— Noteworthy Data Sets —

Note from James D. Thomson, Editor-in-Chief, Journal of Pollination Ecology

This paper inaugurates a new category for the *Journal of Pollination Ecology*. Its history is relevant. Over several decades, Professor C. Eugene Jones oversaw regular censuses of flower-visiting animals to riparian populations of the endangered California plant *Eriastrum densiflorum*, which had become vulnerable because of stream impoundments. This visionary program of study resulted in several master's theses from the California State University at Fullerton. A summary was submitted to *JPE*. Reviewers were unconvinced by the statistical analyses and some aspects of the paper's discussion. These perceived shortcomings would usually be addressed through revision and resubmission, but in this case, exigent personal issues prevented the authors from reworking the paper. I decided that *JPE* could not publish the paper as submitted and retain its status as a peer-reviewed journal. On the other hand, I firmly believe that long-term data sets have special, intrinsic value, particularly because so much attention is now focused on the question of pollinator declines. Therefore, I am proposing a new category of publication, *Noteworthy Data Sets*. For the first such offering, I have edited the Hoffman *et al.* manuscript as follows.

I have made minor adjustments to the Introduction and Methods sections to improve clarity and concision. I have retained all submitted Figures and Tables, along with all cited references. I have removed the description of statistical methods, the Results section, and the Discussion. These portions, basically unedited, will appear as online appendices, accompanied by a disclaimer that these sections should not be regarded as having been endorsed by peer review.

In adopting this unorthodox partitioning of material, I hope to provide an easily found foothold for this study in the peer-reviewed literature. Any researchers who are stimulated to learn more, or who might even want to extend the study with further investigations, should be able to find the information they need in the Fullerton theses and the other cited references. The online materials, despite the caveats, may be useful in outlining the general approach taken by Jones and coauthors.

SPATIOTEMPORAL VARIATION IN POLLINATOR TAXA ON THE SANTA ANA RIVER WOOLY STAR *ERIASTRUM DENSIFOLIUM* SSP. SANCTORUM (MILLIKEN) MASON (POLEMONIACEAE)

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Abstract—Flood control, via the construction of the Seven Oaks Dam in the Santa Ana River in southern California, has altered habitat in the downstream alluvial wash community and jeopardized the persistence of pioneer plant species that rely on periodic flood-scouring and sand recharge. One species, *Eriastrum densifolium* ssp. *sanctorum* ("*Eriastrum*"), an endangered perennial, has been greatly affected and persists in spatially separated populations on successional vegetation terraces. We made "dawn to dusk" observations of pollinators in three phenological stages at four sites, representing young and old seral stages, to identify primary pollinators and to elicit daily, site, and seasonal patterns of visitors. Data were compared to previous observations and correlated with annual rainfall to determine long-term trends. Shifts in pollinator taxa have occurred, with some consistency through time and space, during nine years. The sites with the highest pollinator abundance (older sites) are least suited to *Eriastrum*. Hummingbirds (prevalent in early season) and the Acton giant flower-loving fly (prevalent in late season) have been consistently present across years, whereas other taxa have varied. A shift from native bees to non-native bees has occurred, although native bees in the families Halictidae and Apidae (Micranthophora and Melissodes) remain important. In general, there was no correlation between taxa abundance and rainfall. *Eriastrum* appears to be a generalist able to take advantage of the behaviour, cycling, and availability of diverse pollinators daily, seasonally, and annually.

Keywords: Pollination, Santa Ana River woolly star, pollinators, rare species, Seven Oaks Dam, native bee declin

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INTRODUCTION

Throughout the world, biodiversity is declining at an alarming rate. The principal anthropogenic causes are habitat loss or alteration, fragmentation, and increasing urbanization (Zedler 2001; Burkle et al. 2013). The results are, ultimately, environmental homogeneity and reduced biotic productivity (Stanford et al. 1996), impacting several ecosystem services, e.g. pollination (Kremen et al. 2002; De Marco & Coelho 2004; Díaz et al. 2006; Kremen et al. 2007; Vanbergen & the Insect Pollinators Initiative 2013; Potts et al. 2016). The mutualistic interaction between pollinator-dependent angiosperms and animals may affect community dynamics and terrestrial ecosystem function (Ambrose & Kevan 1990; Kearns & Inouye 1997; Allen-Wardell, et al. 1998; Bronstein et al. 2006; Waser & Ollerton 2006; Tepedino, et al., 2014; Bailey & Kevan, 2017). Worldwide, around 90% of angiosperms are considered to be animal pollinated (Kearns et al. 1998; Ollerton et al. 2011).

One dramatic anthropogenic modification is the regulation and alteration of natural river flows, resulting in impacts to downstream environs and biota, as well as those biota surrounding and underlying the impoundments (Stanford et al. 1996). The Seven Oaks Dam, near the City of Highlands, was inaugurated in 2000 and caused the loss of periodic scouring and clean sand deposition, necessary for the renewal of alluvial wash habitat (Burk et al. 1988). It was constructed despite predicted impacts for flood-plain restricted species, like the Santa Ana River Woolly Star plant (*Eriastrum densifolium* ssp. *sanctorum* (Milliken) H. Mason, Polemoniaceae; hereafter "*Eriastrum*") (U.S. Army Corps 2000), which is considered to be one of California's most endangered plants (York 1987).

Eriastrum occurs and is endemic to the Santa Ana River drainage. Historically, *Eriastrum* occurred from the foothills of the San Bernardino Mountains in San Bernardino County and extended throughout the relic alluvial habitat to northern Orange County (Zembal and Kramer 1984; Burk et al. 1987). However, due to habitat loss and degradation resulting from urbanization, flood control, off-road vehicle use, sand and gravel mining, and colonization by invasive species (Burk et al. 1988), distribution is now restricted to scattered patches just north of Redlands, San Bernardino County, California. *Eriastrum* is specialized to require disturbance for habitat and/or regeneration (Pickett & White 1985) and is therefore restricted to periodically flood-scoured and alluvium-deposited Soboba washed sands, classified as Entisols (Burk et al. 1988; Burk, et al. 2007).

Eriastrum is exclusively reliant on the services of animal vectors for reproduction (Burk, et al. 1989; Burk & Jones 1993; Erickson 1993; Stone 1995; Brunell 1997), thus, the absence of pollinators could quickly result in the extirpation of the already perilously low remnant populations. Populations in fragmented landscapes become progressively more isolated and reduced in size, and face increasing probability of extinction (Young et al. 1996; Tepedino et al. 2014). When plants such as *Eriastrum* are reduced to small and isolated populations, biotic interactions are reduced (Aizen & Feinsinger 1994; Brys et al. 2004) including pollination (Mustajarvi et al. 2001; Aizen et al. 2002), especially when floral displays are reduced (Fischer & Matthies 1997).

Furthermore, rare plants, especially narrow endemics such as *Eriastrum*, are more easily pushed to extinction by stochastic events (Schemske et al. 1994; Fischer & Matthies 1997; Steffen-Dewenter & Tscharntke 1999) including variation in pollinator abundance (Goodwillie 2001; Ashman et al. 2004). Therefore, conservation strategies need to integrate research on the factors that diminish reproductive success (Godt & Hamrick, 1995; Bosch et al. 1998).

Long-term studies of plant pollinator interactions are rare. They have generally been restricted to either an examination of relative visitor abundance or per-visit effectiveness in transferring pollen, but rarely both (Spears 1983; Schemske & Horvitz 1984; Galen et al. 1987; Herrera 1989). Pollinator effectiveness is a combination of both and requires integration of all the factors effecting successful reproduction (Aigner 2005). Few studies address the intra- and interspecific behaviours of pollinators, which would seem to influence the presence of other pollinators daily and seasonally (Aigner 2005) and accordingly become a critical component dictating pollinator demographics.

Spatiotemporal variation in pollinators

In addition, floral visitor assemblages shift through time and space (Potts et al. 2003; Basilio et al. 2006; Alarcon et al. 2008). This spatiotemporal variation occurs annually, seasonally, and daily. In fact, year-to-year variation and seasonal variation in relative abundances are considered the norm in many species due to variable climatic conditions (Herrera 1989; Petterson 1991; Fleming et al. 2001; UNFAO 2008).

In arid and semi-arid areas, plants typically bloom when water resources and temperatures are amenable; therefore, opportunities for sexual reproduction are brief. Weather conditions of high winds, fluctuating temperatures, and variable precipitation can also affect insect visitation (Robertson 1895; Motten 1986; Herrera 1995; Proctor et al. 1996; Ollerton & Crammer 2002). In generalized pollination systems, habitat type has also been found to influence abundance and diversity (Fleming et al. 2001) and population size strongly affected abundance (Sih & Baltus 1987; Brys et al. 2004). Since *Eriastrum* occurs in both young and older vegetation assemblages, these habitat differences would be expected to have an influence on pollinators' presence and abundance. Discrete small populations, as found in *Eriastrum*, also may restrict the array and abundance of flower-visiting fauna (Jennersten 1988; Lamont et al. 1993; Kearns et al. 1998).

The reproductive biology of *Eriastrum* has been studied during nine years; across early, mid, and late phenologies; under variant environmental conditions; and within both young and old seral habitat stages (Muñoz, 1991; Erickson, 1993; Stone, 1995; Dorsett 1996; Atallah 2001; Hoffman, 2010). Rarely has such long-term pollination research been conducted on plant species at the same location.

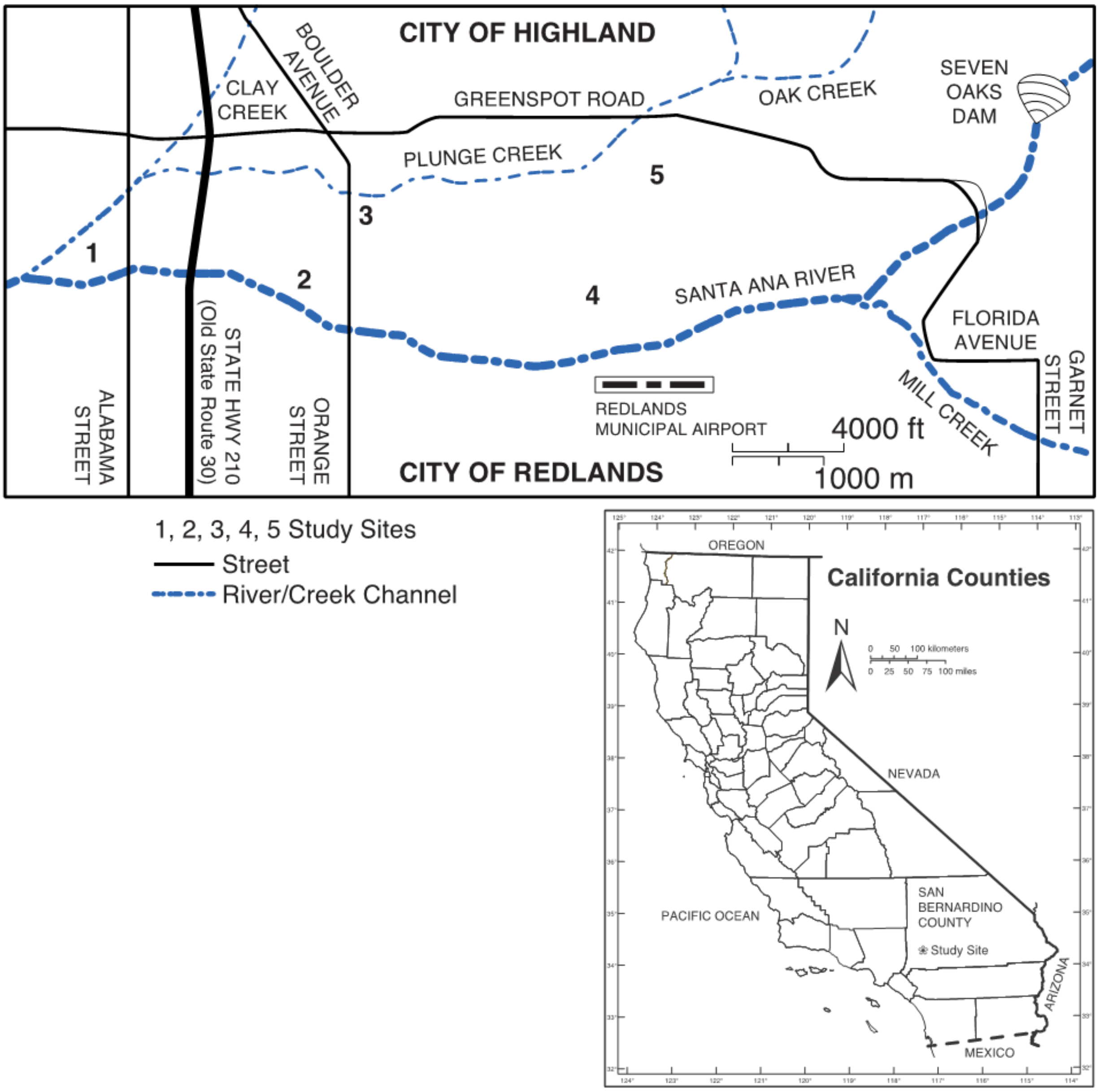

FIGURE 1. The Santa Ana River Wash Area (San Bernardino County, California) in which all known individuals of Eds occur. Sites 1, 2, 3 and 5 indicate locations of permanent demographic plots employed in this study. Site 4, although included in previous research, does not presently support a sufficient population of Eds for study. Coordinates: Site 1 – N 34° 05.727', W 117° 12.584', elevation 360 m; Site 2 – N 34° 05.396', W 117° 11.022', elevation 387 m; Site 3 – N 34° 06.011', W117° 10.832', elevation 396 m: Site 4 – N 34° 05.299', W 117° 10.164', elevation unrecorded; Site 5 – 34° 07.034', W 117° 11.509', elevation 457 m.

The aims of this research were 1) to determine the principal pollinators in each year; 2) assess variation in pollinator taxa and abundances across seasons and years, identifying trends; 3) check for correlation among pollinators' abundances and annual and critical period rainfall (rainfall occurring in the critical months of germination and growth for *Eriastrum*, January, February, and March) and daily temperatures; and 4) assess the relationship between the successional stage of the habitat and pollinator suitability. We examined how pollinator species abundances varied over time, particularly looking for correlations with mean annual precipitation.

MATERIALS AND METHODS

Plant species

Eriastrum is a short-lived perennial, woody, branched subshrub (height ranges from 25-75 cm) with an approximate life expectancy of three to five years (Burk et al. 1987). It has older woody growth and young herbaceous growth, with branching occurring each growing season. The common name refers to the thick pubescence of lannate hairs on the leaves and inflorescences. The flowers are clustered in bracheate heads, have a salver form shape, a light scent, and are protandrous with blue or cream pollen. Corollas are lavender with occasional pinks and whites, with a blooming period from late May to mid-August, with peak flowering in June.

Site location

Dawn-to-dusk pollination studies were conducted at five sites within the Santa Ana River floodplain, north of Redlands, San Bernardino County, California, (Fig. 1). These sites were selected to represent various successional habitat ages and to include the presence of 100 or more plants (Burk et al. 1987). Site 1 and 2 were last scoured in the 1969 flood and are considered to be young successional sites (Burk & Jones 1993); Site 3 is considered an older successional stage terrace created in the 1938 and either the 1862 or 1867 floods; and Site 5 is also considered an older terrace established by either the 1862 or 1867 floods (Burk & Jones 1993).

Site characteristics

The substratum of younger sites comprises deposited alluvium containing little to no silt or clay and is classified as Soboba stony, loamy sand with a high porosity and permeability (Wheeler 1991). The substratum of older sites contains more fine particulate (Wheeler 1991).

Holland (1986) classifies the vegetation as successional stages of Riversidian Alluvial Fan Sage Scrub Community (Holland 1986), variously degraded by human disturbance.

The climate is Mediterranean, consisting of cool wet winters and warm dry summers (Schoenherr 1995). The mean annual rainfall for the city of Redlands is 34.43 cm (maximum = 68.58 cm; minimum = 12.34 cm). The mean annual temperature is 17.54°C (average maximum = 25.61°C; average minimum = 9.56°C) with a statistical monthly high of 34.72°C in July and low of 4.06°C in January (Western Regional Climate Center 2009).

Pollinator studies

We observed flower visitors on *Eriastrum* in a series of three, three-day "dawn-to-dusk" (0600 to 1800) "pollination studies" (nine total periods). A team of observers conducted each of the three-day observation sets during the early (25% of plants in bloom), mid (75-95% of plants in bloom) and late (25% of the plants in bloom) blooming periods, which were compared between 1995 and 2008. A pollinator was defined as an animal that actually landed on and came into contact with the pollen and/or stigma of the flower. Visitors that alighted and did not contact the reproductive structures were not considered.

Three subpopulations at each of the study sites were chosen on the basis of ease with which one person could observe all visitation to 15-20 plants. We identified each pollinator to family, and if possible, to genus, species, and sex. We recorded numbers of visitations at the first of the three subpopulations from the top of the hour, until ten minutes after the hour, then rotated to the next subpopulation and recorded observations from 20 minutes after the hour until 30 minutes after the hour, then rotated to the third population and recorded observations from 40 minutes after the hour to 50 minutes after the hour. This process continued from 06:00 to 18:00, repeating every hour. On each of the three days, the initial subpopulation was rotated to a different starting population. The total observation time for all three observation periods of 234 hours. Total monthly precipitation for the growing season (occurring from July of the previous year to June of the study year) for 1995 and 2008 was recorded in Redlands. Notes on pollinator behaviour and ambient conditions, including hourly temperatures, cloud cover, and wind conditions, were also recorded. Insect visitors were identified using a reference collection developed by Stone for his work on *Eriastrum* (Stone 1995). Data from studies of other years were included to define the pollinators: 2000 (Atallah 2001), 1993 and 1994 (Stone 1995), 1991 and 1992 (Erickson 1993), 1989 and 1990 (Muñoz 1991).

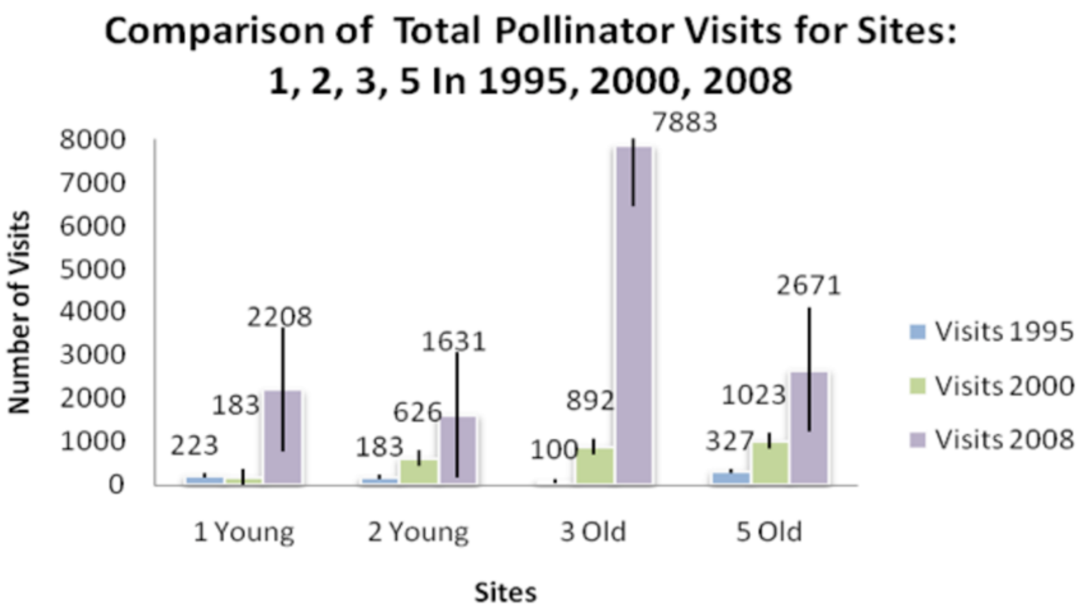

FIGURE 2. Number of recorded visits of all pollinators for Sites 1 & 2 (Young) and Sites 3 & 5 (Old) for observation years of 1995, 2000, and 2008.

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APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I. The description of statistical methods, the Results section, and the Discussion. These sections should not be regarded as having been endorsed by peer review.

TABLE 1. Primary and secondary pollinators from each site arranged by year of observation. MIC – Long-tongued Digger bees, LEP – butterflies and moths, RA – Acton Giant Flower-loving Fly, HUM – Hummingbirds, HYLE – White-lined Spinx Moth, BOM – Bumble bees, BOMC – California bumble bee (*Bombus Californicus*), HAFA – *Halictus farinosus* (Halictidae), HATR – *Halictus tri[artitus* (Halictidae), HAL – Sweat bees (Halictidae), MEL – Longhorned Digger bees), API – Western Honey bee.

Researcher	Year of Pub.	Year of Research	Site 1 Primary	Site 1 Secondary	Site 2 Primary	Site 2 Secondary	Site 3 Primary	Site 3 Secondary	Site 5 Primary	Site 5 Secondary
Muñoz	1991	1989	MIC	LEP, RA, HUM	---	---	---	---	---	---
		1990	MIC	None	---	---	RA, HUM	None	---	---
Erickson	1993	1991	MIC	RA	---	---	---	---	HUM, RA, HYLE	None
		1992	MIC	None	---	---	---	---	HUM, RA, BOM	None
Stone	1995	1993	---	---	---	---	---	---	HUM, BOMC, RA	HAFA, HATR
		1994	---	---	---	---	---	---	HUM, BOMC, RA	HAFA, HATR
Jones et. al	1996	1995	BOM, LEP, HUM	None	HAL, HUM	RA, LEP	HAL, MEL, HUM	None	MEL, HUM, HAL	BOM
Atallah	2001	2000	HAL, MEL, HUM, RA	API	RA, HUM, HAL, MEL	None	HUM, RA	MEL, HAL	HUM, RA	MEL, HAL
Hoffman	2010	2008	MIC, API, HUM	MEL, RA	HUM, RA, API	MEL	HUM, RA, API, HAL, MEL	MIC	HUM, RA, API	MEL

TABLE 2. The percent contribution of each site (1, 2, 3, & 5) expressed in percentage of the ration of the site visits to total visits by select primary pollinators and the raw number of visits across all seasons for years; 1995, 2000, & 2008. Primary pollinator categories are HUM – hummingbirds, HAL – Sweat bees, RA – Acton Giant Flowering-loving Fly, API – Western Honey bees, MEL – Longhorned Digger bees, MIC – Long-tongued Digger bees, & BOM – Bumble bees. Some pollinators were not among the primary pollinators for all years and may have a few to no visits represented.

	Site 1 Pollinator visits		Site 2 Pollinator visits		Site 3 Pollinator visits		Site 5 Pollinator visits		Total Visits by pollinator by year
	%	N	%	N	%	N	%	N	
2008									
HUM	4	183	11.3	516	62	2,832	22.8	1,045	4,576
HAL	1	6	12	72	83.1	497	3.9	23	598
RA	3.3	108	10.2	336	67.2	2,215	19.4	638	3,297
API	22.4	690	16.1	495	40.4	1,240	21	646	3,070
MEL	16	144	12.4	112	47.7	430	24	216	902
MIC	75.5	818	0	0	24.5	266	0	0	1,084
BOM	0	0	0	0	33.3	6	66.7	12	18
2000									
HUM	2.7	35	13.2	171	27	349	57	739	1,294
HAL	14.3	36	33.5	84	31.1	78	21.1	53	251
RA	4.2	32	34.7	263	43.6	331	17.5	133	759
API	100	8	0	0	0	0	0	0	8
MEL	21.2	72	19.8	67	36.7	121	23.3	79	339
MIC	0	0	0	0	0	0	0	0	0
BOM	0	0	0	0	100	13	0	0	13
1995									
HUM	18.1	30	16.9	28	14.5	24	50.6	84	166
HAL	3.8	5	65.8	101	15.2	24	17.1	27	158
RA	21.6	8	35	13	29.7	11	13.5	5	37
API	68.2	15	13.6	3	0	0	18.2	4	22
MEL	9.2	17	2.6	5	10.2	20	78.1	153	196
MIC	0	0	0	0	66.7	2	33.3	1	3
BOM	75.5	83	6.4	7	2	2	16.4	18	110

TABLE 3. Years of pollinator observation, rainfall total for critical months of growing season (January through March) and total growing season rainfall occurring from July of the previous calendar year to June of the study year, with an average rainfall of 34.3 cm and mean annual temperatures with an average annual temperature of 17.54 Celsius.

Year	Rainfall Total for J, F, M (cm)	Rainfall Total for Growing Season (cm) Wet/Dry Above/Below 34.3 cm	Temp Mean Annual Temp 17.54 Celsius
2008	14.22	Dry 27.61	High 18.69
2000	16.87	Dry 19.96	High 21.91
1995	44.65	Wet 54.89	Slightly Low 17.52
1994	20.27	Dry 30.61	Moderate 18.28
1993	53.83	Very Wet 72.31	High 18.88
1992	33.17	Wet 39.93	High 19.14
1991	33.33	Wet 35.74	Moderate 18.29
1990	12.75	Dry 19.79	High 18.66
1989	11.91	Dry 21.03	High 18.83

TABLE 4. The results of linear regression analysis of abundance for primary pollinators standardized by hours of observation correlated to mean annual precipitation for the year of observation and correlated to the mean annual precipitation for the previous year of observation (Asterisk * indicates a significant value of < 0.05, a double asterisk ** indicates a significant value of < 0.01, based on Rohlf and Sokal 1995).

Pollinators	Mean Annual Precipitation for Year of Observation		Mean Annual Precipitation for Year Prior to Observation	
	r value	degree of freedom	*r* value	degree of freedom
Hummingbirds	.71	5	.56	5
Sweat bees	.84	3	.62	3
Acton giant flower-loving flies	.67	5	.61	5
Western honey bees	.35	4	.74	4
Longhorned digger bees	1**	2	.78	2
Long-tongued digger bees	.1	5	.50	5
Bumble bees	.26	4	.1	4
Butterflies and moths	.68	3	.92*	3
White-lined sphinx moths	.22	3	.22	3
Native bees collectively	.68	4	.80	4

PHOTOGRAPHS OF POLLINATORS

Acton giant flower-loving fly, *Rhaphiomidas acton* (Mydidae), male.

Sweat Bee, *Augochlorella pomoniella* (Halictidae)

Digger Bees (Apidae).

Anthophora (subgenus *Heliophila*) sp.

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