and *Kricogonia*, two butterflies which depend upon new growth of the shrubs *Celtis* and *Porlieria* respectively. Differences between these shrubs in seasonal phenology and resistance to, or response to, defoliation result in asynchronous migratory flights and different degrees of sexual dimorphism for onset of migratory flight by the two insects. Adults of both butterfly species may respond to declining resources by entering reproductive diapause locally, or by initiating migratory flight. However, details of such responses vary with species and time of year and remain a fertile direction for future research.

INTRODUCTION

Like many natives of south Texas, I have, since childhood, been fascinated by periodic and often massive migrations of two butterfly species: the pierid *Kricogonia lyside* (Fig 1A) and the snout butterfly, *Libytheana bachmanii* (Fig 1B). From 1965−1980 and especially from 1976−1980, I made sporadic observations sufficient to discern certain patterns in the migratory behaviors of these species and to develop hypotheses concerning the ecological causes of such patterns.

Figure 1
    Two migratory butterflies of southern Texas. A. (above) shows a diapausing *Kricogonia* along Sage Creek, June 1977. B. (below) is a snout butterfly, *Libytheana*, also at Chaparral Wildlife Management Area, July 1976.

Area and Climate

Observations were carried out near Catarina, and 19 km east on the 6,154 ha Chaparral Wildlife Management Area, Dimmitt County, Texas. The study area, like much of southern Texas, is a shrubby grassland dominated by mesquite and prickly pear (Whittaker et al. 1979).

The climate is semi-arid and prone to drought. Rainfall averages about 49 cm per year, with midsummer tending to be the driest period. But in the highly unpredictable climate that characterizes the Rio Grande Plain of Texas, average conditions bear little relationship to the actual conditions faced by organisms in their lifetimes. In addition to such temporal heterogeneity, spatial patchiness in rainfall is

another major feature of the midsummer environment of south Texas which greatly influences the evolution of life history tactics of mobile organisms native there. Stations only 16 km apart may differ by 15−25 cm in July rainfall.

Such spatial and temporal uncertainties, while they select for interesting diapause and migratory tactics, make study difficult. I have been fortunate to have observed and recorded events which may not be repeated during my lifetime on those few areas to which I have access. One goal of this paper is to help focus attention on aspects of this system that present questions of general interest which are also accessible to short term experimental analysis.

Organisms

Kricogonia has been cited as a migrant since the 1940's but only in brief notes by field collectors. *Libytheana bachmanii*, by contrast, has been generally recognized as a migrant from much earlier, and *Libytheana* species are well-known migrants in Africa and Asia (see for example, Williams 1930, 1958).

Hostplants of the two insects, *Porlieria augustifolia* for *Kricogonia*, and *Celtis pallida* for *Libytheana*, are components of shrub clumps which develop around nitrogen-fixing mesquite (Gilbert, in press), and are common in native rangeland of south Texas. Both butterflies restrict oviposition to very new growth of hosts since young larvae can develop only on tender leaves. It appears that the different timing of migrations of the two species relates to phenological differences in new leaf production by the two shrubs, and synchronized migrations of the two species (e.g., Clench 1965) are exceptional.

KRICOGONIA LYSIDE

Kricogonia lyside (Godart) is characterized by spring migrations, female reproductive diapause, and female-biased sex-ratio in migratory populations.

Porlieria (Zygophyllaceae), the hostplant used by *Kricogonia*, is a bonsai-like shrub with thick, succulent stems having sparse foliage of pinnately compound leaves. *Porlieria* flushes new leaves and flowers each spring, even in drought years (personal observation).

By March following a mild winter, overwintering female *Kricogonia* can deposit eggs singly on new leaves of *Porlieria*. Young larvae only grow on new leaves and even last instar larvae prefer, if not require, relatively new foliage. Mature leaves seem highly resistant to *Kricogonia* attack: I have not observed total defoliation of a plant by *Kricognia* larvae. After harsh winters, *Kricogonia* must recolonize by dispersal from northeast Mexico.

Once *Porlieria* new growth is consumed, there is typically a delay before further new growth appears on the plant. Eggs are not placed on plants which lack new shoots even though they may be frequently investigated by mated females. Delay in leafing out after defoliation is one aspect of *Porlieria* phenology which sets it apart from *Celtis* and must account for some of the differences in diapause and migration

tactics evolved by *Kricogonia* and *Libytheana* respectively.

In the case of *Kricogonia*, migratory flights often involve movement of both sexes from areas temporarily devoid of new growth (because of their own larval feeding) to areas *likely* to have new growth available. During most years in southern Texas, moisture and vegetative conditions suitable for *Kricogonia* breeding and development prevail during the spring, and migrations are most often seen from mid-April through late May (Table 1).

Mid-May appears to represent an important switch point for *Kricogonia* reproductive tactics. After that point, deterioration of local conditions (i.e., loss of suitable larval and adult resources) results in sedentary behavior and female diapause. This pattern makes sense in view of long term averages for early summer conditions which face the next brood: this is the period during which the likelihood of rain declines to a yearly low for the area. Dispersal during late May into July from local patches in decline is likely to be futile. Thus from June to July it should be better for individual *Kricogonia* to wait for improvement of the patch in which they originated or to delay migration at least until chances of finding suitable patches improve. I studied a diapausing population along Sage Creek at Chaparral WMA in June 1977. I believe the following account of that population is a reasonable first approximation of diapause biology for this species.

Conditions were favorable for the production of large adult populations of *Kricogonia* in spring 1977 (large overwintering population of 1976—1977 which could effectively utilize the March pulse of new growth). By late May and June, conditions were rapidly deteriorating in what would become a severe drought (June 1977—May 1978). Rather than move, adults retreated to shaded corridors along dry drainages such as Sage Creek. By dissection, I determined that females were in reproductive diapause (Table 2) but males, for the most part, were sexually active. Both sexes spent most of their time perched near the ground, under leaves, along shaded dry gullies and creeks. Roosting sites were 5°C cooler than exposed sites nearby (34°C vs. 39°C).

Males spent much of the day involved with precourtship chases which usually only involved other males. These males would frequent any suitable nectar sources (e.g., *Monardia*).

Most females sampled from the diapausing population, had mated at least once. I dissected 20 females and found that 16 of 17 fresh (young) individuals contained immature eggs and abundant fat body, but only 3/17 were virgin. Only older individuals, presumably from a previous generation, possessed mature eggs and multiple (2—3) spermatophores (see Table 2). In studying these diapausing females, I noted a satellite of the bursa copulatrix (Fig 2) which varied in size and appearance with female reproductive status. Its size ranged from 0.7 mm in two unmated females to 1.3 mm in a female bearing mature eggs and three spermatophores. It was translucent and empty in virgins, but in mated females the structure contained a yellow fluid which turned white in 95% ethyl alcohol. Other pierids possess this structure and its possible role in diapause storage of sperm should be investigated.

Table 1

Summary of migration, diapause, and reproductive activity observed for *Kricogonia* in central and south Texas 1883–1980. Letters N,S,E, and W designate approximate month and direction of noted migration along year rows. Δ indicates notable rain immediately preceeding migratory movement, box (□) indicates sedentary populations in reproductive diapause, R indicates reproductive activity (courtship plus egg laying), and minus (−) indicates that no *Kricogonia* were found in spite of thorough search. Stipled parts of table highlight periods with no recorded migrations. Sources are as follows: A = Aaron (1882), B = Lacey (Kendall and Kendall 1971), C = Sweetman (1940), D = Wilson (1949), E = Kendall (unpublished field notes), F = Clench (1965), G = Gilbert (unpublished field notes), H = Davis (unpublished field notes).

Source & Year	March	April	May	June	July	August	Sept	Oct	Nov
A 1883					N				
B 1902		S							
B 1918			E						
C 1939			ΔSE						
D 1948									
E 1956					SW				
F 1963					N				
G 1965				□¹					
E 1967		ESE							
G 1970				R¹					
G 1973					ΔR¹				
G 1976				ΔR²					
G 1977				□ΔR²		−²			−²
E 1977		WNW							
G 1978		□(?)	ΔN²			□²			
H 1978			ΔESE²						
E 1978					ΔNE				
H 1979		□ΔSE²							
G 1979			□/R²						
G 1980			ΔSE²						

[1] = entries from Chaparral Wildlife Management Area

[2] = entries from Catarina. See text for discussion.

Moderate rainfall (2.7 cm) on 12 June 1977, just prior to my observation period (16–30 June) brought out new growth on a few *Porlieria* near Sage Creek. Coincident with this change in the status of hostplant, a few females were seen to investigate oviposition sites about 800 m from the diapause area. These females were actively courted by males, and one of two dissected females contained a second, fresh spermatophore, indicative of recent mating. In the diapause area at this time one

Table 2

Reproductive status (left column) of females caught along Sage Creek, 16−26 June 1977. Individuals of intermediate condition (i.e., older) are indicated by asterisks. Of 20 females, 15 or 75% possessed 1 spermatophore; of these only one (1/15) carried mature eggs.

Number of Spermatophores

	0	1	2	3	Total
Small Oocytes (0.1−0.3mm), No Vitellogenesis	3	8	0	0	11
Developing Oocytes (0.4−0.7mm) Some Vitellogenesis	0	6	0	0	6
Mature Eggs (0.9mm)	0	1	1*	1*	3
Total	3	15	1	1	20

could observe a few females leaving to visit nearby hostplants, but the majority remained in place. Thus in spite of an average state of diapause, a few individuals, because of age, differential experience, or genetic disposition, appeared to possess different thresholds and/or criteria for breaking diapause. By 30 June 1977, many adults were actively reproducing away from the diapause area. Extensive larval damage on *Porlieria* new growth was evident, but the fate of these larvae is unknown. The area did not receive substantial rain for another year. No *Kricogonia* were found along Sage Creek or elsewhere on Chaparral WMA when I visited the area five months later on 24 November 1977.

Why only a fraction of the Sage Creek population broke diapause in late June 1977 is not certain. Another pattern worth further study is microsite variation in diapause state. During 10−11 May 1979, all female *Kricogonia* seen at Sage Creek appeared to be in diapause. Two miles away along another drainage, ovipositing females were very abundant and no conspicuous diapause population was evident, nor was migratory activity observed.

Even more dramatic differences can be seen during a given month at the same site between years. In contrast to the large diapause population seen in May 1979, *Kricogonia* were virtually absent at Sage Creek, except for individuals moving through the immediate area on migration 26−27 May 1980. Heavy migrations were also seen in May 1978. These and other observations are summarized in Table 1.
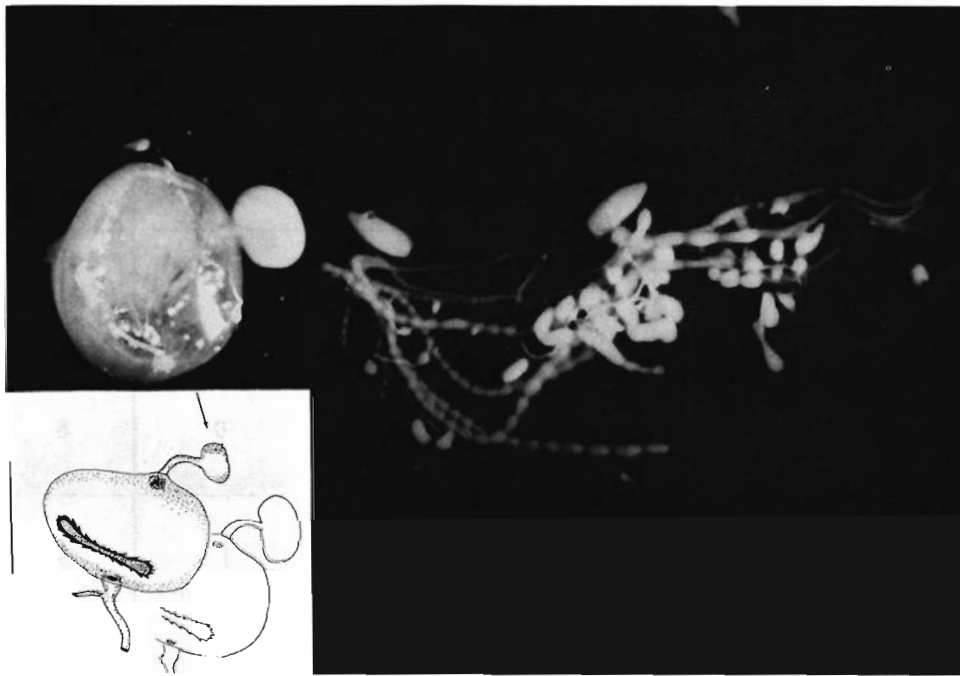
Figure 2
    Field-dissected bursa copulatrix and ovaries of *Kricogonia* female. The bursa satellite varied from 0.7 mm in virgins, to 1.0 mm in once-mated females as shown and 1.3 mm in multiply mated females. Chaparral WMA, June 1977. Scale = 1.7 mm.

Kricogonia migration should occur under two distinct circumstances. First, as in the case of *Libytheana* (see below), migration may immediately follow defoliation of the hostplant's new growth. Second, migration may occur after diapausing populations experience improved conditions such as rainfall and the appearance of new growth on *Porlieria*.

    The first category (Type I) of migration is hypothetical for *Kricogonia*. Such migrations, lacking a prior sedentary phase of reproductive diapause, should only occur in broods emerging from April through early May and possibly from mid-July to mid-September. These are the intervals during which rainfall probabilities are increasing on the Rio Grande Plain (see Fig 7), i.e., when dispersing individuals are likely to find suitable patches (nectar and oviposition sites) for reproduction somewhere in the region.

    Migrations of *Kricogonia* (ESE) were observed on 21 April 1979, by Paul Davis. Later that spring, 10 May 1979, I dissected individuals (assumed to be part of the same population) perching along Sage Creek and found them to be in diapause. Thus it appears that Type I migration may end with individuals becoming sedentary and remaining in diapause if suitable habitats and/or conditions are not encountered, or

if they are seeking diapause sites.

The second category of migration (Type II) exhibited by *Kricogonia* is less hypothetical. It occurs when diapausing individuals terminate their sedentary phase and move to new areas where reproductive activities take place. The evidence for Type II migration is the fact that migrations can be initiated within a few days of rains terminating drought. Sweetman's (1940) report of 30 May 1939 (SE) migrations near Uvalde, TX, and Paul Davis' (personal communication) report of 29 May 1978 (ESE) migration near Sage Creek have in common the fact that the lag between the onset of rain (two days in 1939; 11 days in 1978) and the observed migrations was well short of *Kricogonia*'s generation time. In other words, migrating individuals must have been adults waiting for conditions to change. See other examples in Table 1.

One difference to expect between Type I and Type II migration is the degree of female bias in the sex ratio of migrating groups. For Type I migrations, the sex ratio of migrating individuals should increasingly reflect the primary sex ratio as the migration proceeds. For Type II migrations, heavy female bias should be observed with predominance of females increasing as the preceding diapause period lengthens. This prediction results from the fact that females, not males, diapause and the resulting likelihood that males have much shorter life expectancies. All (25/25) of migrating individuals caught by Davis at Chaparral on 29 May 1978 were female. On the other hand, under conditions for Type I migration, females are predicted to leave first in response to declining oviposition cues, males slightly later as females become more difficult to encounter. It should be noted that degree of protandry, unknown for *Kricogonia lyside*, will influence such predictions.

This account is based on sporadic, short term observations, with almost no careful observations in the August−October period. However, it is safe to say that *Kricogonia*, because of the facultative and diverse nature of its response to changing environments, provides a rich opportunity for the experimental study of the physiology, ecology and evolution of diapause and migration tactics in insects.

If cues which trigger diapause breaking and/or migration act directly on adults and are as sex specific as they seem to be, local manipulations such as irrigation of host patches or presentation of volatiles from host new growth should induce rapid and predictable changes during different times of the year (for example Carlisle, Ellis and Betts 1965). Likewise, careful studies of the dynamics of migrations, both at their origins and through time, will be necessary to verify the hypothesized Type I and Type II migrations and to fully understand differential responses of the two sexes. Alternative explanations for female-biased sex ratios in migrating populations such as so called sexual harrassment (Shapiro 1970) deserve consideration.

In spite of our sketchy knowledge of *Kricogonia*, it is clear that it provides a dramatic and informative contrast to the most conspicuous migratory insect of south Texas: the snout butterfly, *Libytheana bachmanii*.

LIBYTHEANA BACHMANII LARVATA

Libytheana bachmanii (Strecker) is characterized by late summer migration, region-wide movements, and male-biased sex ratio in migratory populations.

Spectacular migratory swarms of *Libytheana*, up to 400 km wide, have been reported numerous times during this century by observers in south Texas. Most reports take the form of brief accounts in entomology journals and do little more than report direction of flight, dates, and recent weather conditions. Virtually none of the many reports document the sex of the migrants, nor is the phenomenon of snout butterfly migration discussed in the broader contexts of insect migration except by Williams (1930, 1958). Neck (1983), by comparing weather records with data on snout migration, was the first to make any sense out of known patterns of snout outbreak and migration: population size is positively correlated with the intensity and duration of dry periods immediately preceding drought-terminating rains.

Migrations of the snout butterfly may not be more frequent than those of *Kricogonia*, but they have been more frequently reported in the literature possibly because the season for *Kricogonia* migration (April−May) ends before the summer field season for lepidopterists begins. Moreover, *Libytheana* host plants are more abundant and are more completely converted to adult butterfly than is the case with *Kricogonia*. *Libytheana* migratory swarms are spectacular for their density, duration and geographical extent. In late September 1921 an estimated 25 million per minute southeasterly-bound snout butterflies passed over a 400 km front (San Marcos south to the Rio Grande River). Gable and Baker (1922) noted that this flight lasted 18 days. It may have involved more than 6 billion (6×10^9) butterflies.

The biotic interactions potentially relevant to *Libytheana* outbreak and migration are more varied and complex than those known for *Kricogonia*. The desert hackberry *Celtis pallida* is one of the most common shrubs of south Texas. It is the primary host for *Libytheana*, *Asterocampa leilia*, and for *A. celtis antonio*, two of several species of so-called hackberry butterflies. Sugar hackberry *Celtis laevigata* is the hostplant for *Libytheana* and *Asterocampa* in central Texas, and exists in semi-arid south Texas only along rivers, creeks, and drainage areas such as Sage Creek. A third hackberry butterfly species (*A. clyton texana*) at Chaparral WMA is found along narrow belts of more mesic vegetation (e.g., Sage Creek) to which its host *C. laevigata* is restricted.

A. clyton and *L. bachmanii* share at least one parasitoid, a chalcid (*Brachymeria*) *sp.* which develops in pupae and which occasionally acts as a major mortality factor for *A. clyton*. For *Libytheana*, *Asterocampa* is potentially a parasitoid reservoir maintaining a significant factor against population increase. In less arid zones, such as central Texas, *Celtis*, *Asterocampa*, and *Libytheana* are all present but *Libytheana* population explosions and migrations are extremely rare and only follow unusual drought as in September 1971 (Helfert 1972). The drought of 1977 that preceded the snout butterfly outbreaks and migrations at Chaparral in 1978, left many *Celtis laevigata* leafless or dead and *Asterocampa clyton* missing from the area where it is usually resident.

By contrast, one *Asterocampa* species that shares *Celtis pallida* with *Libytheana* was negatively affected by *Libytheana* outbreaks. In March 1977 and in May 1979, I found miniature *A. celtis* males (each 20 mm forewing length) in areas where the snout butterfly had defoliated their shared host the previous July (1976) or August (1978) presumably forcing *A. celtis* larvae to pupate well before maximum size was attained. During the same periods,, *A. clyton* were not unusually small as their host plant (*C. laevigata*) was not defoliated by snout larvae. A detailed knowledge of interactions in this system of insect and plant species will be needed before a full understanding of *Libytheana* outbreak and migration cycles is achieved.

A sample of snout butterfly migration records obtained in Texas south of Austin is presented in Table 3. Note that snout migratory activity begins just at the end of *Kricogonia*'s migratory season, i.e., late June−early July (Table 1). It is during this period when the rare joint flights have been observed (e.g., 4 July 1963, by Clench (1965) and 4 July 1956, by Kendall, personal communication). Like Kricogonia, snouts are not typically found migrating during the month of June. Since both species live in the same habitat, the fact that one tends to migrate early and and the other late in the season must ultimately relate to details of their respective life histories, especially their interactions with larval hostplants.

In most years, *Porlieria* and *Celtis pallida* are in the process of leafing out by mid-March at Chaparral WMA. However, *Celtis* seems less well-buffered against extreme dry conditions than does *Porliéria* since development of its new growth can be arrested by extreme drought (personal observation). Thus, regardless of climatic conditions, there is always a spring brood of *Kricogonia* emerging in April, assuming that a population of over-wintering adults is available. By contrast, early spring production of snout butterflies does not appear to be automatic even if adults are available. These differences do not clearly reveal why snout butterflies do not migrate in the spring, but suggest certain approaches to the question such as experimentally supplementing the adult snout population on artificially irrigated patches of *C. pallida* during April and May, simulating conditions that naturally lead to migrations later in the year (July−September) as will now be discussed.

During the summers of 1976, 1977 and 1978, I was able to observe an extreme range of weather conditions and associated migratory responses by snout butterflies. Because no other migrations have been studied at points of origin, my data on these events at Chaparral WMA are the first glimpses into the biology of migration for *L. bachmanii*. Because of the coincidence of unusual weather with my visit to the area, I was able to observe a full range of snout butterfly population events from localized outbreak and migration from drainage areas in July 1976, to low density and no migrations during the drought of 1977−1978, to region-wide outbreak and mass migrations of August 1978.

On 26 July 1976, while involved with a graduate field course at Chaparral WMA, several of my students discovered a narrow drainage zone in South Jay Pasture where snout butterfly larvae had totally defoliated the available *Celtis pallida* shrubs (I call the area "Snout Creek"). Although a few larvae were still in evidence, most individuals were pupae, 2027 and 400 of which were removed from a 3 m diameter

Table 3

Migratory and diapause activity of snout butterflies in south and south-central Texas 1912−1980. Month and year are indicated by column and row of flight direction entry (N,S,E,W). Migrations not having direction specified are indicated M. Diurnal reversals in flight direction are indicated by <. Large populations sitting around are assumed to be in reproductive diapause, □. Reproductive populations are denoted by R. Minus (−) indicates that no *Libytheana* were found in spite of thorough search. Notable rainfall is indicated by Δ. Stipled parts of table indicate periods with no recorded migration. Sources are as follows: I=Smyth (1920), J=Bernheim (1917), K=Parman (1926), L=Gable and Baker (1922), M=Rau (1941), N=Breland (1948), O=Helfert (1972), E=Kendall (unpublished field notes), F=Clench (1965), G=Gilbert (unpublished field notes).

Source & Year	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
I 1912				E						
J 1916							N			
K 1916					Δ Δ	SEΔ ΔSE				
K 1921					SE	SE SE				
L 1921						SE				
M 1940					E					
N 1947						W				
E 1956					SW					
F 1963					NE					
E 1963					P					
O 1971						NE				
E 1971					SE	SE<		NW<□		
E 1975						□	SE			
G 1976					SW	W<				
G 1977									□	
G 1978			Δ	M	Δ	S				
E 1978			−		□ Δ	□ NE<				
G 1979			<−							
G 1980							R			

and a 1.5 m diameter bush respectively (see Figure 3). On 26 July, adult emergence had been underway approximately 1−2 days and a small trickle of migrating adults were heading southwest (230°) 8−13 km per hour at an angle to northwest (320°) 16−24 km per hour winds. The resultant west southwest flow crossed the Artesia Wells-Catarina highway (FM 133) 3 km away. This created a 5.6 km front of migrating snout butterflies which, at peak density on 28 July 1976, were passing a 15 m front at a rate of 25 per minute.

Figure 3
    Pupae of *L. bachmanii* in the defoliation zone called "Snout Creek." A. (left) shows pupae and empty pupal cases on a defoliated *C. pallida* branch. B. (right) shows a fraction of 2027 pupae collected from a single bush.

What were the ecological circumstances of this migration? First, Chaparral WMA received 3 cm of rainfall between 16−20 June. I arrived on the first of two visits in 22 June to find that shrubs including *C. pallida* were already flushing new growth in response to these rains. Although all butterflies, including snouts, were uncommon at that time, eggs laid during the period had high quality host leaves and presumably low parasitoid levels as larvae. Under optimal conditions, the egg to adult period for *L. bachmanii* can be 16 days (R. Kendall, personal communication) so that the brood observed defoliating *C. pallida* and migrating in late July were quite likely the grand offspring of adults seen on 22−25 June.

Two generations were possible because of unusual rains in early to mid-July 1976. Chaparral WMA received 28 cm during that period (about 26 cm above normal for the month). Nineteen kilometers to the west in Catarina, July rains amounted to 18 cm, but June was dry and there were no snout migrations in July. I conclude from these observations that outbreaks involving defoliation and migratory movements require not only a strong pulse of new foliage when parasitoid pressure is probably low (e.g., at the end of a drought) but also the existence of a resident adult population or recent immigrants, capable of opportunistically exploiting the window of optimal

conditions. It follows that the spatial and temporal pattern of new growth availability and the size of prior adult populations are variables that should determine the magnitude of snout outbreak. This simple idea was well supported by the events of August 1978, as will be detailed later in this paper.

Other aspects of the 1976 migration deserve mention here. First, I asked how the two sexes might differ in timing of migration. I reasoned that if these insects, as adults, were responding to changing conditions on short notice, then the sexes might well differ, for example, in what constitutes optimal leaving time. The prediction was that newly emerged females should leave first because the defoliation would eliminate suitable oviposition sites. Conversely, I reasoned that males should wait since virgin females eclose each day at the site. Leaving to search elsewhere seemed risky. With this expectation, I set out with my class to collect sex ratio data from (1) pupae collected at the site, (2) adults feeding on nectar or drinking at mud near the site, (3) the migrating group crossing the highway early in the migration and (4) the same stream of butterflies later in the flight. Two related null hypotheses were, first, that in leaving time the sexes would not be different, and second, that if they were different, males would leave first. Observation rejected the first, but not the second, null hypothesis.

The sex ratio results are shown in Table 4. Since no previous reports of snout migrations had documented the sexes of sampled individuals, I had no warning as to how wrong my initial reasoning on the second hypothesis was. While the sex ratio of adults emerging from collected pupae was near unity, adults migrating the day those pupae eclosed were virtually all males, a sex ratio of 83.5. Only later in the migration did the females begin to join. On 11 August 1976 the sex ratio stood at 7.0 (see Table 4).

Further observation in the emergence zone revealed that rather than being devoid of oviposition sites, defoliated *C. pallida* was breaking new bud as if in spring. Females mated as they emerged and remained to lay eggs on these new shoots. A haphazard sample of 50 shoots revealed 27 eggs. Under typical conditions, 10 to 100 times that number of new shoots would be required to harvest 27 eggs of *Libytheana* at Chaparral WMA.

If females are staying home to reproduce, why were so many males leaving? I believe that newly eclosing males of the snout butterfly have similar problems to juveniles of many birds and mammals. They have little chance to mate in their natal area and disperse to seek better sexual opportunity elsewhere. A look at the progress of an emergence helps explain a male snout butterfly's dilemma. In the first few days of the emergence, older males from a previous brood very likely mate all of the newly eclosing females. Their brothers would be mature enough to compete for new females a few days later, at which time and progressively thereafter, each day's new males are facing increased competition from an accumulating pool of older males for a constant or decreasing daily pool of available virgins. At some point during the emergence, males will fare better if they fly off to compete for females in areas in which the timing of emergence is shifted later relative to their own site of origin.

Table 4
Sex ratio of snout butterflies in area of *Celtis* defoliation, South
Jay Pasture ("Snout Creek"), Chaparral Wildlife Management Area,
July—August 1976.

	Males	Females	Sex Ratio
Pupae on *Celtis* 27 July 1976	79	69	1.15
Adults on *Condalia* flowers 27 July 1976	26	14	1.86
Adults on Mud 27 July 1976	47	3	15.67
Adults Migrating 28 July 1976, 1100 hours 11 August 1976, 1130 hours	167 76	2 11	83.50 6.91

The requisite spatial and temporal heterogeneity of rainfall favoring the evolution of such tactics is a salient feature of south Texas during the summer months. A rancher may watch his neighbor receive heavy rains while his own pastures wither and blow away. Such patchiness in convectional thunderstorm activity can be detected in official weather records. In June 1965, Encinal received 0.0 cm, Cotulla 4.3 cm, Carrizo Springs 0.8 cm, and Catarina 0.0 cm of rainfall. In July 1959, the same stations received 1.8 cm, 1.9 cm, 7.3 cm, and 2.2 cm respectively. Flying at a speed of 8—13 km per hour, a snout butterfly could easily move between any two of these stations in less than one day (see Fig 4). For its hostplant, and thus for this insect, a difference of 5 cm rainfall from time to time or place to place is highly significant when the range is 0—5 cm!

Since the July 1976 migration appeared to be the local patch to patch type flight, I attempted to negate the null hypothesis, i.e., that it was a long range flight. On 31 July 1976 a minimum of 35 hours of prime flying time since our first sightings of the migration, my brother, Thomas Gilbert, a resident of Laredo, drove the public roads from Artesia Wells, past Chaparral and through the continuing flight (Fig 4) to Catarina and south to Hilltop. From there, he drove east to Encinal. No other migrations were encountered. The Snout Creek migrants, capable of traveling over 100 miles in the available time, had settled somewhere in the private ranch land circumscribed by Texas FM 133, Highway 83, FM 44, and IH 35. One possible destination is the San Rogue Creek drainage indicated in Figure 4.
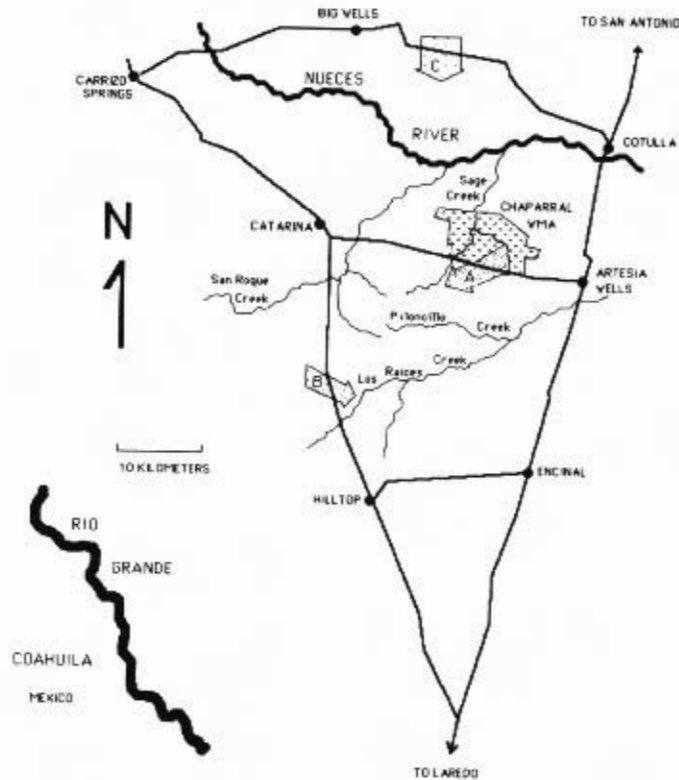
Figure 4
    Map of localities discussed in text. Chaparral Wildlife Management Area lies just to the west of Interstate Highway 35 which connects San Antonio and Laredo.

A later survey of the area, carried out on 11 August 1976 by a field assistant, Howard Locker, revealed an additional migration entering the same area south of Catarina (Fig 4, arrow B), a sparse southward migration north of the Nueces River (Fig 4, arrow C), and continued movement at Chaparral (Fig 4, arrow A), but with direction of flight reversing between morning and afternoon.

Both the male-biased sex ratio as well as magnitude of the 1976 Snout Creek outbreak result first from the fact that *C. pallida*, in contrast to *Porlieria*, flush new growth in response to defoliation, and second, from the fact that regrowth is not better defended as is the case with some woody plants having inducible defenses (Haukioja and Niemela 1979). Thus the plant can be (and was) defoliated at least twice in one season. It seemed important to pursue further the biology of this plant in order to understand more fully the biology of *Libytheana* in this region. I therefore wished to assess the consequences to individual plants of the 1976 defoliation.

In March 1977, the production of new growth was compared between *C. pallida* in the 1976 zone of defoliation versus plants not defoliated (Fig 5A), i.e., those away from lower drainage areas. Table 5 shows those results. Twelve bushes had 5 branches of 46 cm length removed for shoot census. Plants living "upland" away from the defoliation zone had more new shoots and approximately 5 times the new

shoot dry biomass as compared to the snout-defoliated sample. Comparison of a single bush known to have been totally defoliated with an untouched counterpart showed a 31-fold difference in new shoot biomass.

By June 1977, many branches alive but defoliated in July 1976 were dead. I walked through Chaparral WMA looking for other such zones and found them. One area along Sage Creek had apparently been defoliated a few years earlier since many *C. pallida* had lost most or all aboveground woody growth. Some were dead, being overgrown by *C. laevigata*, others were producing suckers from the root crown. Had other shrub species been so affected, I would have concluded that fire or herbicide had affected the area.

By 1979, many of the *C. pallida* first observed along the Snout Creek drainage at Chaparral WMA resembled those of Sage Creek (see Fig 6) in having lost most or all aboveground woody growth. Remarkably, the snout butterfly, a small specialist herbivore which would be missing or highly inconspicuous in beat samples from *C. pallida* over at least 90% of the area at Chaparral and during no less than 95% of the years, can periodically reduce the density of the plant, especially in wetter areas. A map of snout-killed or damaged *C. pallida* is a map of the drainage system at Chaparral (e.g., Fig 5B).

There are at least two good reasons for the differential impact of snout butterflies on *C. pallida* in wetter areas. First, these are likely to be the first areas where leafing out begins after rains and the last areas to cease new production. Indeed drainages are often the only areas where new growth can be found on *C. pallida*. Second, other habitat requirements such as nectar plants or diapause sites may be best along these corridors of thick shrubbery (Fig 5B). *Alosysia* (whitebrush) flushes new flowers soon after rains on periodically dormant inflorescences which may last from March to August. This shrub, a favorite nectar plant for snout adults, is very dense along drainage zones and may help concentrate egg laying on *C. pallida* which grow near.

The consequence of snout damage to *C. pallida* in drainage zones is interesting to contemplate. Since these are the prime areas for generating local migrations, it may be that an area would gradually cease to be a source area for migrations as hostplants there are repeatedly defoliated and killed during exceptional episodes of weather. For such an area to return to its previous status as a snout-outbreak zone might require a long period of reinvasion or regeneration by *C. pallida* in bottom areas.

Are upland *C. pallida* defoliated or otherwise seriously affected by snout butterflies? The answer is yes, if the uplands are sufficiently wet and if a large snout population is already present when the *C. pallida* flush new growth. It is such an event that triggers regionwide movements encompassing several thousand square kilometers.

The ingredients for such an event came together in 1977 and 1978. Chaparral WMA was lush but drying out rapidly in June 1977, when I studied the diapausing *Kricogonia* along Sage Creek. From that time until May 1978, Chaparral WMA and the region generally suffered one of the most severe droughts on record. Although

Table 5

Consequences of defoliation by snout butterflies at Chaparral Wildlife Management Area, July 1976, in terms of new growth in mid-March 1977.

	"Creek"	Upland	"Creek"	Upland
	N = 12 bushes 60 branches	N = 12 bushes 60 branches	N = 1 bush 5 branches. Total Defoliation July 1976	N = 1 bush 5 branches No Defoliation July 1976
New Shoots	2282	7192	47	988
New Shoots/ Branch	38	120	9	198
Dry Wt. New Growth/ Branch	0.32g	1.5g	0.08g	2.48g
Biomass Advantage	4.7 ×		31 ×	

Kricogonia was numerous, all other butterflies were extremely rare by early May 1978. I saw a single snout butterfly during six hours at Chaparral on May 7. By late August, an estimated half billion snout butterflies were produced and virtually every *Celtis palida* bush was defoliated—*except* along drainages!

Figure 7 summarizes drought, rainfall, and butterfly migrations at Chaparral WMA during 1978. The steps leading to the massive August flights were as follows. First, an unusual drought presumably eliminated, at least temporarily, parasitoid controls. Next, rains in May and June were well above average, thus allowing rapid increase of the snout butterfly population over 2–3 generations. The result was drainage-zone defoliation and the production of large resident populations of females as well as migratory males during early July. Had conditions returned to normal at this point, 1978 would have been very similar to 1976 in terms of the pattern and extent of snout butterfly outbeak.

However, at the end of July a low pressure system, called tropical storm "Amelia," moved from the Gulf of Mexico into the region, thus insuring that for a third straight month, rainfall would be well above normal. According to Bomar (1983), Amelia was responsible for the 24 hour record rainfall total for Texas, 76 cm in Albany, TX, 4 August 1978. The response by snout butterflies was spectacular. Most *C. pallida* at Chaparral WMA and in the region generally were defoliated. Snouts were migrating throughout the region. At Chaparral WMA, they were moving

Figure 5
A. (above) shows C. *pallida* in 1976 defoliation zone being censused for new shoots by T.R.E. Southwood in March 1977. B. (below) shows dense growth of shrubs along drainage zones (usually dry gullies) at Chaparral WMA.
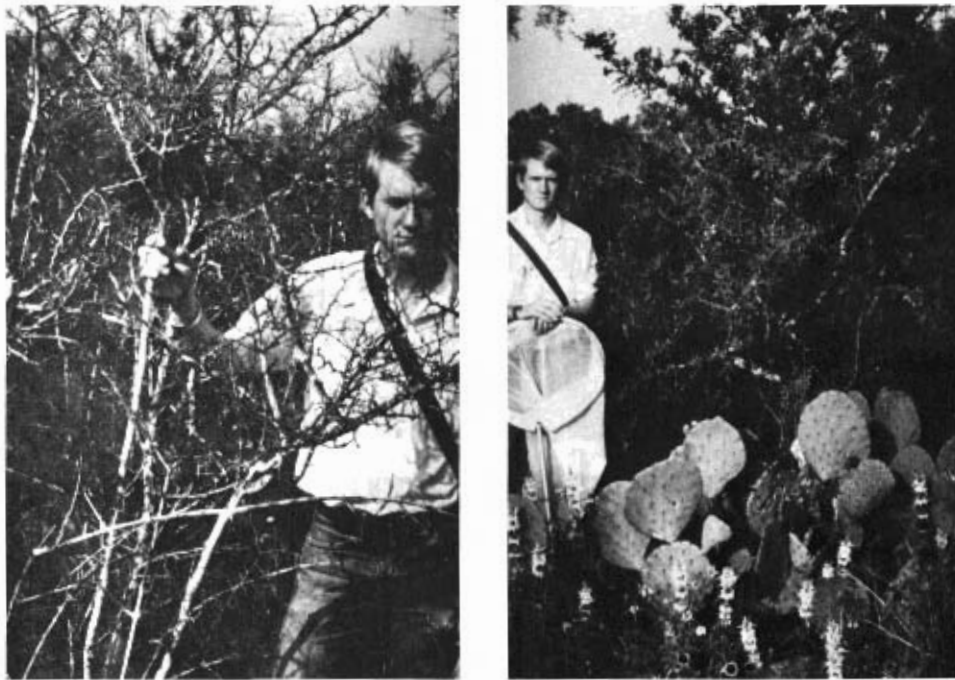
south by tacking into a southwest wind. Sex ratio of migrant population was male biased, but females were clearly a component of the migration when I observed it on 24–25 August 1978. A sample collected near Chaparral contained 85 males and 51 females and a collection from Catarina contained 99 males and 27 females. Eight migrating females were dissected from the Chaparral sample. All eight were mated but none contained mature eggs.

Figure 6
     Effects of different levels of defoliation on *C. pallida* by *L. bachmanii* in May 1979. A: J. Longino stands next to a typical "upland" individual which was free of defoliation in 1976 and only partly defoliated in August 1978. B: This bush, along Snout Creek, was defoliated in 1976 and 1978, and when photographed (May 1979), had only a few living large branches (e.g., see cluster of leaves above and behind Longino's hand).

     The August 1978 migration culminated about 100 days of astronomical population increase by the snout butterfly. A rough estimate of this increase was obtained as follows. First, it is possible to extract an estimate of the *C. pallida* population from previous Texas Parks and Wildlife surveys on the vegetation of the area. This results in an estimate of 1.56 million hackberry shrubs on the area (an average of 255 per ha, see Table 6). Of these, no less than 85% or 1.32 million were defoliated in August 1978 (this is a conservative guess). From the 1976 defoliation, it was determined that no less than 2000 and 400 snout adults were produced on 3 m diameter and 1.5 m diameter *C. pallida* respectively. Assuming that the 1.5 m bush is approximately average size for Chaparral WMA, the total snout population generated would be approximately one half billion (1.32×10^6 bushes $\times$ 400 snouts·bush^{-1} = 5.28×10^8 snout butterflies). This amounts to about 84,000 butterflies per hectare (8.4 m^2) produced over the emergence period. Can snout butterfly life history characteristics account for this increase?
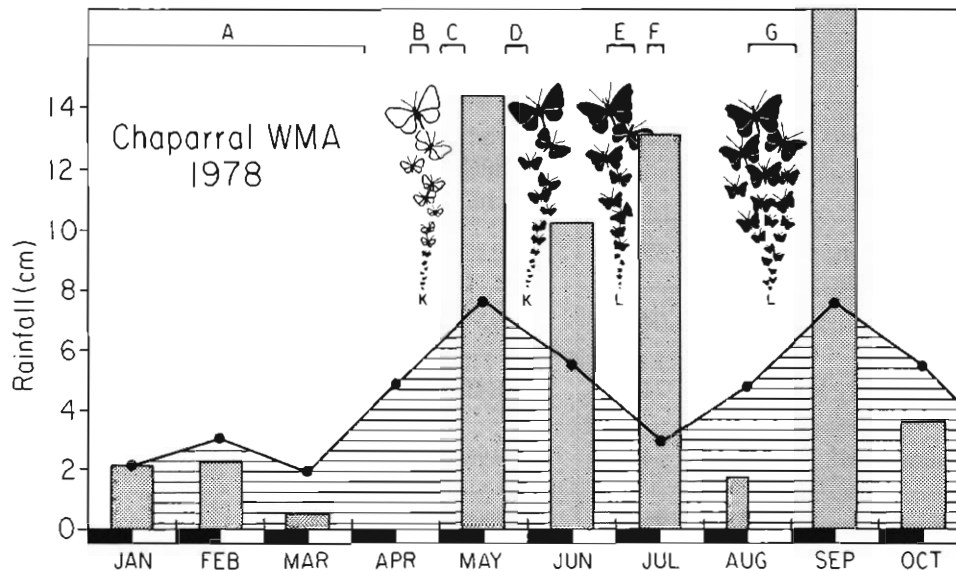
Figure 7

Libytheana and *Kricogonia* migrations at Chaparral WMA, 1978, related to longterm averages at nearby Encinal, TX (solid line) and the unusual rainfall of May−July 1978 (stippled bars). Interval A above was a continuation of drought which began in June 1977. Actual migrations are shown as three swarms of black butterflies. During interval C, *Libytheana* were very rare, on the order of one per hectare. During interval D, all-female migration of *Kricogonia* took place. These were the diapausing individuals responding to the May rains (Type II migration). During interval E, *Libytheana* erupted, defoliated *Celtis pallida* along drainages and some migrated locally (Type I migration). During interval F, a large population of *Libytheana* was resident in the area, probably in diapause. This population laid eggs on new growth flushed by late July rains. Less than 20 days later, these had defoliated > 85% of *C. pallida* at Chaparral WMA and entered migratory phase (G). Note that August was relatively dry until the 30th, after migrations were underway. August 30−31 rain totals were added to September's to prevent confusion of causation of the large Type I migration (G). Interval B was not observed in 1978, but was a period of migration by both sexes of *Kricogonia* in 1979, a year with 6.5 cm and 18.3 cm of rain in March and April respectively.

To answer this question, I assume that snout population growth was virtually unchecked from May to late August 1978, and that it can be described by the simple discrete generation model: $N_t = N_0 R^t$. Given a starting population in May 1978 of one female per hectare (N_0) growing to 42,000 females per hectare (N_t) 100 days later in late August 1978, it is possible to see whether biologically realistic combinations of R and t are consistent with such numbers. R, the replacement rate, is simply the average number of female offspring produced per mother in each generation, while t is the number of elapsed generations. Since the egg to adult time for snout butterflies is no less than 16 days, 6 is the maximum value t could assume within the 100 day period and, by observation, t was greater than 2. Thus given t values of 6, 5, 4, or 3, I found that R values of 5.89, 8.41, 14.32, and 34.76 respectively gave the 42,000-fold increase estimated for the Chaparral WMA snout population. These

Table 6

Number of *C. pallida* at Chaparral Wildlife Management Area. Extracted from Ellisor (1970). (Metric conversion of totals are used in text.)

	A	B	C	A × B × C
Zone	Acreage	Woody shrubs/ acre	% *C. pallida*	Total *C. pallida*
Sandy loam	11,570	1,232	9.93	1.33×10^6
Shallow ridge	1,048	1,934	2.70	5.47×10^4
Tight sandy loam	718	3,847	4.53	1.25×10^5
Loamy sand	540	496	3.51	9.4×10^3
Cleared area	1,324	846	3.78	4.23×10^4
Total	15,200			1.56×10^6

values are all well within the reproductive potential of these insects. Thus even larger migratory swarms can be expected under similar conditions from areas having more *C. pallida* biomass.

These crude calculations underscore the efficiency with which parasitoids, predators, predators, poor host quality, host phenology, and other natural controls must be limiting the population growth, and thus the occurrence of conspicuous migratory swarms of *L. bachmanii* over much of its range, most of the time. Host plants of the genus *Celtis* are very common over much of the snout's distribution, yet migrations are extremely rare in the more mesic areas. The impact of the south Texas drought cycle on the natural controls of this species probably accounts for its more frequent migratory behavior there (see Neck 1983). I have assumed this to be true in the present account, but careful studies of larval demography will be necessary to confirm my assumption. The relatively low parasitoid rate of 8% ($n = 658$) in snout pupae collected in the 1976 outbreak zone supports this assumption. Another possibility, not mutually exclusive, is that other species of *Celtis*, which replace *C. pallida* in more mesic areas (e.g., *C. laevigata*) are intrinsically more resistant to herbivory by snout butterfly larvae.

A final aspect of snout migration worthy of further study is the problem of directionality. It is frequently observed that these insects are actively working to move in particular directions, often into light breeze (e.g., Parman 1926, pp. 104–105; Gable and Baker 1922, p. 265) and against substantial wind (e.g., Breland

1948, p. 130; Smyth 1920, p. 259). Southeast and east southeast are very commonly observed flight directions, but most other compass headings are represented (e.g., Table 3). 180° reversals of flight direction between morning and afternoon are occasionally observed (e.g., Breland 1948, Kendall personal communication). However, this may occur in some latter phase of a migration. Thus, at Chaparral WMA 26−28 July 1978, (early) migrations were consistently southwest and west southwest. Two weeks later, 11 August 1978, morning migrations were roughly west, those of afternoon roughly east. Much more data will be required to ascertain the pattern, if any, in migratory direction as it relates to environmental factors such as wind direction and velocity.

SUMMARY

Two shrub-feeding butterflies of south Texas frequently initiate migratory flights. For *Kricogonia*, the pierid that uses *Porlieria* as larval host, migrations may be of two types: Type I migrations follow exhaustion of suitable leaves on larval hostplant early in the season (April). Type II migrations involve the directional movements of previously diapausing populations and are triggered by rainfall. For reasons that are not clear, *Kricogonia* migrations are primarily restricted to April−May. Type II migrations are female biased.

Libytheana bachmanii, which uses *Celtis pallida* in south Texas, undergoes Type I migration and primarily males are involved. This appears to result from the rapid flushing of new growth by recently defoliated *Celtis pallida* which holds females in the area. Type II migrations also occur in *Libytheana*. Kendall (personal communication) has observed large populations sitting around for weeks prior to large migrations.

Two other categories of migration were identified for snout butterflies: (1) local, involving defoliation, population outbreak, and migration on a scale of a few kilometers and (2) regional, involving widespread defoliation of hosts, population explosions, and migrations over thousands of square kilometers, involving billions of insects. I suspect that both Type I and II migrations can occur at these different spatial scales.

In contrast to *Kricogonia*, *Libytheana* migrates late in the season (July−October). It is not clear why snout butterflies have not been seen moving before June.

Differences between these two butterflies in migratory patterns result from different leafing-out phenologies of hostplants, different degrees of resistance by mature leaves of hosts, and perhaps from differential ability to diapause through south Texas winters or to recolonize from Mexico after harsh Texas winters.

Snout butterflies may be the most significant mortality factor for mature *C. pallida*, especially in some habitats, and therefore alter the potential of such areas to support subsequent population growth and migration. *Kricogonia* appears incapable of completely defoliating *Porlieria*. *Kricogonia* migrations are less conspicuous than those of the snout butterfly because there are fewer *Porlieria* than *Celtis* and because

a relatively small fraction of *Porlieria* standing crop can be converted into adult *Kricogonia* by their larvae.

In order to develop this relatively complete view of the ecological context of migration in these two insects, I have had to draw from scattered and incomplete information. I have woven facts together with assumptions, extrapolations, and my own intuition for habitats and organisms in south Texas. I prefer to think that this process is akin to the computer enhancement of fuzzy photographic images. Pattern is made clear by replacing grey with black or white. I am not sure what the precise patterns are, but I have tried to generate a coherent picture or model of the system, well summarized by the actual events of 1978 in Figure 7. Hopefully, this model will help organize and focus research that will further elucidate the patterns and their causes.

The danger inherent in such a wonderfully rich biological system which is so poorly known is that there are few facts to constrain imagination. With this in mind, I have avoided any discussions on aspects of *Kricogonia* and *Libytheana* biology that are free of factual information. For example, I did not suggest that the snout (labial palps) on a migrating snout butterfly functions like a divining rod to help it locate some distant oasis. But the fact is, *Libytheana* almost always migrate into a breeze, and since prevailing winds are from the southeast in July and August, migrations are typically seen to be in that direction. *Libytheana* really do seem to be following their snouts for some reason!

LITERATURE CITED

AARON, E.M. 1885. Collecting on the Gulf coast of southern Texas. *Papilio* 4: 159-161.

BERNHEIM, J.L. 1917. Swarms of butterflies (Lep.). *Entomological News* 28: 339-340.

BOMAR, G.W. 1983. *Texas Weather*. University of Texas Press, Austin. 265 pp.

BRELAND, O.P. 1948. Two migrations of the snout butterfly, *Libytheana bachmanii larvata* (Strecker). (Lepidoptera: Libytheidae). *Entomological News* 59: 128-131.

CARLISLE, D.B., P.E. ELLIS and E. BETTS. 1965. The influence of aromatic shrubs on sexual maturation in the Desert Locust *Schistocerca gregaria*. *Journal of Insect Physiology* 11: 1541-1558.

CLENCH, H.K. 1965. A migration of *Libytheana* and *Kricogonia* in southern Texas. *Journal of the Lepidopterists' Society* 19: 223-224.

ELLISOR, J.E. 1970. *Job Progress Report: Federal Aid Project no. W-101-R-1: Job no. 2, Vegetative Trends. (Chaparral Wildlife Management Area).* Texas Parks and Wildlife Department, Austin, TX.

GABLE, C.H. and W.A. BAKER. 1922. Notes on a migration of *Libythea bachmanni* Kirtl. *The Canadian Entomologist* 54: 265-266.

GILBERT, L.E. In press. An ecosystem perspective on the role of woody vegetation, especially mesquite, in the Tamaulipan biotic region of south Texas. In D.H. Riskind and G.W. Blacklock (eds.) *The First Symposium on the Tamaulipan Biotic Province.* Texas Parks and Wildlife Department.

HAUKIOJA, E. and P. NIEMELA. 1979. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. *Oceologia* 39: 151-159.

HELFERT, M.R. 1972. Migratory behavior of the snout butterfly, *Libytheana bachmanii larvata* (Strecker). *Entomological News* 83: 49-52.

KENDALL, R.O. and C.A. KENDALL. 1971. Lepidoptera in the unpublished field notes of Howard George Lacey, Naturalist (1856–1929). *Journal of the Lepidopterists' Society* 25: 29-44.

NECK, R.W. 1983. Causal analysis of a migration of the snout butterfly, *Libytheana bachmanii larvata* (Strecker) (Libytheidae). *Journal of the Lepidopterists' Society* 37: 121-128.

PARMAN, D.C. 1926. Migrations of the long-beaked butterfly, *Libythea bachmani* Kirtland (Lepid.: Libytheidae). *Entomological News* 37: 101-106.

RAU, P. 1941. Migrating butterflies, *Libythea bachmanii larvata* Stkr. in Texas. *Entomological News* 52: 277-278.

SHAPIRO, A.M. 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. *American Naturalist* 104: 367-372.

SMYTH, E.G. 1920. Butterfly migrations. *Journal of Economic Entomology* 13: 259: 260.

SWEETMAN, H.L. 1940. The migration of a pierid butterfly in Texas. *Bulletin of the Brooklyn Entomological Society* 35: 173-174.

WHITTAKER, R.H., L.E. GILBERT and J.H. CONNELL. 1979. Analysis of two-phase pattern in a mesquite grassland, Texas. *Journal of Ecology* 67: 935-952.

WILLIAMS, C.B. 1930. *Migration of butterflies.* Oliver and Boyd, Edinburgh. 473 pp.

WILLIAMS, C.B. 1958. *Insect Migration.* Macmillan, New York.