Journal of the Lepidopterists' Society
39(4), 1985, 299–312

SKIPPERS: POLLINATORS OR NECTAR THIEVES?

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ABSTRACT. The hypothesis that butterflies as a group are primarily nectar thieves, rather than pollinators, of many flowers that they visit was tested by observing skippers and quantifying their pollen loads. Two species of skippers, *Atalopedes campestris* and *Epargyreus clarus*, were studied.

Adult *A. campestris* visited 23 flower species and *Epargyreus clarus* visited 27 flower species. Fifty-nine male and female *E. clarus* carried a mean of 45.1, and 283 male and female *A. campestris* carried a mean of 68.4 pollen grains from eight species of very frequently visited flowers. Skippers carried most of the pollen in their facial cavities and on their proboscides. At least one skipper of each species carried pollen from each of these flowers in its genital cavity, a newly documented pollen-carrying structure for butterflies.

The skippers may have occasionally pollinated their nectar flowers, because they were constant to particular species during foraging bouts; they transported pollen; and they contacted stigmas with their pollen-bearing proboscides. Nevertheless, the skippers evidently functioned mainly as nectar thieves. They foraged mostly on asteriads rather than other kinds of flowers, primarily probing innermost (male-stage) disk florets, and they tended not to contact the outermost (female-stage) florets with their more pollen-laden parts. Moreover, they carried pollen loads that were too small to make them significant pollinators. Thus, our skipper data do not reject the above hypothesis.

Many butterfly species visit flowers from which they imbibe nectar (Faegri & van der Pijl, 1966; Shields, 1972; Barrows, 1976, 1979; Schemske, 1976; Wiklund et al., 1979; Schemske & Horwitz, 1984). For example, 197 butterfly species found in eastern North America use at least 5.9 ± 0.55 SE (1–15) genera of flowers as nectar sources (Opler & Krizek, 1984). Butterflies undoubtedly pollinate some flower species (Grant & Grant, 1965; Levin, 1972; Levin & Berube, 1972; Barrows, 1979; Cruden & Hermann-Parker, 1979), and they are definitely nectar thieves of others (Spears, 1983; Schemske & Horvitz, 1984). An individual nectar thief is an animal that takes nectar through a natural orifice of a flower without pollinating it (Inouye, 1980). Further, if an animal species thieves nectar during more than 50% of its visits to a particular flower species, the entire animal species could be classified as a thief species with regard to this plant species.

Delpino (1874) suggested that male butterflies are likely cross pollinators of their nectar plants, but decades later Robertson (1924: 100–101) stated that butterfly "relations to flowers are often that of nectar thieves." Subsequently, Wiklund et al. (1979) studied the flower visiting of the pierid *Leptidea sinapsis* L. in Sweden. From this species they generalized that, "Butterflies as a group may have evolved to occupy a parasitic mode of life as adults, feeding on the nectar of flowers without pollinating them," but they did not refer to Delpino's

or Robertson's assertions. All in all, however, pollination effectiveness and efficiency of butterflies is little known (Gilbert & Singer, 1975; Kevan & Baker, 1983; Spears, 1983). In an attempt to test further the butterflies-as-nectar-thieves hypothesis, we studied foraging behavior of two common skippers, *Atalopedes campestris* (Boisduval) and *Epargyreus clarus* (Cramer), in Washington, D.C. The identities and relevant characteristics of the skippers' nectar flowers, skipper foraging behavior, and the locations and amounts of pollen that skippers carried were examined to test the hypothesis. Both skipper species that we studied are native to the Washington, D.C., area, where they have three broods per season (Clark, 1932). *Atalopedes campestris* fly in the garden from mid-July through September; *E. clarus,* from mid-June to early August. A future paper will discuss whether butterflies, in general, are nectar thieves or pollinators.

MATERIALS AND METHODS

In our study, we define "foraging bout" as a skipper's feeding activity on one or more flower species, starting when it was first discovered on a flower until it could no longer be followed due to its flying out of sight. A "visit" is a skipper's alighting upon or near a flower, extending its proboscis into it for at least 1 sec, and presumably feeding. An "infrequently visited flower species (IVFS)" is a flower that we saw only one individual skipper visit during only one of the ten 2-week observation periods of our study. A "frequently visited flower species (FVFS)" is a flower that we saw two to four conspecific skippers visit, and a "very frequently visited flower species (VFVFS)" is a flower that we saw five to hundreds of skippers visit during two or more of the 2-week observation periods. A "clear day" is one over 75°F, with no rain, and with less than 20% cloud cover. A "facial cavity" is a concavity into which a skipper's proboscis coils; a "genital cavity," one at the end of a skipper's abdomen, formed in a female by scales surrounding her papilla analis above and lamella antevaginalis below and in a male by scales surrounding his uncus above and valvae below.

Skippers were studied from May through October 1982 in the 0.9-ha vegetable and flower garden where Lazri and Barrows (1984) investigated flower visiting in *Pieris rapae* L. The garden is a community garden used in 1982 by about 146 gardeners, and it contains about 265 species of entomophilous plants, including vegetables, ornamentals, herbs, wildflowers, and weeds.

Flowers visited by the skippers and the relative numbers of skippers present at each species were noted during a total of 12 30-min meandering walks made through the garden twice each month in June, July, August, and September. The walks were made once every 2 weeks on

a clear day, every hour on the hour, from 0800 to 2000 h (EDT). At each skipper-frequented flowering plant or group of such plants, we made short (10 sec) counts to standardize the amount of time spent at a plant or group of plants. A total of 564 skippers of both species was counted during the entire census.

To measure flower corolla lengths, we collected flowers in plastic bags and kept them moist until they could be examined. Dial calipers, accurate to 0.01 mm, were used to measure corollas (Lazri & Barrows, 1984). We made a pollen reference collection from pollen collected in the study area.

In studying possible flower constancy, frequency of flower use, and pollen deposition of skippers, we observed 22 foraging *A. campestris* and 60 foraging *E. clarus*. A stopwatch and tape recorder were used when needed. To discriminate focal individuals from other nearby skippers when they were common, we marked forewings of focal individuals with small spots of enamel paint, which did not appear to affect their behavior. Forty additional skippers were each observed for 10 min as they foraged at asteriad disk and ray florets.

In examining possible pollen transport and deposition, we collected 285 *A. campestris* and 77 *E. clarus*; 3 to 23 males and 5 to 25 females were taken from each VFVFS. Before it was captured, each skipper was followed as it visited two consecutive flower heads, extending its proboscis into a flower in each head for at least 1 sec. After it was netted, a skipper was paralyzed by carefully pinching the sides of its thorax between a thumb and forefinger and then placed into a glassine envelope on which relevant data were recorded. The enveloped skipper was immediately put into an insulated bag filled with frozen cold packs. Within the hour, all skippers in the bag were put into a cooler filled with more frozen cold packs. At the end of a collecting day, the skippers were put into a freezer until they could be examined for pollen (Turnock et al., 1978).

In searching for pollen on a skipper, we removed its legs and proboscis, placed them on a clean glass slide, and covered them with a drop of Permount® and a coverslip. The rest of the skipper was placed on a watchglass. Its proboscis, legs, body, glassine envelope, slide, and watchglass were examined for pollen under a compound microscope (up to 400 power), a dissecting microscope (up to 30 power), or both. Pollen adhering to the skipper's labial palpi were included in its facial cavity count. Free floating pollen grains on the slide and watchglass and in the envelope were also counted. Adult skipper age was estimated to be young, middle-aged, or old, based on the amount of scale loss and wing tattering that was present on a skipper's wings and body. A young skipper was one that was almost totally intact; a middle-aged

one had slight wing tattering and a few scales missing; and an old one had very tattered wings and many scales missing.

Quantitative analyses were made with the Statistical Analysis System (SAS) computer package (Ray, 1982a, b). Pollen count and corolla depth values were log transformed to obtain homoscedastic data for the Duncan's multiple range test (DMRT). Possible differences between groups were analyzed with the *t*-test (TT) or paired *t*-test (PTT) corrected for heteroscedasticity when necessary, the Fisher exact probability test (FEPT), and the Chi-square test (CST). Kendall's rank correlation coefficient (KRCC) was used to test for significant correlations.

RESULTS AND DISCUSSION

Flowers Visited

Atalopedes campestris visited 23 species of flowers (including two hybrids), in eight plant families (Table 1). Thirteen of these flowers (57%) were in Asteraceae, making it the most visited family. All but one of *A. campestris*' eight very frequently visited flower species (VFVFS) were asteriads. The other VFVFS was the dipsacaciad *Scabiosa atropurpurea* which has florets that are morphologically similar to asteriad disk flowers. *Atalopedes campestris* also abundantly visited the asteriad *Cosmos sulphureus*, but since they did so for only 1 week, this flower was not classified as a VFVFS.

Epargyreus clarus visited 28 species of flowers (including three hybrids), in 16 plant families (Table 1). Eight of the flowers (29%) were asteriads. This skipper used only two VFVFS, both also VFVFS of *A. campestris*. Seven frequently visited flower species (FVFS) were used by *E. clarus*. Of these, *Consolida orientalis* and *Dianthus barbatus* were visited early in the season when few other flowers were in bloom. *Epargyreus clarus* visited *Phaseolus vulgaris* and *Cucurbita* sp. in midseason when its VFVFS were commencing to bloom. All of the flowers visited by the skippers are introduced ones, except for *Oenothera biennis*, upon which only one *E. clarus* was seen and *Eupatorium coelestinum* which was visited by many *A. campestris*.

Based on the censuses made during walks through the garden, we found three *A. campestris* adults in June, 40 in July, 65 in August, and 176 in September on its VFVFS. These observed frequencies were significantly different from a hypothetical situation with equal monthly frequencies of 71 (the 4-month average) skippers ($P < 0.001$, CST). Twenty *E. clarus* visited their VFVFS in June; 34 in July; 72 in August, and 18 in September. These empirical frequencies were also different from a hypothetical situation with equal monthly frequencies (36) of skippers ($P < 0.001$, CST). These observed differences from equal

TABLE 1. Flowers visited by *Atalopedes campestris* (AC) and *Epargyreus clarus* (EC). Flower species are listed in systematic order by families (Bailey and Bailey, 1976) and alphabetical order by genera.

Family Species, common name	Butterfly visitors
Liliaceae	
Allium vineale L., field garlic	EC
A. schoenoprasum L., chives	AC
Amaryllidaceae	
Amaryllis belladonna L., belladonna lily	EC
Caryophyllaceae	
Dianthus barbatus L., sweet william	AC, EC
Ranunculaceae	
Consolida orientalis (J. Gray) Schrödinger, larkspur	AC, EC
Oxalidaceae	
Oxalis corniculata L., creeping oxalis	AC
Bassicaceae	
Rhaphanus sativus L., radish	EC
Fabaceae	
Phaseolus vulgaris L., snap bean	EC
Balsaminaceae	
Impatiens balsamina L., garden balsam	EC
Impatiens wallerana Hook., "Liegnitzia"	EC
Violaceae	
Viola × *wittrockiana* Gams., garden pansy	EC
Lythraceae	
Lythrum salicaria L., purple or spiked loosestrife	EC
Onagraceae	
Oenothera biennis L., evening primrose	EC
O. fruticosa L., sundrops	EC
Boraginaceae	
Myosotis scorpioides L., true forget-me-not	EC
Laminaceae	
Lavandula sp., lavendar	EC
Mentha × *piperita* L., peppermint	AC
M. spicata L., spearmint	AC, EC
Ocimum basilicum L., common or sweet basil	AC, EC
Origanum vulgare L., marjoram or oregano	AC, EC
Solanaceae	
Capsicum sp., bell pepper	AC
Petunia × *hybrida* Hort. Vilm.-Andr., petunia	EC
Dipsacaceae	
Scabiosa atropurpurea L., sweet scabious	AC,[a] EC[a]

TABLE 1. Continued.

Family	Butterfly visitors
Polemoniaceae	
Phlox paniculata L., phlox	EC
Asteraceae	
Ageratum houstonianum Mill., floss flower	EC
Aster cv., aster	AC,[a] EC
Callistephus chinensis (L.) Nees., China aster	AC[a]
Centaurea cyanus L., bachelor's button	AC, EC
Chrysanthemum leucanthemum L., ox-eye daisy	AC, EC
Chrysanthemum sp., chrysanthemum	AC
Cosmos bipinnatus Cav., cosmos	AC, EC
C. sulphureus Cav., cosmos	AC
Dahlia pinnata × *coccinea* Cav., dahlia	AC,[a] EC
Eupatorium coelestinum L., hardy ageratum	AC,[a] EC
Rudbeckia fulgida Ait., gloriosa daisy	AC
Tagetes erecta L., African marigold	AC[a]
T. patula L., French marigold	AC[a]
Zinnia elegans Jacq., zinnia	AC,[a] EC[a]

[a] Very frequently visited flower species.

frequencies are expected due to seasonality of flowering and fluctuating skipper population levels.

The skippers used VFVFS of different colors and similar shapes. Corolla tubes of many of these flowers were significantly different in length (Table 2).

Flower Constancy

Seventy-eight of the 82 observed skippers showed flower species constancy by visiting individual conspecific flowers or capitula twice in a row. This is significantly different from a hypothetical group in which by chance, 41 skippers visited conspecific flowers and 41 visited heterospecific flowers in sequence ($P < 0.001$, CST). All four of the skippers that visited heterospecific flowers were *E. clarus* foraging early in the season at their FVFS or IVFS (*Dianthus barbatus* and *Lythrum salicaria*, respectively).

Further, 32 of the 82 skippers were observed as they made up to 14 consecutive visits to flowers or capitula (Table 3). Fourteen of these skippers visited only 1 flower species; 14, 2 species; and four, 3 to 4 species. Thus, the skippers tended to visit less than three flower species during a foraging bout.

In asteriads, skippers preferred disk florets to ray florets. Forty randomly chosen *A. campestris* were each observed foraging for at least 10 min on the flowers of *Aster* cv., *Eupatorium coelestinum*, *Tagetes*

TABLE 2. Corolla depths of very frequently visited flower species of *Atalopedes campestris*. Disc florets were measured for all flowers except *Scabiosa atropurpurea* for which regular florets were measured. Means followed by the same letter are not significantly different from one another ($P < 0.05$, DMRT).

Flower species	Corolla depth (mm) Mean ± S.E., range, n
Tagetes patula	26.74 ± 0.214, 23.7–29.0, 34
T. erecta	20.87 ± 0.237, 17.7–25.0, 35
Scabiosa atropurpurea	12.73 ± 0.481, 8.0–18.0, 38b
Zinnia elegans	12.04 ± 0.350, 7.3–15.8, 26bc
Dahlia pinnata × *coccinea*	11.82 ± 0.320, 7.7–17.4, 35bc
Callistephus chinensis	11.26 ± 0.204, 9.5–15.0, 35c
Aster spp.	7.67 ± 0.145, 6.3–9.9, 35
Eupatorium coelestinum	3.34 ± 0.117, 1.8–5.0, 35

patula, and *Zinnia elegans*. All foraged significantly more ($P < 0.05$, FEPT) on the innermost mature disk flowers than on ray flowers when empirical data were compared to hypothetical cases in which skippers foraged at equal numbers on each of the two kinds of flowers.

Stigma Contact

All of the VFVFS of both skipper species have narrow corolla tubes with stigmas and anthers in positions that should promote proboscis contact as skippers imbibe nectar. Feeding skippers usually placed only their proboscis tips into corolla tubes, the remainders of their proboscides bending above corolla tube openings. Some skippers feeding at flowers with longer corolla tubes, such as *Tagetes erecta*, *T. patula*, and the infrequently visited *Consolida orientalis*, *Viola* ×*wittrockiana*, and *Capsicum* sp., occasionally pushed their proboscides deep into corolla tubes, possibly effecting stigma and anther contact with their "faces" and palpi.

Pollen Transport

From their VFVFS, 283 *A. campestris* carried 68.35 ± 3.250 (0–357) pollen grains, and 59 *E. clarus* carried 45.05 ± 3.760 (0–143) pollen grains. *Atalopedes campestris* carried the greatest mean amount of pollen from *Eupatorium coelestinum*, the only VFVFS that is native to the study-site region. The pollen loads that *A. campestris* carried from some species were significantly different from one another (Table 4). Regarding their VFVFS, *E. clarus* carried significantly more *Scabiosa atropurpurea* than *Zinnia elegans* pollen grains ($P < 0.05$, DMRT).

Selected examples of significant differences in numbers of grains

TABLE 3. Sequential flower visits of individual skippers. AH, *Ageratum houstonianum*; CA, *Capsicum* sp.; CC, *Callistephus chinensis*; CS, *Cosmos sulphureus*; DB, *Dianthus barbatus*; DX, *Dahlia pinnata* × *coccinea*; EC, *Eupatorium coelestinum*; IW, *Impatiens wallerana*; LS, *Lythrum salicaria*; SA, *Scabiosa atropurpurea*; TE, *Tagetes erecta*; TP, *Tagetes patula*; ZE, *Zinnia elegans*.

Skipper number	Sequence of flower visits
	Atalopedes campestris
1	SA (14 times)
2	ZE (10)
3	ZE (6), SA (2), TE (3)
4	TP (9)
5	TE (4), EC (2), TE (2), EC (1), TE (1), EC (2)
6	TP (5), DX (1), TP (6), CA (1)
7	ZE (8), CC (1), ZE (2)
8	ZE (5), SA (2), ZE (3)
9	TP (5), SA (1), TP (5)
10	TE (6), EC (4), TE (1)
11	EC (10)
12	ZE (11)
	Epargyreus clarus
1	ZE (10)
2	ZE (1), LS (3), ZE (5)
3	SA (1), DB (5), SA (3)
4	ZE (1), DB (2), ZE (6)
5	SA (10)
6	DB (8)
7	ZE (1), DB (4), ZE (5)
8	ZE (11)
9	ZE (11)
10	ZE (5), SA (1), ZE (5)
11	IW (4), ZE (2), SA (1), ZE (2)
12	SA (13)
13	ZE (10), IW (2)
14	SA (11)
15	SA (12)
16	SA (5), CS (2), SA (2)
17	SA (10)
18	ZE (5), SA (1), AH (1), SA (4)
19	ZE (4), SA (1), ZE (2), SA (2)
20	ZE (13)

carried by different skipper parts are listed in Table 5. Individual skippers carried significantly more pollen of these flowers in their facial cavities than on, or in, other structures, except for pollen of *Tagetes patula*. The most pollen any one *A. campestris* carried in its facial cavity (and in fact on, or in, any part) was 161 grains from *Eupatorium coelestinum*. For seven of their eight VFVFS, *A. campestris* carried the second largest amounts of pollen on their proboscides. *Epargyreus clarus* carried more pollen from *Scabiosa atropurpurea* and *Zinnia*

TABLE 4. Mean number of pollen grains carried by *Atalopedes campestris* and *Epargyreus clarus* from very frequently visited flower species and *Cosmos sulfureus*. Within a skipper species, means followed by the same letter are not significantly different from one another ($P > 0.05$, DMRT).

Flower species	Mean ± SE, range, n
Atalopedes campestris	
All very frequently visited flower species	68.35 ± 3.250, 0–357, 283
Cosmos sulphureus	135.83 ± 15.662, 11–240, 16a
Eupatorium coelestinum	116.22 ± 9.298, 21–357, 45ab
Aster cv.	91.55 ± 9.350, 0–259, 42bc
Dahlia pinnata × *coccinea*	73.50 ± 13.132, 8–168, 12c
Zinnia elegans	59.04 ± 4.042, 16–132, 48cd
Callistephus chinensis	56.75 ± 15.554, 12–132, 8cde
Tagetes patula	40.41 ± 3.755, 8–142, 35de
Scabiosa atropurpurea	37.29 ± 4.222, 7–108, 35e
Tagetes erecta	26.60 ± 3.821, 0–103, 35
Epargyreus clarus	
Both flower species	48.05 ± 3.760, 0–143, 59
Scabiosa atropurpurea	54.28 ± 6.172, 0–135, 43
Zinnia elegans	38.06 ± 4.371, 9–143, 25

elegans in their facial cavities than on, or in, any other parts. They carried significantly more *Scabiosa atropurpurea* pollen than *Zinnia elegans* pollen in their facial cavities ($P < 0.001$, TT). *Epargyreus clarus* from both flowers carried the second largest amounts of pollen on their proboscides.

The significant differences in Table 5 indicate that skippers generally carried more pollen anteriorly and less posteriorly. In order of decreasing amounts of pollen, *E. clarus* carried pollen in facial cavities, on proboscides, on hindlegs, on forelegs, in genital cavities, and on middle legs from *Zinnia elegans* and in facial cavities, on proboscides, forelegs, hindlegs, and middle legs and in genital cavities from *Scabiosa atropurpurea*. When mean numbers of pollen grains of two kinds of legs (or legs versus genital cavity) were compared, they were not usually significantly different from one another. In contrast, pollen loads carried in skipper facial cavities and on proboscides were significantly greater than those carried by legs and genital cavities. Pollen of VFVFS was distributed similarly on *A. campestris*.

The skippers usually carried more pollen of VFVFS on their proboscides or in their facial cavities compared to on, or in, other parts; this probably resulted from their more frequently putting their tongues rather than tips of their legs or other parts into flowers. Pollen from proboscides then builds up in facial cavities as skippers recoil their proboscides between flower visits. In cavities, pollen is likely to stick

TABLE 5. Selected examples of significant differences ($P \leq 0.05$, PTT) in the pollen loads carried between two body parts of an individual skipper from very frequently visited flower species. AC, *Aster* cv.; see Table 3 for other plant abbreviations.

Compared parts	Plants with significant differences
Atalopedes campestris	
Facial cavity > proboscis	AC, ZE
Proboscis > hindleg	AC, CC, DX, EC, TE, TP, ZE
Hindleg > foreleg	AS, TE
Hindleg > middle leg	AC, EC, SA, TE, ZE
Foreleg > middle leg	EC, SA, TE, TP, ZE
Hindleg > genital cavity	AC, EC, SA, ZE
Foreleg > genital cavity	AC, EC, SA, ZE
Middle leg > genital cavity	AC, SA, ZE
Eparygreus clarus	
Facial cavity > proboscis	SA
Hindleg > foreleg	ZE
Hindleg > middle leg	ZE
Foreleg > middle leg	SA, ZE
Hindleg > genital cavity	SA, ZE
Foreleg > genital cavity	SA, ZE
Middle leg > genital cavity	ZE

to scales and other pollen already present and remain relatively undisturbed. Skipper posture and movement on asteriad heads could also account for the pollen distribution on their bodies. On these capitula, they often have their heads over innermost, polliniferous disk florets and their thoraces and abdomens over outermost (female stage) disk florets and ray florets with little or no pollen. Further, skippers are likely to have smaller pollen loads on their legs and other more exposed parts due to pollen loss during locomotory and grooming behaviors.

Some pollen was found in the genital cavity of at least one skipper collected from each of the VFVFS. This pollen was confined to the hairlike scales on females' papillae analis and males' valvae (Ehrlich, 1960). The mean number of pollen grains borne in genital cavities for all VFVFS ranged from 0.17 ± 0.171 (0–6, N = 35) grains of *Scabiosa atropurpurea* to 4.12 ± 1.880 (0–15, N = 8) grains of *Callistephus chinensis*. Females of both skipper species carried significantly more pollen of these flowers, except for *Dahlia pinnata* × *coccinea*, in their genital cavities than males ($P < 0.05$, TT). Of the 41 skippers that carried pollen in their genital cavities, only eight were males. The most pollen any one female skipper carried in her genital cavity was 67 pollen grains of *Tagetes patula*. The most pollen any one male skipper carried in his genital cavity was seven grains from *Tagetes erecta*. Pollen is likely to enter genital chambers when skippers touch pollen on flowers with their abdominal tips during foraging. Perhaps groom-

ing movements also cause pollen to enter genital chambers. Since the amount of pollen that a skipper carries might increase with its age, we examined our data for possible positive correlations between age and the pollen load of VFVFS on a skipper's forelegs, middle legs, hindlegs, and proboscis, and in its facial and genital cavities. In *A. campestris*, age was positively correlated ($P < 0.05$) with the amount of pollen in facial cavities (3 flower species) and genital cavities (4), and on forelegs (1), hindlegs (1), and proboscides (5). In *E. clarus*, age was positively correlated with the amount of pollen in facial cavities (2 flower species) and on proboscides (2). Thus, pollen loads were generally not positively correlated with age, because out of a possible 48 correlations, only 13 were found for *A. campestris*, and out of a possible 12 such correlations only four were found for *E. clarus*.

In our study, the skippers visited *Zinnia elegans* more than other flowers. However, they carried more pollen from *Eupatorium coelestinum* and *Scabiosa atropurpurea* than from *Zinnia elegans*, which might not be expected (Heinrich & Raven, 1972). This finding might be due to *Zinnia elegans* having larger (55-μ-diameter) and spinier pollen than the other two species which have 35-μ-diameter pollen (Erdtman, 1966; Kapp, 1969). Pollen with a smoother exine surface adheres better to parts of Lepidoptera, such as tongues, than pollen with a spinier surface (Kislev et al., 1972). Further, pollen of smaller rather than larger diameter is generally picked up by a butterfly's proboscis during feeding and is retained when its proboscis is recoiled and not in use (Levin & Berube, 1972). Besides skipper-visitation frequency and pollen size and surface characteristics of a particular flower species, the pollen load of a skipper is likely to be affected by many other variables which have not been studied.

In conclusion, three lines of evidence suggest that the skippers were pollinators of their VFVFS. First, they were ordinarily constant to particular species during foraging bouts. Second, they transported pollen. Finally, they were likely to contact stigmas frequently with their proboscides, since they mainly visited flowers with narrow, tubular corollas. They contacted some flowers with their facial cavities and may have contacted stigmas with their pollen-bearing legs and genital cavities, as well, because they sometimes walked over stigmas.

However, two more important lines of evidence indicate that the skippers probably functioned mainly as nectar thieves. First, they mostly foraged upon asteriads rather than upon other kinds of flowers and primarily probed innermost (male-stage) disk florets, tending not to contact female-stage florets with their more pollen-laden parts. Second and more importantly, the skippers carried pollen in loads that appear too small for efficient pollination. In the *Colias-Phlox* pollination sys-

tem, Levin and Berube (1972) found that only 0.5% of the *Colias*-transported pollen, that was transferred to receptive stigmas, germinated and produced pollen tubes. In our study, 0.5% of the mean number of pollen grains from VFVFS that was carried by an entire individual skipper was always less than one grain. Making the liberal assumption that all pollen grains in the skippers are available for pollination and extrapolating from the *Colias-Phlox* system, we find that it would take an average of at least four flower visits for a skipper to deposit a pollen grain. If one considers an efficiently working capitulum to be one with many florets that can be pollinated by a single foraging insect (Burtt, 1961), capitula of the VFVFS are not efficiently working ones with regard to the skippers we studied.

The butterflies-as-nectar-thieves hypothesis is not rejected by our observations on skippers and quantification of their pollen loads. Emmel (1971) presents strong circumstantial evidence that the Ecuadorian skipper *Perichares philetes dolores* (Reakirt) is a pollinator of the orchid *Maxillaria "ontoglossom"* (which is not in Index Kewensis). However, because he does not present direct evidence that this skipper is indeed a pollinator, his data do not reject the hypothesis. A further test of the hypothesis based on an extensive literature survey will be presented in a future paper.

The hypothesis that the skippers might indirectly increase pollination and seed set of their thieved flowers remains to be tested. This increased pollination might occur because pollinators have to visit more flowers to obtain adequate resources from thief-depleted flowers compared to ones not depleted by thieves (Heinrich & Raven, 1972; Barrows, 1976). An alternative hypothesis to consider is that skippers somehow cause pollinators to forage less on patches of thieved flowers, thereby reducing pollination of these patches (McDade & Kinsman, 1980; Roubik, 1982).

ACKNOWLEDGMENTS

We are grateful to the following persons who helped us with this study: R. S. Blanquet, F. M. Harrington, F. C. Thompson, L. Venables, and members of the Glover Park Garden Club.

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