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DIVERSITY AND TEMPORAL CHANGE IN THE EFFECTIVE POLLINATORS OF *ASCLEPIAS TUBEROSA*¹

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Abstract. Although pollination effectiveness is a central process underlying the evolution of plant and pollinator traits, it is difficult to measure and has rarely been reported for a diverse spectrum of visitors under natural conditions. We measured the effectiveness of all common flower visitors to *Asclepias tuberosa* (butterfly weed) at a site in southeastern Arizona, in terms of visitation rate, per-visit rate of pollinia removal and insertion, and pollinia load. *Bombus* and *Apis* (Hymenoptera) were the most effective pollinators, counter to predictions that *A. tuberosa* is butterfly-pollinated. We also documented large differences between 2 yr in the pollination effectiveness of visitors, primarily due to changes in visitation rate. *Bombus* were the most frequent and effective pollinators in 1992. In 1993, *Apis* were equivalent to *Bombus. Battus* (Lepidoptera) were the second most effective pollinators in 1992, but were scarce in 1993. Thus, conclusions about the identity of effective pollinators based on floral traits, casual observations of visitation, or even precise measurement of effectiveness in a single season are all potentially suspect. We compare our results to those of previous studies of *Asclepias* pollination.

Key words: Arizona; *Asclepias*; Hymenoptera; Lepidoptera; mutualism; pollination effectiveness; randomization test.

INTRODUCTION

Quantifying pollination effectiveness is central to many questions in pollination biology. These include the measurement of selection on floral traits (e.g., Campbell et al. 1994), examining the utility of pollination syndromes (e.g., Bawa 1994), and, in the case of pollen consumers, explanations of the foraging behavior of flower visitors (e.g., Strickler 1979). Unfortunately, the measurement of pollination effectiveness has been hampered by intrinsic difficulties in observing the pollination act, which is often brief, occurs on a small scale involving large numbers of male gametophytes, and is often followed by the rapid movement of the pollinator out of range of the observer (Primack and Silander 1975, Snow and Lewis 1993).

Recent studies have demonstrated that pollinators can select for floral traits that are correlated with reproductive success, such as corolla size/shape (e.g., Campbell et al. 1991, but see Andersson 1994), flower color (e.g., Stanton et al. 1986, 1989), nectar production (e.g., Mitchell 1993), pollen presentation (e.g., Thomson and Thomson 1992), and inflorescence size (e.g., Broyles and Wyatt 1990; M. Fishbein and D. L. Venable, *unpublished manuscript*). Because of the difficulties in assessing pollination effectiveness, the identities of the pollinators responsible for selection in natural populations are often assumed to be commonly observed flower visitors (e.g., Campbell 1989, Stanton et al. 1989, Andersson 1991).

Indirect measures have usually been employed to assess the pollination effectiveness of particular taxa of flower visitors. These include measuring pollen loads of foraging animals (e.g., Willson et al. 1979, Young 1988, Liede 1994), measuring the movement of pollen analogs during single or multiple flower visits (e.g., Campbell et al. 1991), and determining the seed set obtained in the presence of a given pollinator relative to other pollinators (e.g., Motten et al. 1981, Tepedino 1981, Spears 1983). Although it has not been used in this manner, paternity exclusion analysis (reviewed in Snow and Lewis 1993) could also be applied to this problem, by exposing plants to particular pollinators and determining the number of seeds produced and sired. Direct methods of quantifying pollination effectiveness involve the measurement of pollen removal and deposition for single visits (e.g., Bertin 1982, Herrera 1987, Pettersson 1991, Wilson and Thomson 1991). Few studies have measured both per-visit pollen removal and deposition under nearly natural conditions or in multiple seasons that may differ in composition of the visitor fauna (Snow and Roubik 1987, Wolfe and Barrett 1989, Murcia 1990, Young and Stanton 1990, Wilson and Thomson 1991).

Pollination effectiveness can be partitioned into components, including rates of visitation, pollen removal, and pollen deposition (Herrera 1987, Waser and Price 1990, Inouye et al. 1994). Because of difficulties in measuring overall effectiveness, often only one or two components are measured. The distinction between overall effectiveness and components is important because some visitors may be effective at one component

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(e.g., visitation rate), but ineffective or detrimental at another (e.g., pollen removal). Thus, frequent visitors may consume pollen, nectar, or other floral tissues, reducing the reproductive success that would occur in their absence (McDade and Kinsman 1980, Wilson and Thomson 1991). They may also increase self-pollination, which may result in pollen wastage, stigma clogging, or the production of inferior offspring (de Jong et al. 1993). The net effect on reproductive success of an association of floral visitors may be very different than that predicted by summing the effect of each visitor species in isolation (Thomson and Thomson 1992); i.e., the ranking of taxa by pollination effectiveness can depend on the composition and relative abundance of the taxa that comprise the flower-visiting fauna.

The goals of this study are: (1) to test whether the milkweed, *Asclepias tuberosa* (butterfly weed), is most effectively pollinated by butterflies, as suggested by its floral traits and the great variety and numbers of butterflies observed to visit its flowers; (2) to accurately measure several components of pollination effectiveness for each flower-visiting taxon; and (3) to determine whether the pollination spectrum (i.e., the ranking of flower visitors by pollination effectiveness) of *A. tuberosa* is constant across 2 yr of study.

METHODS

Study site and species

We studied the pollination effectiveness of flower visitors to *Asclepias tuberosa* L. var. *interior* (Woodson) Shinnery (Asclepiadaceae) at The Nature Conservancy's Canelo Hills Cienega Preserve, ≈ 75 km south-east of Tucson, Arizona, USA ($31^{\circ}33\frac{1}{2}'$ N, $110^{\circ}31\frac{1}{2}'$ W, elevation 1500 m), at the lower elevational limit of Madrean oak woodland. The study site was located on the edge of a marsh, in the bottom of a shallow canyon. The study population of *A. tuberosa* occupied an area of ≈ 0.1 ha on the lower margin of a moderate east-facing slope.

A. tuberosa is a herbaceous, perennial milkweed common throughout the eastern two-thirds of the United States, reaching southeast Canada and northwest Mexico. Flowers in the study population are typically orange (ranging from yellow to red-orange), but individuals exhibit uniform flower color. The combination of reddish flowers, with nectar contained in narrow tubes, and a dense aggregation of flowers that can be visited at one time, is considered indicative of butterfly pollination (Proctor and Yeo 1972, Faegri and van der Pijl 1979:115–117). *A. tuberosa* is, in fact, commonly referred to as “butterfly weed,” presumably because of the large number of butterflies attracted to the flowers (Robertson 1891, Wyatt 1976, this study). *A. curassavica*, a species with similar morphology and flower coloration, has been reported to be butterfly-pollinated (Proctor and Yeo 1972, Bierzychudek 1981).

Because of their unusual pollination system, milk-

weeds are ideally suited for the study of pollen movement. Pollen in each anther sac is amassed in discrete structures termed pollinia that function as single dispersal units (Wyatt 1978). Each pollinium carries sufficient pollen to produce a mature fruit (Wyatt 1976); thus, it is meaningful to quantify pollen movement via pollinia. In the field, pollinia are easily observed with the aid of a hand lens, in flowers and on the bodies of captive pollinators. This feature has been appreciated by pollination biologists and entomologists, who have measured pollinia loads of insects (Robertson 1928, Frost 1965, Macior 1965, Lynch 1977, Willson et al. 1979, Morse 1982), net pollinia removal from and insertion in flowers (reviewed in Wyatt and Broyles 1994), and net retention and loss of pollinia from flower visitors (Morse 1982).

Data collection

Data were collected during 2-wk periods in June–July of 1992 and 1993, during the flowering peak of *A. tuberosa* at this site. The earliest individuals began flowering ≈ 2 wk prior to observation periods, and the last flowers were produced ≈ 4 wk following observations. The observation periods were concluded in both years when the first sustained “monsoonal” storms occurred, after which visitor activity drastically diminished. Observations were made on 77 individual plants in 1992 and 100 in 1993.

Pollinia transfer.—We observed each plant for two consecutive days to measure pollinia transfer rates and visitation rates. On the first day, we monitored each plant for the first four (1992) or five (1993) visits, totalling 272 visits in 1992 and 430 visits in 1993. For each visit, we recorded the taxon of the visitor, the duration of the visit, and the number of pollinia inserted and removed (removal observations actually record the movement of two paired pollinia, which, for the sake of clarity, we will refer to as single pollinia removals). The visitor “taxon” was either a species or a broader category such as “medium-sized bees.”

We bagged all inflorescences on experimental plants prior to anthesis with a coarse mesh cloth that prevented transfer of pollinia, but that did not exclude nectar consumption by some visitors (i.e., *Bombus*, *Battus*). This type of pollination bagging has been shown to minimally affect the physical environment (Wyatt et al. 1992). At the beginning of the sampling period, the observer removed the pollination bag from a plant, and the numbers of pollinia missing (due to malformation or removal within the bag) and inserted were recorded for the entire display. Observers monitored visits from 8 m away using field glasses. Following each visit, the observer recorded the numbers of pollinia inserted and removed. Pollinia removal was scored by noting the number of corpuscula missing from each flower (a corpusculum is the black structure that connects paired pollinia; it is readily visible in the flower prior to removal). Pollinia insertion was scored

by noting the number of pollinia projecting from the stigmatic chamber. A projecting pollinium indicates that another connected pollinium is inserted in the chamber. Because pollinaria observed on insect legs often have one pollinium broken off (Robertson 1886, Woodson 1954, Wyatt 1976, M. Fishbein and S. Buchmann, *unpublished data*), it is likely that counting projecting pollinia underestimates the total number of insertions. In *A. tuberosa*, the number of projecting pollinia is significantly correlated with the actual number of insertions and underestimates insertions by a factor of 2.3 (M. Fishbein and D. L. Venable, *unpublished data*). Thus, the estimate of pollinia insertions is conservative and assumes that the proportion of broken pollinia does not vary across taxa.

In each year, observations were staggered throughout the day when visitors were active (generally between one-half hour after sunrise and one-half hour before sunset) and in a variety of weather conditions ranging from sunny, hot, still, and dry to cloudy, cool, breezy, and humid. Flower visitation by all taxa ceased during steady rain. No observations were made at night since nocturnal visitors to *A. tuberosa* were very uncommon.

Since pollen loads have been used as a measure of pollination effectiveness (e.g., Willson et al. 1979), but do not necessarily correspond to effectiveness (e.g., Pettersson 1991), we measured them for comparison with actual removal and deposition rates. To measure pollinia loads, flower visitors of *A. tuberosa* were captured haphazardly in insect nets, sampled for the number of attached pollinia, and released. Paired and single pollinia were scored equally. Visitors were chosen to represent the entire spectrum (except birds), but individuals of abundant taxa, and those of taxa that rarely carry pollinia, were sampled more intensively to more accurately estimate their pollinia loads. Voucher specimens of visitors have been deposited in the Department of Entomology, University of Arizona.

Visitation rate.—Approximately 24 h following the pollinia-transfer observations, each plant was observed for 30 min to determine visitation rates and visit durations. During each observation period, the observer recorded the identity of each visitor to the focal plant and the duration of the visit. Total observation time was 105 h in 1992 and 127.5 h in 1993.

Analysis

We tested for differences among taxa in components of pollination effectiveness with analysis of variance (ANOVA) procedures of SAS system under Windows (SAS Institute 1989). Because more than one visit was recorded for each plant, it could be argued that those observations are pseudoreplicates (Hurlbert 1984). We compensated for the potential lack of independence of observations from the same plant by reducing the denominator degrees of freedom for *F* tests to reflect the number of plants observed rather than the number of visits recorded. This is a conservative approach. We

combined visitor taxa into seven categories. Because we were interested in whether *A. tuberosa* was accurately classified as butterfly-pollinated, we tested for differences between Lepidoptera and Hymenoptera a priori by the method of orthogonal comparison (Sokal and Rohlf 1981). Otherwise, taxon means were compared by Tukey's Honestly Significant Difference (HSD) test, which controls the experiment-wise error rate to $\alpha = 0.05$. Modifications of these procedures for particular analyses are discussed.

Visitation rate and visit duration.—We tested for differences among visitor taxa in visitation rate (number of visits per 30-min observation period) and mean visit duration. Data were analyzed by two-way ANOVA using taxon and year as fixed main effects. Year was treated as a fixed effect because we were interested in differences in pollination effectiveness in the particular years of the study and not in long-term, among-year variation in effectiveness (cf. Bennington and Thayne 1994).

Pollinia transfer.—We tested for differences among visitor taxa in number of pollinia removed and inserted per flower per visit. In some cases additional visitors arrived before the first visitor left. To account for the possibility that some of the observed pollination events were due to these additional visitors, we reanalyzed the data after weighting number of pollinia removed or inserted during multiple visits by the proportion of the summed visit durations assignable to the first visitor. Because taxa varied between years in visitation rate, combining pollinia transfer data from both years yielded a highly unbalanced design. Under such circumstances, it is possible to fail to detect a truly significant effect due to collinearity in the data (Shaw and Mitchell-Olds 1993). Thus, we also conducted separate one-way analyses for each year. Statistical analyses of transfer rates were conducted only for pollinia removal, since sample sizes were too low for insertion. For the single-year analyses of removal, we eliminated *Battus* and medium-sized Lepidoptera in 1993 because of small sample size ($n < 5$).

Because of highly non-normal distributions (i.e., most observations equal to zero, but with several relatively large values), pollinia transfer data violated assumptions of both standard and rank-transformed ANOVA (Conover 1971, Potvin and Roff 1993). Such data have highly non-normal distributions of residuals and are prone to deviate strongly from the assumption of homogeneous variances. A likely consequence of ignoring this problem is inflated statistical significance. While rank transforming tends to stabilize homogeneity of variance (Potvin and Roff 1993), the large number of zeros results in many tied ranks, which compromises this approach (Conover 1971:256). To determine robust probability values for these *F* tests, we utilized a randomization procedure (Manly 1991). An empirical *F* distribution was created by repeatedly randomizing taxon identity and reanalyzing the untransformed data.

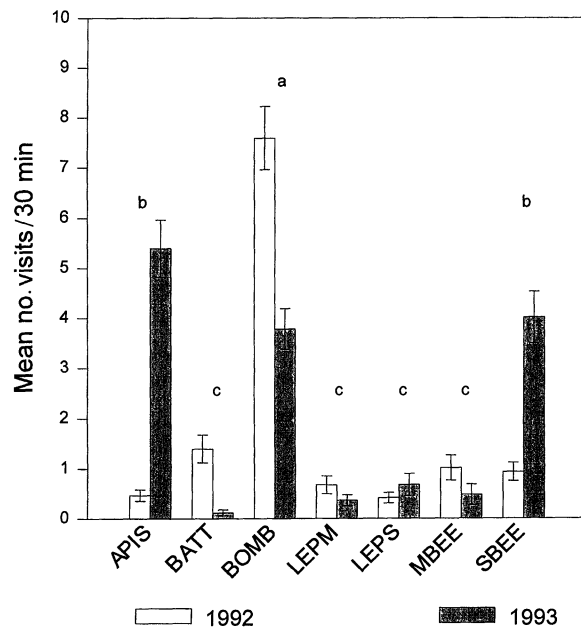


FIG. 1. Mean visitation rate of seven "taxa" of insects to inflorescences of *A. tuberosa* during 30-min observation periods in 1992 ($n = 210$) and 1993 ($n = 255$). Bars indicate ± 1 SE. Taxa labeled with the same letter are not significantly different in visitation frequency averaged across years (Table 1A). Taxa codes are as follows: APIS = *Apis mellifera* (Hymenoptera: Apidae), BATT = *Battus philenor* (Lepidoptera: Papilionidae), BOMB = *Bombus sonorus* (Hymenoptera: Apidae), LEPM = "medium-sized Lepidoptera" (including Hesperidae, Nymphalidae, Pieridae), LEPS = "small-sized Lepidoptera" (including Hesperidae, Lycaenidae, Nymphalidae, Pieridae), MBEE = "medium-sized bees" (including Anthophoridae, Megachilidae), SBEE = "small-sized bees" (including Halictidae).

After 1000 random reanalyses, the actual value of F was compared to the distribution generated by the randomization procedure to determine the probability of obtaining a value of F that large or larger.

To explore further the mechanisms for differences in effectiveness among visitors of different taxa, we decomposed the mean rate of pollinia transfer into two quantities: (1) the probability of a transfer event occurring, and (2) the mean number of pollinia transferred given that a transfer occurred. Because of the small number of observations of pollinia insertion, we only partitioned pollinia removals in this manner.

To test for differences among taxa in the probability of any pollinia being removed, we scored each visit as 0 if no pollinia were removed, or 1 if any pollinia were removed. Because binary data do not satisfy the distributional assumptions of least-squares ANOVA/regression, we utilized maximum likelihood logistic regression (Aitkin et al. 1989, Crawley 1993, SAS Institute 1993). Year of observation, taxon identity, and visit duration were the explanatory variables. Tests for a significant contribution of each explanatory variable and first- and second-order interactions among the vari-

ables were conducted following the model simplification recommendations of Crawley (1993: Chapter 12) utilizing SAS/INSIGHT Fit Analysis (SAS Institute 1993).

To test for differences among visitor taxa in the number of pollinia removed, given that any pollinia were removed, we deleted all observations for visits with no removals, and reanalyzed the data by analysis of covariance (ANCOVA) in the manner described above for the complete data set, but with the addition of visit duration as a covariate. As with the analysis of the unpartitioned data, combining the data for both years would have yielded a highly unbalanced design, so data were analyzed for each year separately. For taxa that were well represented in both years, we utilized ANOVA to test for an overall difference between years.

RESULTS

We observed 80 species of visitors to *Asclepias tuberosa* flowers, including one hummingbird and 79 insects (Appendix). Several of these were casual visitors, not recorded during formal observation periods. However, many were directly observed to transfer or carry pollinia. These pollinating species form a phylogenetically diverse assemblage including seven families of Hymenoptera, six families of Lepidoptera, and a total of 34 species.

Visitation rate and visit duration

Visitation rate.—The mean number of visits per 30-min period differed strikingly for several of the important flower-visiting taxa in 1992 and 1993 (Fig. 1, Table 1A). There also were differences between years in visitation rate, which varied among visitor taxa (year \times taxon interaction). Overall visitation rate was similar between the 2 yr (year main effect not significant). Hymenoptera visited at a significantly higher rate than Lepidoptera (a priori contrast: $F_{1,145} = 171$, $P < 0.0005$). *Bombus sonorus* (Hymenoptera: Apidae; Plate 1) visited at a significantly higher rate than all other

TABLE 1. ANOVA of visitation rate and visit duration of seven insect taxa to *A. tuberosa* in 1992 and 1993 (see Figs. 1 and 2). Significance tests based on type III sums of squares. Significant effects ($\alpha < 0.05$) indicated in bold. Degrees of freedom adjusted to account for multiple observations per plant.*

Source	df	MS	F	P
A) Visitation rate				
Taxon	6	581	66	<0.0005
Year	1	31	3.5	0.07
Taxon \times Year	6	327	37	<0.0005
Residual	145	8.7		
B) Visit duration				
Taxon	6	78.2	13	<0.0005
Year	6	1.68	0.3	>0.25
Taxon \times Year	6	3.04	0.5	>0.25
Residual	145	6.2		

* Total number of observations = 465.

PLATE 1. *Bombus sonorus* visiting flowers of *Asclepias tuberosa* at Canelo Hills Cienega Preserve, Arizona. Photograph by M. Fishbein.



taxa, and *Apis mellifera* (Hymenoptera: Apidae) and small-sized bees (Hymenoptera: Halictidae) visited at higher rates than each of the remaining taxa (Tukey's HSD test; Fig. 1).

Between-year differences were due to changes in visitation by *Bombus*, *Apis*, *Battus philenor* (Lepidoptera: Papilionidae), and small-sized bees (Fig. 1). Overall, there was a shift from a flower-visiting fauna dominated by *Bombus* in 1992 to one with more equal representation by *Apis*, small-sized bees, and *Bombus* in 1993. *Bombus* were responsible for 59.4% of visits in 1992, but only 23.6% in 1993. The most frequent visitors in

1993 were *Apis*, which accounted for 33.8% of visits, an almost 10-fold increase from 1992. The only frequent butterfly visitors in 1992, *Battus* (11.0%), were infrequent visitors in 1993. *Danaus gilippus* (Lepidoptera: Danaidae) were abundant at this site but made very few visits.

Visit duration.—In contrast to the between-year differences in visitation rate, visit duration of each taxon was remarkably constant between years (Fig. 2, Table 1B). Taxa differed significantly in visit duration (Table 1B). Mean visit duration of Lepidoptera was longer than that of Hymenoptera (a priori contrast: $F_{1,145} = 8.4, P < 0.005$). The only significant difference among seven visitor taxa was that small-sized Lepidoptera (Hesperiidae, Lycaenidae, Nymphalidae, Pieridae) conducted longer visits than those of each other taxon (Fig. 2; Tukey's HSD test).

Pollinia transfer

Pollinia removal.—When data from both years were analyzed together, there was no evidence for differences in pollinia removal per flower per visit among taxa (Fig. 3, Table 2A). However, visitation rates varied between years so that the statistical design is highly unbalanced when data from both years are combined.

In separate analyses for each year, taxa differed in pollinia removal rate in 1993, but not 1992 (Fig. 3, Table 2A). In 1993, *Bombus* removed pollinia at a significantly higher rate than small-sized bees (Tukey's HSD test). In both years there was a trend for Apidae (*Bombus* and *Apis*) to remove pollinia at the highest rate (Fig. 3). *Battus* also removed pollinia at relatively high rates in 1992; however, they removed no pollinia in relatively few visits in 1993. Medium-sized bees (Anthophoridae and Megachilidae), small-sized bees, small-sized Lepidoptera, and medium-sized Lepidoptera (in 1992; Hesperiidae, Nymphalidae, Pieridae) tended to remove pollinia at lower rates than Apidae. In 1993, medium-sized Lepidoptera removed pollinia

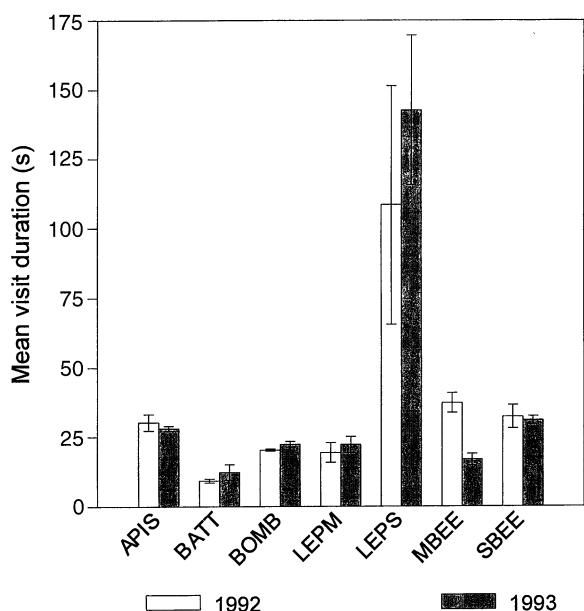


FIG. 2. Mean visit duration of seven taxa during 30-min observation periods in 1992 ($n = 210$) and 1993 ($n = 255$). Bars indicate ± 1 SE. LEPS is significantly different than all other taxa in visit duration across years (Table 1B, Results). Taxa codes as in Fig. 1.

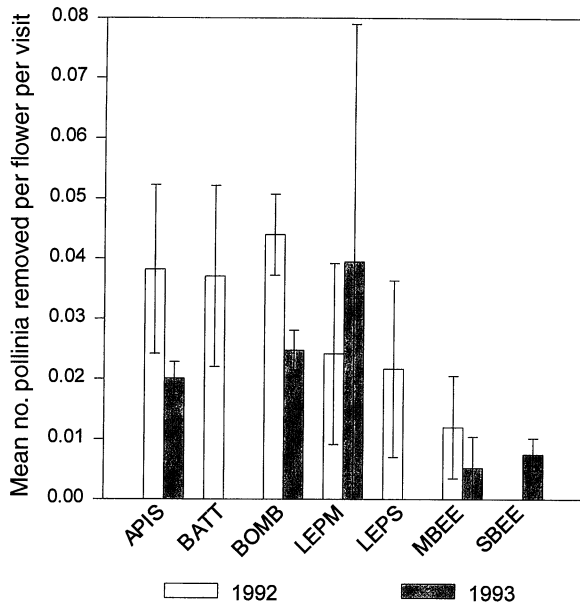


FIG. 3. Mean pollinia removal rates (per-flower per-visit) of seven taxa in 1992 and 1993 (Table 2A). Bars indicate ± 1 SE. Taxa codes as in Fig. 1. Sample sizes (1992, 1993) for each taxon are APIS (24, 198), BATT (21, 3), BOMB (206, 192), LEPM (10, 2), LEPS (10, 6), MBEE (10, 8), SBEE (12, 54).

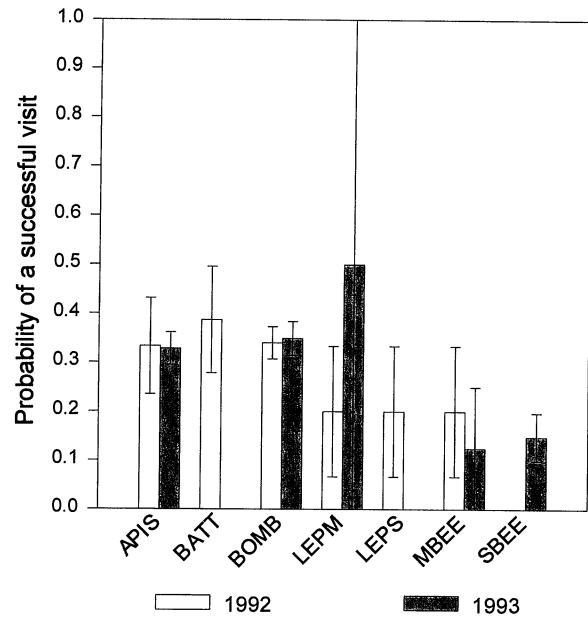


FIG. 4. Probability of a visit resulting in any pollinia being removed for seven taxa in 1992 and 1993 (Table 2). Bars indicate ± 1 SE. Taxa codes as in Fig. 1. Sample sizes as in Fig. 3.

TABLE 2. ANOVA of pollinia removal by seven insect taxa from *A. tuberosa* in 1992 and 1993 (see Figs. 3 and 5). Probabilities of *F* determined by randomization procedure (see *Methods*). Conventions follow Table 1.*

Source	df	MS	<i>F</i>	<i>P</i>
A) Removal rate				
Overall				
Taxon	6	0.0083	2.1	0.15
Year	1	0.0039	1.0	>0.25
Taxon \times Year	6	0.0016	0.4	>0.25
Residual	162	0.0040		
1992				
Taxon	6	0.0062	0.8	>0.25
Residual	69	0.0083		
1993†				
Taxon	4	0.0052	2.7	0.05
Residual	95	0.0020		
B) Mean pollinia removed				
1992‡				
Taxon	2	0.0034	0.2	>0.25
Duration	1	0	0.0	>0.25
Residual	45	0.0018		
1993§				
Taxon	2	0.0006	0.3	>0.25
Duration	1	0.0057	2.7	>0.25
Residual	82	0.0013		

* Sample sizes (n = number of observations): (A) $n = 756$ ($n_{1992} = 293$, $n_{1993} = 463$), (B) $n_{1992} = 86$, $n_{1993} = 140$.

† Observations for medium-sized Lepidoptera and medium-sized bees excluded.

‡ Only observations for *Apis*, *Battus*, and *Bombus* included.

§ Only observations for *Apis*, *Bombus*, and small-sized bees included.

at a high rate, but this was based on only two observations, and thus had a very large standard error. *Danaus gilippus*, milkweed bugs (Hemiptera: Lygaeidae: *Lygaeus* and *Oncopeltus*), wasps (Hymenoptera: Pompilidae, Scoliididae, Sphecidae, Vespidae), and Diptera (Bombyliidae, Conopidae, Stratiomyidae) were not observed removing pollinia in either year (Fig. 3), although pollinia were found in small quantities on some of these visitors in our haphazard collections.

Taxa differed significantly in the probability of a successful visit (Fig. 4), and this probability was positively related to visit duration, independent of taxon identity (logistic regression, all interactions nonsignificant, Table 3). However, the probability of pollinia removal was constant between years. Given a successful visit (i.e., at least one pollinium was removed), taxa did not differ significantly in the mean number of pollinia removed, and there was no linear relationship be-

TABLE 3. Analysis of deviance from a logistic regression model fit to the probability of successful pollinia removal (Fig. 4). Explanatory variables are year, taxon, and visit duration ($n = 773$). Data were analyzed by model simplification (Crawley 1993). Conventions follow Table 1. All second- and higher-order interactions between explanatory variables are not significant.

Source	df	Scaled deviance	<i>P</i>
Taxon	6	21.4	<0.005
Duration	1	66.8	<0.001
Year	1	1.0	>0.25
Residual	745	856	

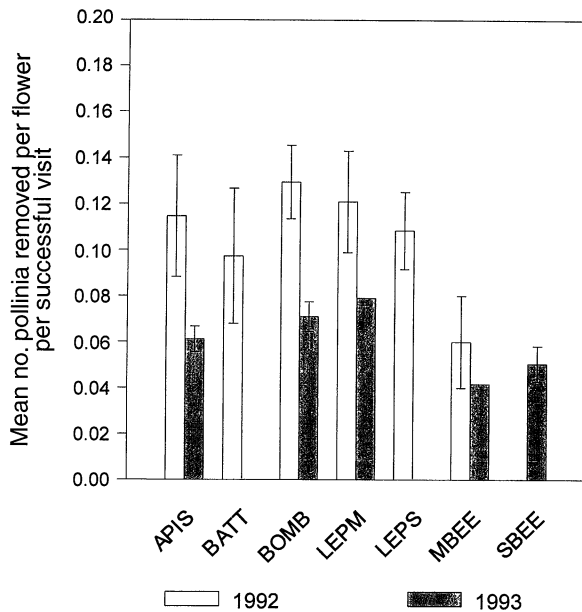


FIG. 5. Mean pollinia removal (per-flower per-visit) for visits in which at least one pollinium was removed for seven taxa in 1992 and 1993 (Table 2B). Bars indicate ± 1 SE. Taxa codes as in Fig. 1. Sample sizes (1992, 1993) for each taxon are APIS (8, 65), BATT (8, 0), BOMB (70, 67), LEPM (2, 1), LEPS (2, 0), MBEE (2, 1), SBEE (0, 8).

tween the number of pollinia removed and visit duration (interaction nonsignificant, Table 2B, Fig. 5). For these analyses only *Apis*, *Battus* (1992 only), *Bombus*, and small-sized bees (1993 only) were included, as other taxa had too few (<5) observations to warrant statistical analysis. Thus, differences among taxa are due mostly to the probability of a successful visit. Only *Apis* and *Battus* made sufficient visits to test for overall differences between years in number of pollinia removed during successful visits. Mean pollinia removed were significantly higher for these taxa in 1992 (ANOVA on raw data: $F_{1,113} = 9.6$, $P = 0.002$, Fig. 5).

An estimate of the population-level, pollinia-removal effectiveness of each visitor taxon (cf. Waser and Price 1990) can be calculated by multiplying visitation rate (number of visits per 30-min sampling period) by pollinia removal rate (number of pollinia removed per flower per visit) and multiplying by two (to express this quantity as a per hour rate). This measure clarifies the overall importance of *Bombus* as pollinia removers in 1992 (Fig. 6). They removed approximately six times as many pollinia per hour as the next highest ranked taxon, *Battus*. In 1993, however, we observed a shift to *Apis* and *Bombus* being equally important (Fig. 6).

Pollinia insertion.—Pollinia insertion rates also differed among taxa, although direct observation was so infrequent as to limit statistical analysis. In 1992, there were only four observations of pollinia insertion, three by *Bombus* and one by a medium-sized bee (Fig. 7). In 1993, of 23 total observations of insertions, 12 were

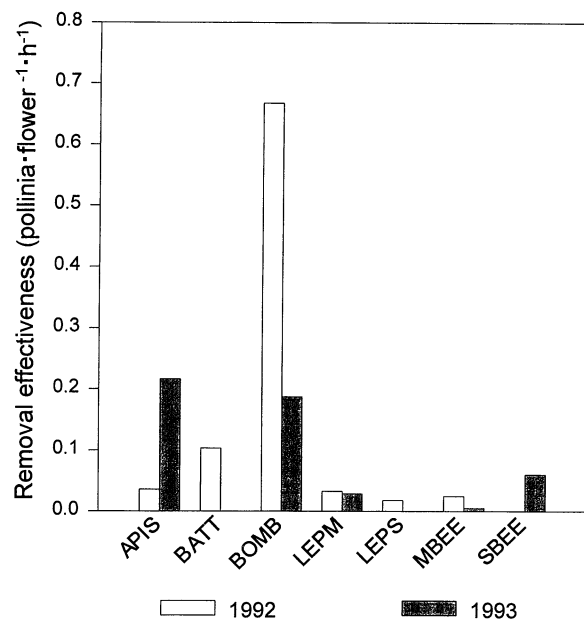


FIG. 6. Population-level, pollinia-removal effectiveness (product of mean per-flower per-visit removal rate and mean visitation rate per hour) of seven taxa in 1992 and 1993. Taxa codes as in Fig. 1.

by *Bombus*, 8 were by *Apis*, and 3 were by small-sized bees. The mean insertion rate per visit for these three taxa was approximately equal in 1993, about one pollinium inserted per flower in 500 visits. Since real insertion rates are 2.3 times greater than our estimate from field-collected data (M. Fishbein and D. L. Venable, unpublished data), the actual insertion rate for the above taxa is about one in 217 visits.

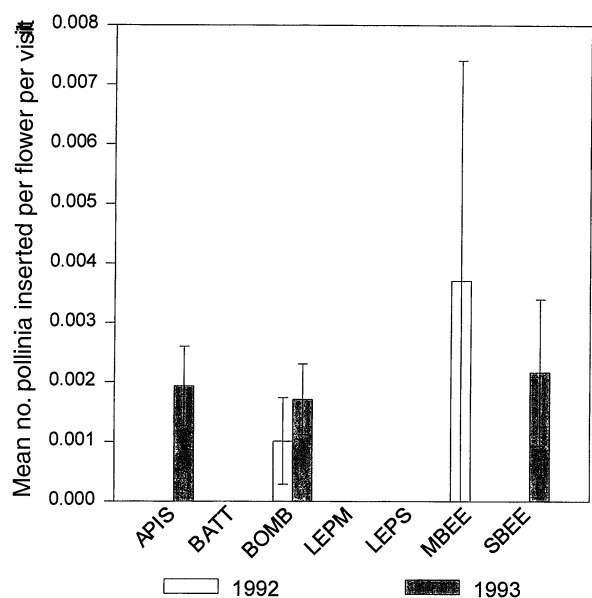


FIG. 7. Mean pollinia insertion rates (per-flower per-visit) of seven taxa in 1992 and 1993. Bars indicate ± 1 SE. Taxa codes as in Fig. 1. Sample sizes are the same as in Fig. 3.

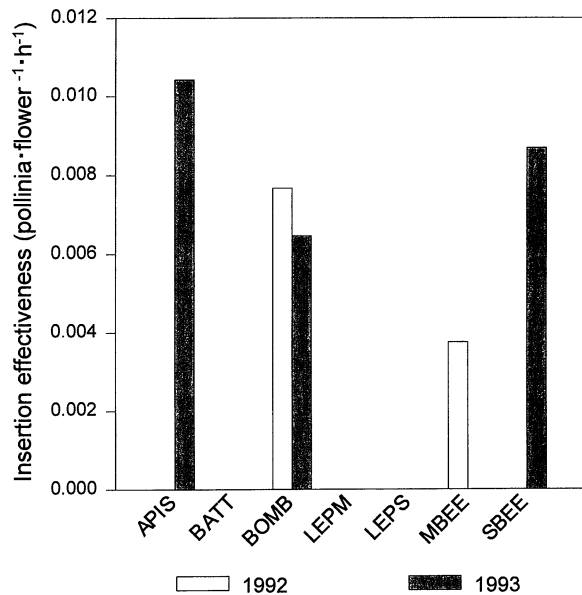


FIG. 8. Population-level, pollinia-insertion effectiveness (product of mean per-flower per-visit insertion rate and mean visitation rate per hour) for seven taxa in 1992 and 1993. Taxa codes as in Fig. 1.

We calculated the population-level, pollinia-insertion effectiveness of each taxon in the same manner as described above for removal effectiveness (Fig. 8). The results suggest that *Bombus* and *Apis* are most important in terms of pollen delivery.

Pollinia loads.—Haphazardly chosen insects were found to vary substantially among taxa in the number of pollinia carried (Fig. 9). Pollinia were carried on middle tarsal segments without exception. Hymenoptera (except Halictidae) and *Battus* bore relatively large pollinia loads (four–nine pollinaria), medium-sized lepidopterans bore smaller loads (three pollinaria), and *Danaus gilippus*, small-sized lepidopterans, small-sized bees, and milkweed bugs were found to carry pollinia rarely.

DISCUSSION

We have documented taxonomic variation and differences between two years in pollination effectiveness of visitors in a natural population of *Asclepias tuberosa*. Pollination effectiveness was measured by pollinator visitation rates and per-visit pollen removal and deposition rates. Although floral traits and casual visitor observation suggest butterfly pollination of this species, bees (*Bombus* and *Apis*) were the most effective visitors. These insects generally visited flowers and transferred pollen at higher rates than butterflies. However, visitor effectiveness was not constant between years. *Bombus* were the most effective pollinators in 1992, but *Apis* were equally effective in 1993. Butterflies (*Battus*) were of secondary importance in 1992, but were unimportant in 1993. Differences among pollinating taxa were due

largely to variation in visitation rate and the per-visit probability of pollinia removal, but not mean number of pollinia transferred per visit. Pollinia loads were often poor predictors of effectiveness (compare Figs. 6 and 9; e.g., *Battus*, medium-sized bees).

Taxonomic variation in pollination effectiveness is not unusual. Schemske and Horvitz (1984) found that Hymenoptera had a significantly higher probability of initiating fruit set than Lepidoptera. Waser and Price (1990) found per-visit differences in effectiveness between *Bombus* spp. and hummingbirds, but these differences were not apparent at the population level. Ashman and Stanton (1991) detected significantly higher pollen-deposition rates by *Bombus bifarius* than *Bombus* spp. These authors also documented temporal variation in components of pollination effectiveness, as was found for pollinating moths by Pettersson (1991) and for pollinators of *A. tuberosa* (this study). Variation in pollination effectiveness has been suggested to affect both the strength and direction of selection on floral characters (Schemske and Horvitz 1989, Ashman and Stanton 1991, Eckhart 1991).

Thomson and Thomson (1992) have demonstrated that net effectiveness of each pollinator species depends on the composition of the entire spectrum. Using the terminology of Thomson and Thomson (1992), *Bombus* were “good” pollinators for this population of *A. tuberosa* because they removed pollinia at rela-

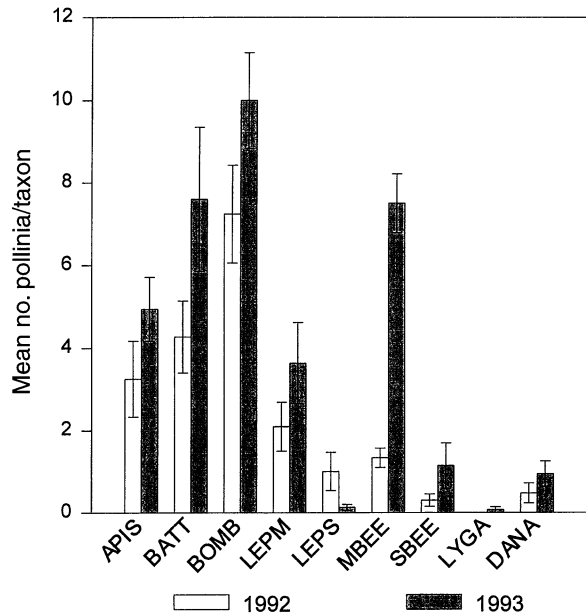


FIG. 9. Mean pollinia loads of nine taxa in 1992 and 1993. Bars indicate ± 1 SE. Sample sizes (1992, 1993) for each taxon are APIS (8, 17), BATT (15, 5), BOMB (29, 3), LEPM (22, 18), LEPS (30, 32), MBEE (9, 14), SBEE (10, 7), LYGA (13, 15), DANA (17, 17). Taxa codes as in Fig. 1 with the addition of DANA = *Danaus gilippus* (Hymenoptera: Danaidae) and LYGA = *Lygaeus kalmii* and *Oncopeltus fasciatus* (Hemiptera: Lygaeidae).

TABLE 4. Proportion and total number of species of five insect orders recorded as visitors to six species of *Asclepias* (see Discussion). Proportion and number of species that were observed to carry pollinia in parentheses.

Order	<i>A. tuberosa</i> (this study)	<i>A. tuberosa</i>	<i>A. incarnata</i>	<i>A. purpur-</i> <i>ascens</i>	<i>A. sullivantii</i>	<i>A. syriaca</i>	<i>A. verticillata</i>
Coleoptera	.03 (0)		.05 (.03)	.02 (0)	.02 (.02)	.05 (.03)	.02 (.01)
Diptera	.08 (.03)	.05 (.07)	.13 (.07)	.08 (.18)	.16 (.10)	.19 (.19)	.31 (.14)
Hemiptera	.05 (.06)		.01 (.02)	.02 (.06)	.02 (0)	.04 (.03)	.01 (0)
Hymenoptera	.30 (.38)	.41 (.46)	.57 (.64)	.30 (.29)	.55 (.59)	.38 (.51)	.49 (.64)
Lepidoptera	.54 (.53)	.54 (.46)	.25 (.24)	.58 (.47)	.25 (.29)	.34 (.23)	.16 (.14)
Total species of visitors	79 (34)	41 (28)	134 (109)	53 (17)	105 (41)	167 (105)	185 (116)
Flower color	orange	orange	pink, white	deep rose	deep rose	rose, white	white
Flower size*	large	large	small	large	large	large	small
Sources†	a	g, h, i, l	c, d, h, i	i	h, i	b-j	c, d, h, i, k

* Large flowers: corolla lobes >7 mm long, corona segments >4 mm long; small flowers: corolla lobes <4 mm long; corona segments <2 mm long (Woodson 1954; M. Fishbein, unpublished data).

† Sources: (a) this study, (b) Jennersten and Morse 1992, (c) Kephart 1983, (d) Macior 1965, (e) Morse 1982, 1986a, 1986b, Morse and Fritz 1983, 1989, (f) Ralph 1976, 1977, (g) Robertson 1886, (h) Robertson 1887, (i) Robertson 1891, 1928, (j) Willson and Rathcke 1974, Willson and Price 1977, Willson and Bertin 1979, (k) Willson et al. 1979, (l) Wyatt 1976. These data are adapted from a larger data base which is available from the authors, upon request.

tively high rates and were responsible for most of the observed pollinia insertions. It is also clear that some of the taxa are "bad" pollinators (e.g., Lygaeidae, *Dan- aus gilippus*), due to low visitation rates and/or low per visit removal rates. These bad pollinators carry very few pollinia (Fig. 9). They may be mismatched morphologically to *A. tuberosa* inflorescences (e.g., few tarsal hairs, small body) or have inappropriate behavior (e.g., idleness). *Apis* have been suggested to be "ugly" pollinators for other species because they remove large amounts of pollen, preventing its transport by good pollinators, but fail to deposit it (Wilson and Thomson 1991), perhaps due to their active pollen collection and effective grooming. There is no indication from our data that *Apis* were ugly pollinators for *A. tuberosa*; *Apis* were among the most effective pollinia inserters in 1993 when they were frequent visitors. Because *Asclepias* pollinia are probably not used as a food source by *Apis*, we would not expect *Apis* to be ugly pollinators. Our data suggest that some small-sized Lepidoptera (e.g., Lycaenidae) may be ugly pollinators because of their long residence time on a single inflorescence. The long visits of small-sized lepidopterans may result in more geitonogamous pollination, which may waste pollinia or preempt stigmatic chambers that would otherwise be available for outcross pollinia (de Jong et al. 1992, 1993, Broyles and Wyatt 1993). Self-pollination is potentially detrimental to *A. tuberosa* because it is known to be largely self-incompatible (Wyatt and Broyles 1994).

Although it is often recognized that inferences of pollination effectiveness based solely on floral traits can be suspect (e.g., Haber and Frankie 1989, Bawa 1994; Wasser et al., in press), "pollination syndromes" (Faegri and van der Pijl 1979) are still commonly used. Pollination syndromes are typically invoked when data on pollination effectiveness are not available, as in community level studies of multiple species (e.g., Bawa 1994, Pe-

tanidou 1995). Often, they are invoked in comparative studies of relatively few species (e.g., Cocucci 1995). Utilization of syndromes, however, is rarely substantiated by direct measurement of effectiveness.

The pollinator spectrum of *A. tuberosa* is different than that suggested by floral traits and initial observations of the composition of the flower-visiting fauna. The dense, flat-topped inflorescence of orange to reddish flowers with narrowly recessed nectar chambers implies the butterfly-pollination syndrome (Faegri and van der Pijl 1979). Further, the list of flower-visiting taxa at Canelo Hills Cienega includes many species of butterflies, more than any other order of visitors (Appendix). Our finding that *Bombus* and *Apis* were the most effective pollinators during the period of study strongly reaffirms caveats regarding the inference of effective pollination from floral traits, even when supported by observations of visitation (Schemske and Horvitz 1984). Based only on observations of fruit set and flower visitor abundance among several populations of *A. tuberosa*, Wyatt (1976) also speculated that Hymenoptera were more effective pollinators than Lepidoptera.

As in previous studies of *Asclepias* pollination, we found that *A. tuberosa* is visited by numerous species of insects that are capable of transporting pollinia (Appendix). A survey of pollinator records for six species of *Asclepias* reveals that between 41 and 185 insect species have been recorded as flower visitors to each species (Table 4). These data were obtained by compiling a list of all species recorded as flower visitors (or pollinia carriers) for these species (M. Fishbein, unpublished data). Comparison of the species in Table 4 reveals substantial variation in taxonomic composition of the pollinating fauna. Proportional composition by insect order of visitors to *A. tuberosa* at our study site was remarkably similar to that recorded by Robertson (1886, 1887, 1891) in southern Illinois. Both faunas are composed of ≈50% Lepidoptera with somewhat fewer Hy-

menoptera. Among *Asclepias* species, those with similar floral traits may differ in taxonomic composition of visitors (e.g., *A. sullivantii* vs. *A. purpurascens* and *A. incarnata* vs. *A. verticillata*). *Asclepias* species with very different floral traits may share similar taxonomic composition of visitors (e.g., *A. purpurascens* vs. *A. tuberosa* and *A. sullivantii* vs. *A. incarnata*). Comparison of taxonomic composition of pollinia-bearing visitors gives the same result. The 79 flower-visiting and 34 pollinia-bearing species recorded in this study are not unusual for *Asclepias* and underscore the tentativeness of classifying the pollination syndrome of a plant based on floral traits or casual observation alone.

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APPENDIX

FLOWER VISITORS TO *A. TUBEROSA* AT CANELO HILLS CIENEGA IN 1992 AND 1993

Records based on haphazard sampling and observation of flower visitation (see *Methods*). Pollinia carrier codes as follows: Y = pollinia observed on the visitor, or pollination observed during pollinia transfer observations (see *Methods*); N = pollinia never observed on visitor, and pollination never observed during pollinia transfer observations; ? = pollinia never observed on visitor, but members of its taxon (e.g., small-sized bees; see *Methods*) were observed to transfer pollinia. Nomenclature follows Scott (1986), Bailowitz and Brock (1991), Michener et al. (1994), and standard entomological texts.

Class	Order	Family (subfamily)	Species	Year	Pollinia carrier
Aves	Apodiformes	Trochilidae	<i>Archilochus alexandri</i>	1992, 1993	N
Insecta	Coleoptera	Cerambycidae	<i>Tetraopes femoratus</i>	1992, 1993	N
		Coccinellidae	<i>Hippodamia convergens</i>	1993	N
	Diptera	Bombyliidae	<i>Geron</i> sp.	1993	N
		Calliphoridae	<i>Phaenicia</i> sp.	1993	N
		Conopidae	<i>Physoconops townsendii</i>	1992	N
			<i>Zodion obliquefasciatum</i>	1992, 1993	Y
		Stratiomyidae	<i>Hedriodiscus</i> sp. 1	1992	N
		<i>Hedriodiscus</i> sp. 2	1993	N	
	Hemiptera	Alydidae	<i>Alydus pluto</i>	1992	N
		Largidae	<i>Largus</i> sp.	1992	N
		Lygaeidae	<i>Lygaeus kalmii</i>	1992, 1993	Y
	Hymenoptera	Reduviidae	<i>Oncopeltus fasciatus</i>	1992, 1993	Y
		Anthophoridae (Anthophorinae)	<i>Zelus renardii</i>	1992	N
			<i>Anthophora</i> sp.	1992	N
			<i>Centris</i> sp.	1992, 1993	N
			<i>Diadasia rinconis</i>	1993	Y
			<i>Melissodes</i> sp.	1992	Y
			<i>Xeromelecta californica</i>	1992	Y
		Anthophoridae (Nomadinae)	<i>Nomada</i> sp.	1993	N
			<i>Triepeolus verbesinae</i>	1992	N
		Anthophoridae (Xylocopinae)	<i>Xylocopa californica arizonensis</i>	1992, 1993	?
		Apidae (Apinae)	<i>Apis mellifera</i>	1992, 1993	Y
		Apidae (Bombinae)	<i>Bombus sonorus</i>	1992, 1993	Y
		Halictidae (Halictinae)	<i>Agapostemon</i> sp.	1992, 1993	Y
			<i>Halictus</i> sp.	1992, 1993	?
			<i>Lasioglossum</i> sp.	1993	?
	Megachilidae (Megachilinae)	<i>Coelioxys</i> sp.	1992, 1993	Y	
		<i>Megachile</i> sp. 1	1992	Y	
		<i>Megachile</i> sp. 2	1992	?	
	Pompilidae	<i>Pepsis</i> c.f. <i>elegans</i>	1993	N	
	Scoliidae	<i>Scolia ardens</i>	1992	N	
		<i>Campsomeris tolteca</i>	1992	Y	
	Sphecidae	<i>Ammophila</i> sp.	1992	Y	
			<i>Astata occidentalis</i>	1992	N
			<i>Prionyx</i> sp.	1992	Y
			<i>Steniola</i> sp.	1992	Y
			<i>Polistes major</i>	1992	Y
	Lepidoptera	Vespidae	<i>Danaus gilippus strigosus</i>	1992, 1993	Y
		Danaidae	<i>D. plexippus</i>	1992, 1993	Y
			<i>Chioides catillus albofasciatus</i>	1993	?
			<i>Copaeodes auranticus</i>	1992	N
			<i>Erynnis funeralis</i>	1992	?
			<i>Erynnis tristis tatus</i>	1993	?
			<i>Hesperia pahaska</i>	1992	?
			<i>Hylephila phyleus</i>	1992	Y
			<i>Pyrgus albescens</i>	1993	Y
			<i>Chlorostrymon simaethus sarita</i>	1992	?
	Lycaenidae	<i>Hemiargus isola alce</i>	1992, 1993	?	
			<i>Icaricia acmon texana</i>	1993	?
			<i>Leptotes marina</i>	1993	?
			<i>Ministrymon leda</i>	1992, 1993	?
			<i>Strymon melinus franki</i>	1992, 1993	?

APPENDIX. Continued.

Class	Order	Family (subfamily)	Species	Year	Pol- linia carrier	
Insecta	Lepidoptera	Nymphalidae	<i>Agraulis vanillae incarnata</i>	1992, 1993	Y	
			<i>Chlosyne lacinia crocale</i>	1992	Y	
			<i>Euptoieta claudia</i>	1992, 1993	Y	
			<i>E. hegesia huffmanni</i>	1992	?	
			<i>Junonia coenia</i>	1992, 1993	?	
			<i>J. nigrosuffusa</i>	1992, 1993	Y	
			<i>Phyciodes pictus pictus</i>	1992, 1993	?	
			<i>Ph. texana texana</i>	1992	Y	
			<i>Ph. tharos tharos</i>	1992, 1993	?	
			<i>Ph. vesta</i>	1993	?	
			<i>Vanessa cardui</i>	1992, 1993	Y	
			<i>V. virginensis</i>	1992	Y	
			Papilionidae	<i>Battus philenor philenor</i>	1992, 1993	Y
				<i>Papilio acauda</i>	1992	Y
				<i>P. multicaudatus</i>	1992, 1993	N
			Pieridae	<i>P. polyxenes asterius</i>	1992	Y
				<i>Colias cesonia</i>	1992, 1993	Y
		<i>C. eurytheme</i>		1992, 1993	Y	
		<i>C. philodice eriphyle</i>		1993	?	
		<i>Eurema mexicanum</i>		1992, 1993	?	
		<i>E. nicippe</i>		1992, 1993	?	
		<i>Nathalis iole</i>		1992, 1993	N	
		<i>Pheobis agarithe agarithe</i>		1992	?	
		<i>Pieris protodice</i>		1992, 1993	Y	
		<i>P. rapae</i>		1993	Y	
		?		moth sp. 1	1993	N
		? -		moth sp. 2	1993	N
		?	moth sp. 3	1993	N	