

ECOLOGICAL SEPARATION IN FORAGING SCHEDULE AND FOOD TYPE BETWEEN POLLINATORS OF THE CALIFORNIA WILDFLOWER, *CLARKIA XANTIANA* SSP. *XANTIANA*

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Abstract. The co-occurrence of several dimensions of resource separation between coexisting consumers strengthens the hypothesis that the separation arose from and/or ameliorates interspecific competition. The two most common pollinators of the California endemic plant *Clarkia xantiana* ssp. *xantiana* (Onagraceae), the bees *Hesperapis regularis* (Melittidae) and *Lasioglossum pullilabre* (Halictidae), are known to partition flower resources by flower colour. Here we asked whether *H. regularis* and *L. pullilabre* also partition flower resources by diurnal foraging schedule and by food type (pollen versus nectar). We also quantified diurnal patterns of nectar availability, expected to be related to foraging schedules and forager responses to flower colour. The diurnal schedules of the two species differed distinctly and significantly. The majority of *L. pullilabre* foraging visits occurred before midday, while the majority of *H. regularis* visits occurred afterwards. The two species foraged for alternative food types at significantly different frequencies—nectar and pollen approximately equally frequently for *H. regularis*, pollen almost exclusively for *L. pullilabre*. Nectar standing crop declined with time of day, but it did not clearly reflect or explain previously identified colour-morph preferences. The major pollinators of *C. xantiana* ssp. *xantiana* exhibit multiple forms of ecological separation that likely reduce the intensity of competition for floral resources.

Keywords: Pollination, resource partitioning, coexistence, foraging, solitary bees, nectar

INTRODUCTION

Flowers of insect-pollinated plants are often shared as food sources by diverse pollinator assemblages (e.g. MacSwain et al. 1973, Real 1981, Eckhart 1992, Torres and Galletto 1998, Kandori 2002; reviewed in Waser et al. 1996) that might be expected to experience interspecific competition (Palmer et al. 2003). Circumstantial evidence of such competition is the ecological separation of coexisting pollinators known to occur by space (Herrera 1995, Emms and Arnold 2000), diurnal time (Real 1981, Cotton 1998, Stone et al. 1999), season (MacSwain et al. 1973, Heinrich 1976, Ginsberg 1983), food type (MacSwain et al. 1973, Tepedino and Parker 1982), flower sex expression (Eckhart 1992), flower colour (Paige and Whitham 1985, Emms and Arnold 2000, Medel et al. 2003), flower shape (Inouye 1978, Graham and Jones 1996), and ambient temperature (Willmer 1983).

Frequent ecological separation suggests that pollinator competition is important and widespread, though little is known about direct consequences of competition and resource partitioning for pollinator abundance and community structure (Steffan-Dewenter and Tschardt 2000, Goulson 2003, Palmer et al. 2003). It remains poorly resolved whether ecological separation of pollinators represents (1) incidental species differences that do not affect species interactions, (2) incidental species differences that facilitate competitor coexistence, or (3) species differences that evolved because they reduce interspecific competition.

Clarkia xantiana ssp. *xantiana* is a California-endemic winter annual that possesses a diverse bee assemblage of flower visitors but receives most visits and pollination services from three species: *Clarkia* specialist *Hesperapis regularis* Cresson (Melittidae), *Clarkia* specialist *Ceratina sequoiae* Michener (Apidae), and *Clarkia* near-specialist *Lasioglossum pullilabre* (Vachal) (Halictidae) (Moeller 2005, Eckhart et al. 2006). *Clarkia xantiana* ssp. *xantiana* populations are polymorphic in flower colour. Most populations consist of a majority of individuals with red spots at the centres of pink petals and a substantial

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minority of individuals with unspotted petals, while some populations have higher frequencies of unspotted than spotted morphs (Eckhart and Geber 1999; Eckhart et al. 2006). The three bee species listed above exhibit contrasting frequency-dependent preferences for flower colour morphs. The most common and widespread species, *H. regularis*, prefers to visit locally common morphs, while the less common *L. pullilabre* and *C. sequoiae* prefer locally rare morphs (Eckhart et al. 2006). Some resource competition models predict such contrasting preferences, as, for example, when the most abundant pollinator species is expected to prefer the most common (and easier to remember and forage on) flower morph, making it more profitable for less abundant species to prefer rare flower morphs (Possingham 1992; Mesterson-Gibbons 1992, Rodríguez-Gironés and Santamaría 2004). It is therefore likely that these pollinators effectively partition floral resources via contrasting frequency-dependent preferences for floral variants.

The present study investigates whether other forms of ecological separation occur in the pollinator assemblage of *C. xantiana* ssp. *xantiana*, specifically between the two most common pollinators, *H. regularis* and *L. pullilabre*. Separation in diurnal foraging schedule could, hypothetically, explain contrasting frequency-dependent flower colour preferences. If the species that prefers the locally common flower colour morph, *H. regularis*, forages earlier in the day than *L. pullilabre*, then *L. pullilabre* may prefer the rare flower colour morph because it retains greater food rewards. Apart from this specific scenario, finding multiple forms of ecological separation in the same system would strengthen the inference that separation is related to competition, either as a direct response or as species differences that facilitate coexistence though they evolved for other reasons. In other words, as more axes of separation are found, it becomes less plausible that ecological separation is independent of competition.

Interspecific separation in resource use is usually hypothesized to involve separation by habitat, time, and/or food type (Amarasekare 2003, Kronfeld-Shor and Dayan 2003). Separation of *H. regularis* and *L. pullilabre* on *C. xantiana* ssp. *xantiana* may occur in all three forms. The above-mentioned flower colour preferences can be considered segregation by habitat (Possingham 1992). A survey of pollination of the genus *Clarkia* (MacSwain et al. 1973) hints that, at a coarse scale and across several *Clarkia* species, the foraging of this study's focal bee species may differ temporally (*L. pullilabre* being active very early in the day) and in food type (*L. pullilabre* taking pollen almost exclusively; *H. regularis* frequently taking nectar as well). Note that these reported diurnal patterns contrast with the scenario we propose to explain flower colour preferences of *C. xantiana* ssp. *xantiana*'s pollinators.

Here we address three questions. First, does the foraging of *H. regularis* and *L. pullilabre* on *C. xantiana* ssp. *xantiana* occur on distinct diurnal schedules? Second, do individuals of these species forage for *C. xantiana* ssp. *xantiana*'s food resources (pollen and nectar) at different frequencies? Finally, do patterns of daily foraging and food-type selection, plus the diurnal schedule of nectar availability in *C. xantiana* ssp. *xantiana* populations, help explain bees' contrasting frequency-dependent flower colour preferences?

MATERIALS AND METHODS

Study species

The winter annual *Clarkia xantiana* A. Gray (Onagraceae) is endemic to inland central and southern California, and populations are most frequent in the Kern River drainage of the southern Sierra Nevada (Eckhart and Geber 1999). Subspecies *xantiana* is self-compatible but highly outcrossing, in contrast to the highly self-pollinating subspecies *parviflora* (Lewis and Lewis 1955, Moore and Lewis 1965, Raven and Lewis 1992, Runions and Geber 2000). Populations of *C. xantiana* ssp. *xantiana* occur mainly in loose slopes in grassland, pine-oak savannah, and chaparral. Flowering across the geographic range occurs from late April through early July, with single populations flowering for several weeks. As in other outcrossing species of *Clarkia*, the protandrous, four-petaled flowers persist several days (Lewis and Lewis 1955, MacSwain et al. 1973, pers. obs.). The eight anthers dehisce over several hours immediately following anthesis, complete dehiscence sometimes taking more than 1 day, and anthers present pollen (until bees remove it) for several days, as filaments gradually wither. Several (usually about 7) days after anthesis, the style reaches its maximum length and the four stigma lobes open fully and become receptive (Runions and Geber 2000). If stigmas do not receive pollen, they remain receptive for up to a week. If they do receive pollen, then they generally wither by the next day. We considered flowers to be in "male phase" before stigmas became receptive and considered them in "female phase" as soon as stigmas became receptive.

Hesperapis regularis (Melittidae) and *Lasioglossum* (*Evyllaesus*) *pullilabre* (*pullilabris*) (Halictidae) are both considered "*Clarkia* bees" (MacSwain et al. 1973) though they differ in their degree of food-plant specialization. *Hesperapis regularis*, a strict oligolege on the genus *Clarkia*, is restricted to low- and mid-elevation mountainous areas in cismontane southern California and in a ring around California's Central Valley (Burdick and Torchio 1959, MacSwain et al. 1973). This range coincides with the region of greatest *Clarkia* abundance and diversity (Lewis and Lewis 1955). Female *H. regularis* provision their single-cell ground nests exclusively with *Clarkia* pollen, while male *H. regularis* search for potential mates in patches of *Clarkia* flowers, visit *Clarkia* flowers for nectar,

and use *Clarkia* flowers as resting sites. *Lasioglossum pullilabre* has a geographic range that overlaps with *H. regularis*' range but also extends north of California, and it sometimes collects pollen from genera besides *Clarkia*; where *L. pullilabre* does take *Clarkia* pollen it only takes *Clarkia* pollen (MacSwain et al. 1973, Moeller 2005). *Lasioglossum pullilabre* visitors to *Clarkia* flowers are mainly female (MacSwain et al. 1973, Moeller 2005).

Foraging schedules and food type

For this investigation we studied pollination in seven *C. xantiana* ssp. *xantiana* populations at elevations between 600 and 950 m (Fig. 1). At the easternmost population (Middle Kern), random transect sampling indicated that unspotted flower-colour morphs constituted a slight majority (55%), while at the other six sites, spotted morphs were in the majority (75-85%), (Eckhart et al. 2006; D. Carter, unpublished data). At each study population we spent one day, between Julian days 150-162, observing pollinators for 20 minutes of each hour, from 0700 to 1500 hours solar time. During each 20 min observation period, 1-3 observers watched separate haphazardly selected patches of 10 plants and recorded the identity, number of flowers visited, and food type (pollen, nectar, or both pollen and nectar) for each individual forager (but without scoring colour-morph frequencies in patches, the flower-colour phenotypes of plants visited, or forager sex). We distinguished visits by *H. regularis*, *L. pullilabre*, and nine other visitor taxa, including *Ceratina sequoiae* and *Bombus* spp. (Apidae). The activity of the two focal species accounted for 70% of foragers. For each of the seven site-date combinations, we estimated the visitation rates (visits per 10 plants per 20 min) by *H. regularis* and *L. pullilabre* during each sampling period by averaging across observers' findings. Across observation periods and populations, ambient air temperature (in full

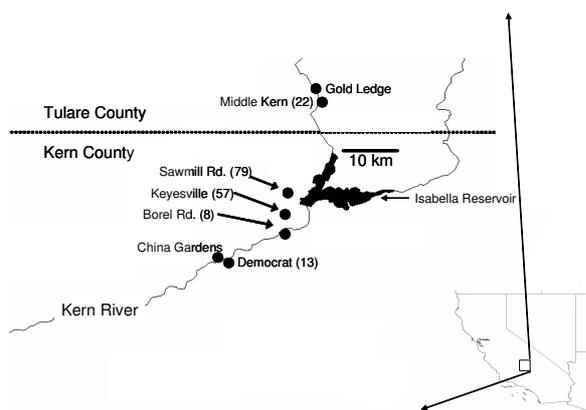


FIG. 1. Locations of *C. xantiana* ssp. *xantiana* populations (in California, USA) used for pollinator observations and nectar analysis.

sun, approx. 1 meter above ground level) ranged from 16°C to 39°C (median = 33°C). Temperature rose until 1100 or 1200 hours and then levelled off, except at one site (Sawmill Road) where temperature declined after midday with the arrival of a rare summer cold front (Fig. 2). The close association between temperature and time of day prevented our assessing possible independent effects of temperature on pollinator activity.

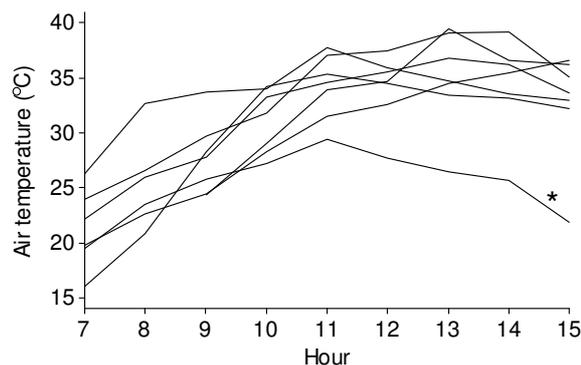


FIG. 2. Daily courses of ambient air temperature at seven sites where pollinator activity was scored. Each line connects temperature estimates at a single site. The asterisk marks data from the Sawmill Road site (see text).

We analyzed ln-transformed visitation rates with an ANOVA that included site-date combination (with seven levels) as a random blocking factor, and two crossed, fixed factors: bee species (*H. regularis* or *L. pullilabre*) and time of day (with nine levels). The main question in this analysis was whether the two focal bee species differed in diurnal foraging schedule, a question assessed by species by time of day interaction term.

We evaluated possible differentiation in food-type foraging by performing χ^2 tests of heterogeneity. We simplified foraging observations by placing them into two categories, (1) nectar or nectar plus pollen versus (2) pollen alone, to distinguish foragers collecting some nectar from those that did not. We restricted statistical testing to the two study sites where *H. regularis* and *L. pullilabre* were sufficiently common that all cells in the analysis had expected frequencies greater than 5.

Diurnal variation in nectar standing crop

We quantified variation in *C. xantiana* ssp. *xantiana* nectar standing crop at three of the seven sites (two majority-spotted sites—China Gardens and Democrat—and the unspotted-majority site, Middle Kern). At each site we collected nectar on a single day from 120 flowers, 40 each at 0700, 1100, and 1500 hours, with 20 male-phase and 20 female-phase flowers in each set of 40. At each time interval we sampled flowers by selecting two individuals at each of 10 haphazardly selected positions:

one individual of each flower colour morph, and one female-phase flower and the nearest male-phase flower from each individual. This sampling design was not intended to produce nested pairs of plants for comparison but rather to produce representative, equal-sized samples of spotted- and unspotted-flowered plants. We therefore ignored spatial structure in sampling, a decision expected to make our statistical tests more conservative.

We used McKenna and Thomson's (1988) method to estimate total nectar sugar in small volumes of *C. xantiana* ssp. *xantiana* nectar. In brief, we collected nectar in the field by gently squeezing flower receptacles and using filter paper wicks to absorb nectar. We allowed wicks to dry and then stored them individually in airtight containers. In the lab we dissolved nectar sugar from the wicks by placing them in known volumes of boiling distilled H₂O and then mixed sugar solutions with Anthrone reagent (Sigma, St. Louis, MO, USA) in concentrated H₂SO₄. Linear regressions of absorbance at 620 nm on the concentration of sucrose standards allowed us to estimate nectar sugar in field samples.

We transformed sugar content (in μg) into natural logarithms and then analyzed the data with ANOVA, with site (including day) as a random factor, and with time and petal spotting as fixed factors. As conclusions from the analysis did not differ whether we assigned petal spotting according to the presence of spots (spotted versus unspotted) or relative to local morph frequency (common versus uncommon), we present the absolute assignment. Accidents during sugar analysis reduced the total sample size of male-phase flowers from 180 to 176.) Data for each sex phase were analyzed separately. Petal length correlated with nectar sugar (both variables ln-transformed) in the Middle Kern population but not the others, and it had no significant effect as a covariate in the complete analysis. Therefore we did not include it.

RESULTS

Foraging schedules and food type

Hesperapis regularis and *L. pullilabre* used *C. xantiana* ssp. *xantiana*'s floral resources on different daily schedules. *Lasioglossum pullilabre* foragers were most active before midday, while *H. regularis* foragers were most active from late morning through mid afternoon (Fig. 3). The time-of-day by species interaction was highly significant (Tab. 1). The visit rate of *H. regularis* was significantly greater than that of *L. pullilabre* (Tab. 1, Fig. 3), *H. regularis* accounting for approximately five times as many foragers (452 of 770) as *L. pullilabre* (90 of 770). The former species was also more widespread, being found at all seven sites, compared to five for *L. pullilabre*. There was no overall main effect of time of day on the combined visit rate of the two species, but variation among site-day combinations was large and significant (Tab. 1).

TABLE 1. Analysis of variance in forager visit rate to flowers (visits per 10 plants per 20 min).

Source	df	SS	MS	F
Site	6	26.28	26.28	16.44***
Species	1	16.65	16.65	62.48***
Time-of-day	8	2.11	0.26	0.99
Species X Time-of-day	8	11.79	1.47	5.53***
Error	102	27.18	0.27	
Total	125			

*** $P < 0.001$

The two species also differed in their pattern of foraging for alternative floral resources (Tab. 2). Within foraging bouts, *Hesperapis regularis* foragers collected nectar or nectar plus pollen approximately as often as they collected pollen alone, while almost all *Lasioglossum pullilabre* foragers sought only pollen. These differences between species were highly statistically significant in both *C. xantiana* ssp. *xantiana* populations analyzed (China Gardens: $\chi^2_{[1]} = 21.67$, $P < 0.0001$; Democrat: $\chi^2_{[1]} = 36.75$, $P < 0.0001$).

TABLE 2. Frequencies of flower resource selection by individual *Hesperapis regularis* and *Lasioglossum pullilabre* foragers in two *Clarkia xantiana* ssp. *xantiana* populations.

Site		<i>H. regularis</i>	<i>L. pullilabre</i>
China Gardens	Nectar or nectar plus pollen	47	1
	Pollen only	56	35
Democrat	Nectar or nectar plus pollen	76	0
	Pollen only	49	31

Diurnal variation in nectar standing crop

Nectar standing crop varied among flowers from undetectable (and considered zero) to almost 1 mg, with a mean of approximately 20 μg . The only consistently significant source of variation in nectar standing crop was time-of-day (Tab. 3), with afternoon declines in nectar sugar, on average (Fig. 4). For flowers in male phase, there was also significant among-site variation (Tab. 3, Fig. 4). Though there are hints of interesting variation associated with flower colour—for example, reverses in which flower colour morph had more sugar between mornings and afternoons at the two spotted-majority sites (China Gardens and Democrat)—petal spotting and the interaction between time of day and petal spotting had no significant effects on nectar sugar (Tab. 3, Fig. 4).

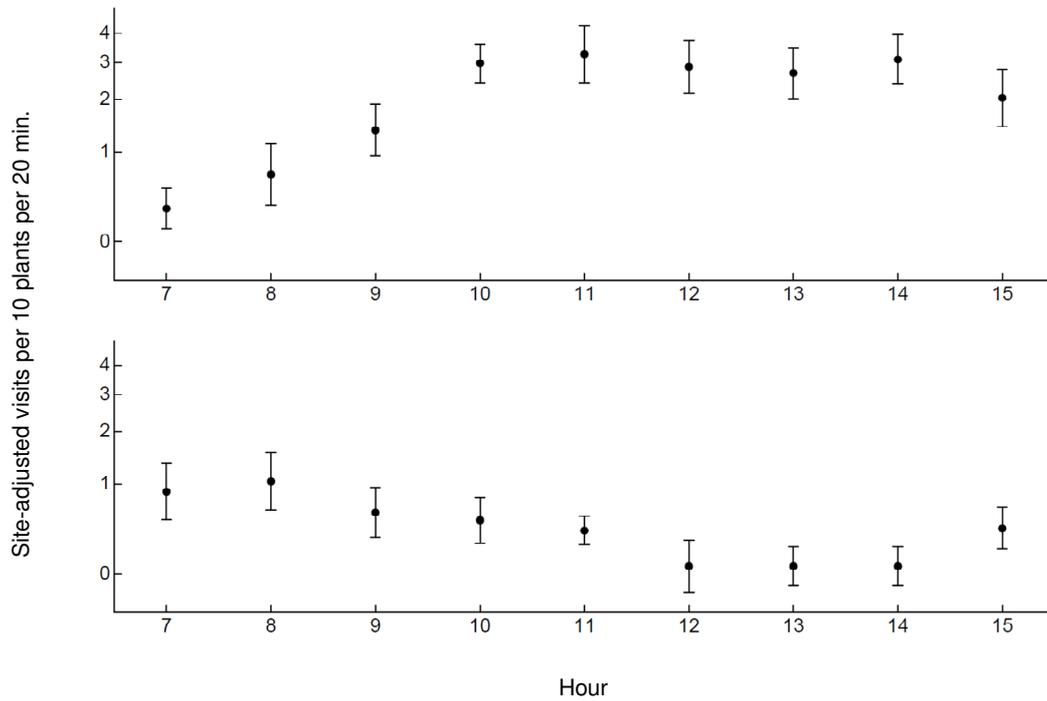


FIG. 3. Diurnal schedules of the visit rates of the two most common pollinator species of *C. xantiana* ssp. *xantiana*. Upper panel: *Hesperapis regularis*. Lower panel: *Lasioglossum pullilabre*. Symbols are least-squared means adjusted for among-site variation. Error bars represent ± 1 standard error.

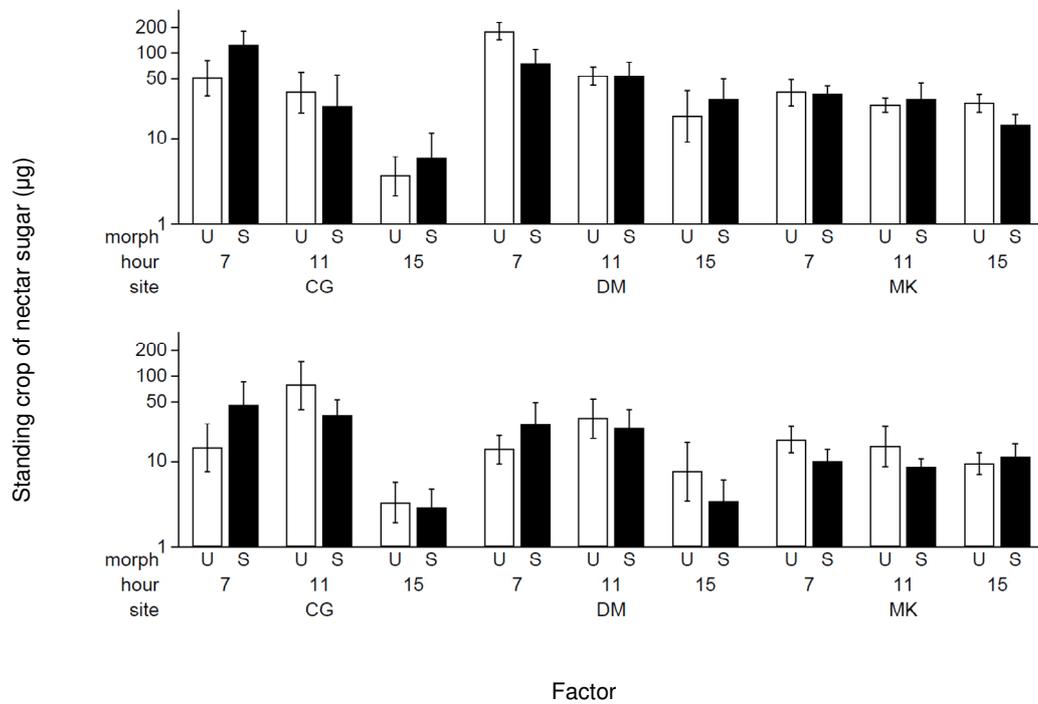


FIG. 4. Per-flower nectar standing crop in *C. xantiana* ssp. *xantiana*, measured as weight of sucrose equivalents, for male-phase (top panel) and female-phase (bottom panel) flowers, unspotted (U) and spotted (S) flower color morphs, at three sampling times (0700, 1100, and 1500 hours), at three sites (CG: China Gardens, DM: Democrat, MK: Middle Kern). Bars are means. Error bars represent ± 1 standard error.

TABLE 3. Analysis of variance in nectar sugar per flower in three *Clarkia xantiana* ssp. *xantiana* populations.

	Source	df	SS	MS	F
Male-phase flowers	Site	2	4.62	2.31	5.69**
	Time-of-day	2	15.90	7.95	19.59***
	Petal spotting	1	0.001	0.001	0.00001
	Time-of-day x Petal spotting	2	0.048	0.024	0.06
	Error	168	27.18	0.27	
	Total	175			
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Female-phase flowers	Site	2	0.50	0.25	0.47
	Time-of-day	2	14.79	7.40	13.94***
	Petal spotting	1	0.12	0.12	0.23
	Time-of-day x Petal spotting	2	1.26	0.63	1.19
	Error	172	91.23	0.53	
	Total	179			

** $P < 0.01$; *** $P < 0.001$

DISCUSSION

Ecological separation

In *Clarkia xantiana* ssp. *xantiana* populations, the bee *Hesperapis regularis* differs from *Lasioglossum pullilabre* in foraging later in the day and in foraging for both pollen and nectar, rather than almost exclusively for pollen. An earlier study discovered that these bees also use *Clarkia xantiana* ssp. *xantiana* flower resources differently by exhibiting contrasting preferences for flower-colour morphs (Eckhart et al. 2006). Thus at least three forms of ecological separation occur between these species. The co-occurrence of so many forms has rarely been documented, and it suggests that species differences likely ameliorate competition and facilitate coexistence. These findings support the idea that competition plays an important role in structuring pollinator communities (Palmer et al. 2003).

Confirming that ecological separation affects species coexistence ultimately requires a demonstration of long-term population-dynamic consequences of competition (Thomson 1980, Palmer et al. 2003). It is also pertinent to investigate shorter-term responses, to ask whether *H. regularis* and/or *L. pullilabre* modify their diurnal activity (i.e. shift their temporal niches) in response to the abundance of other pollinators (Pleasants 1981, Thomson et al. 1987, Palmer et al. 2003). As *H. regularis* exhibited higher visitation rates in this study than *L. pullilabre*, one

might expect the foraging of the rarer species to have shifted earlier in the day at sites where *H. regularis* exhibited especially high visit rates. Among the five sites where we observed both species, there were negative correlation coefficients between *H. regularis* activity (summed across hours) and the mean ($r = -0.805$, $P = 0.10$) and mode ($r = -0.943$, $P = 0.016$) foraging hour of *L. pullilabre*, as expected on this hypothesis.

It is possible that diurnal differences between these pollinators evolved in response to predictable competition, as their association with the genus *Clarkia* evolved. Investigating evolutionary responses to competition requires reconstructing the phylogeny of character evolution and species interactions (Webb et al. 2002), characterizing natural selection under interspecific competition (e.g. Schluter 2003), and/or investigating geographic patterns of character displacement (e.g. Schluter 1986). The near ubiquity of *H. regularis* as a *Clarkia* pollinator in California (MacSwain et al. 1973) suggests that *L. pullilabre* (and other less abundant *Clarkia* bee species) frequently coexist with it. It should be possible to search for evidence of geographic character displacement of foraging schedules and food type between *H. regularis* and *L. pullilabre*, comparing behaviour in regions of allopatry (e.g. the central Coast Ranges of California, where *L. pullilabre* appears rare or absent) with behaviour in sympatry.

Scaling relations may be informative in interpreting the behaviour and coexistence of these and other *Clarkia* bees. *Hesperapis regularis* is about 50% longer (ca. 11–12 mm) than *L. pullilabre* (ca. 8 mm). Body size would be expected to affect bee thermal relations and temperature relations (Stone et al. 1999). In this study the larger-bodied *H. regularis* foraged later, at higher temperatures, than the smaller *L. pullilabre*. All else equal, larger-bodied bees would tend to lose heat more slowly and therefore perform better in cold conditions, at a cost of greater risk of overheating in warm conditions (Stone and Willmer 1989, Stone 1993). This is in accord with the frequent finding (in contrast to this study) that larger-bodied bees in temperate areas tend to forage earlier in the day than smaller-bodied species (e.g. Heinrich 1976, Real 1981, Willmer 1983, Graham and Jones 1999). But while small-bodied bees might have reduced risks of over-heating in hot conditions, hot, dry conditions might constrain foraging by small bees via the risk of excess water loss, created by small bees' high surface areas per unit volume (Willmer 1988). Reduced foraging by *L. pullilabre* in hot afternoons is consistent with this idea, raising the possibility that the diurnal foraging differences observed in this study arose from water relations physiology, not resource competition (or not resource competition alone).

Nectar dynamics and flower colour

If *H. regularis* foragers, which express a preference for locally common flower-colour morphs (Eckhart et al. 2006), were active earlier in the day than *L. pullilabre* foragers, and if both species commonly collected nectar, then *L. pullilabre*'s rare-morph preference might be explained because the rare morph would offer higher nectar rewards later in the day. This simple scenario does not apply. Our pollinator observations showed that the general species differences noted by MacSwain et al. (1973) apply specifically to these bees' behaviour in *C. xantiana* ssp. *xantiana* populations. *Lassiglossum pullilabre* individuals forage earlier in the day than *H. regularis* individuals, and they primarily collect pollen (though they do visit female-phase flowers and often deposit pollen on stigmas when they do, Eckhart et al. 2006). Thus our analysis of nectar standing crop would not be expected to reflect, and cannot explain, morph-specific pollinator visitation. The findings instead suggest that early-day visits by *L. pullilabre* (perhaps primarily by females) deplete pollen of the rare flower-colour morph, leading *H. regularis* females to favour the common morph for pollen collection. Perhaps *H. regularis* foragers (or perhaps just males) do not discriminate by colour morph when they collect nectar. As *Clarkia* pollen is an essential resource for *Clarkia* specialists, it should be informative to estimate the schedules of pollen release and pollen standing crop in *C. xantiana* and other *Clarkia* (cf. Stone et al. 1996, Stone et al. 1999). What the nectar data do show is diurnal declines and only hints of more interesting dynamics involving flower colour. Nectar standing crop, of course, should be influenced by nectar secretion rates and by nectar collection rates by all pollinator species (Pleasants and Zimmerman 1983), not just nectar collection by the two most frequent visitor species. Manipulative experiments and additional careful observations would be necessary to tease apart and quantify these separate influences.

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