NECTAR SECRETION AND BEE GUILD CHARACTERISTICS OF YELLOW STAR-THISTLE ON SANTA CRUZ ISLAND AND LESVOS: WHERE HAVE THE HONEY BEES GONE?

Santa Cruz ve Midilli Adasinda Güneşçiçeği Bitkisinde Balözü Salgısı ve Arı Çeşitliliği: Bal Arıları Nereye Kayboldu?

(Genişletilmiş Türkçe Özet Makalenin Sonunda Verilmiştir)

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Anahtar kelimeler: *Centaurea solstitialis,* istilacı tür, Midilli, tozlaşma, Santa Cruz adası, Güneşçiçeği

ABSTRACT: We compared nectar secretion rates and bee guilds of yellow star-thistle, *Centaurea solstitialis*, on Santa Cruz Island (USA) and the Northeast Aegean Island of Lesvos (Greece). This plant species is non-native and highly invasive in the western USA but native to Eurasia (including Lesvos). "Nectar flow" was assessed by measuring nectar volumes in florets of flower heads covered with mesh bags (preventing visitation by bees); "nectar standing crop" data were taken from open (unbagged) flower heads to which all bees could gain access. We censused bees at *C. solstitialis* during comparable periods on both islands and determined the bee guild composition of the plant on Lesvos. Significant differences in nectar levels occurred between bagged and unbagged florets at each locale, especially during the period that pollinators were most common. Nectar flow and nectar standing crop volumes were lower on Lesvos than on Santa Cruz Island. The bee guild diversity at Lesvos was higher relative to Santa Cruz Island. Surprisingly, however, honey bees were not recorded during our monitoring periods on Lesvos.

INTRODUCTION

Yellow star-thistle, *Centaurea solstitialis* L., a highly invasive, non-native plant species, now inhabits much of the extreme western United States, especially California (Pitcairn et al. 2006). It is an obligate outcrossing species with its origin in Eurasia, including Turkey (Sun and Ritland 1997, Uygur et al. 2004). Because of its breeding system requirements, the ability to attract pollinators is critical to its reproductive success. Plants can attract pollinators (bees) with rewards that include nectar, pollen and oils (Proctor et al. 1996), and may depend upon these inducements to "market" themselves to potential pollinators (Chittka and

Schürkens 2001). Nectar is one such inducement that may be a key attribute of a successful plant invader (Ghazoul 2002), and at least one experimental study shows that non-native flowering plant species can draw potential pollinators away from native plants to effect pollination (Brown et al. 2002). The other requirement is that at least one reliable pollinator species is available to take advantage of the reward; in the case of *C. solstitialis*, the honey bee, *Apis mellifera* L., can serve in this role (Maddox et al. 1996, McIver et al. 2009).

We have been studying the relationship between honey bees and thistles for over two decades on Santa Cruz Island (SCI) where over 25 percent of the flowering plant species are non-native, including *C. solstitialis* which was first detected there in 1930 (Junak et al. 1995). This species is the near antithesis of the successful, self-compatible weed species predicted by Baker (1965) because of its dependence on strong-flying pollinators to effect pollination (Maddox et al. 1996, Sun and Ritland 1997, Gerlach and Rice 2003). Early studies on SCI showed that the exclusion of the non-native honey bee from flower heads of this species caused a significant decline in reproduction for *C. solstitialis* (Barthell et al. 2001). However, the same effect was not observed on the obligate outcrossing native gumplant, *Grindelia camporum* Greene, which drew relatively few honey bees to its flower heads (Thorp et al. 1994, Barthell et al. 2000). Another study on SCI of the self-compatible *Centaurea melitensis* L., or tocalote, demonstrated no seed set differences when honey bees were excluded from its flower heads (Porras and Álvarez 1999, Barthell et al. 2005). So, although Baker's hypothesis aptly describes this latter species' invasion success, *C. solstitialis* stands out as a clear exception to this generalization on SCI (but see Memmott and Waser 2002).

Honey bees were recorded on SCI in the late 1800s (Wenner and Thorp 1993 and 1994). By the year 2000 honey bee colonies had declined to below detectable levels there due to a biological control program (begun in December of 1993) that used the varroa mite, *Varroa destructor* Anderson & Trueman, to kill or disable developing and adult honey bees (Wenner et al. 2000); this ectoparasitic species had already established itself six years earlier in the United States and continues to be a major factor in the decline of commercial and feral honey bee colonies throughout the USA (Sammataro et al. 2000). A concomitant decline in seed set of *C. solstitialis* has accompanied this reduction in honey bee numbers (Barthell et al. 2004). *Centaurea solstitialis* became established in California during the mid-1800s (Hendry and Bellue 1936, Gerlach et al. 1998) and, in the western USA, its nectar has long been considered a favorite of honey bees and beekeepers alike (Pellet 1976). The strong association of honey bees with *C. solstitialis*, coupled with our studies cited above, suggest a mutualistic invasion mechanism by these two species (Barthell et al. 2001). This viewpoint is bolstered by the fact that both species are Eurasian in origin (Hickman 1993, Michener 2000).

In order to better understand the relationship between the invasive *C. solstitialis* and its most visible pollinator in California, the honey bee, we examined these species in a region where they are both native, predicting that they should remain close counterparts there (e.g., Olesen et al. 2002). The island of Lesvos (Greece), a Northeast Aegean island near the western coast of Turkey, was chosen for the comparison. Below, we present preliminary information on 1) "nectar flow" and "standing crop" levels of *C. solstitialis* over the course of a day, 2) bee visitation levels of this plant during the day, and 3) pollinator guild composition of *C. solstitialis* plants on Lesvos. This information is relevant to invasiveness since a self-incompatible plant species must 1) have an ability to attract (using nectar or other rewards) pollinators and 2) have a sufficient pool (guild) of pollinators to draw from in order to succeed in a new environment. Indeed, we intend that these avenues of investigation will inform future studies of plant invasion in island and mainland ecosystems, including in Greece, Turkey and the USA.

STUDY LOCALES

Lesvos, Greece (Latitude 39^{o}N–Longitude 26^{o}E)

The largest of the Northeast Aegean islands (Fig. 1a), Lesvos is 1,614 square km and 986 m at its highest point (Foufopoulos and Mayer 2007). Lesvos has a large, resident human population (ca. 100,000), and scientific history on the island dates back over two millennia with the marine biological studies of Aristotle near the ancient city of Pyrra (Tipton 2006). Our nectar and visitation studies were located near this same city, along the eastern shore of Kalloni Bay. Along with its many municipalities, Lesvos has an agricultural history that includes the production of grapes, wine, figs and, most recently, olives, as well as grazers (Marathianou et al. 2000, Dalaka and Petanidou 2006). Efforts spearheaded by one of us (TP) have yielded a growing base of knowledge about plant-pollinator communities on Lesvos (Petanidou and Lamborn 2005, Potts et al. 2006). Non-native species of plants and bees found on SCI are native to Lesvos and the surrounding region (Theophrastus 1916, Michener 2000), including the honey bee and its host plant *C. solstitialis*.

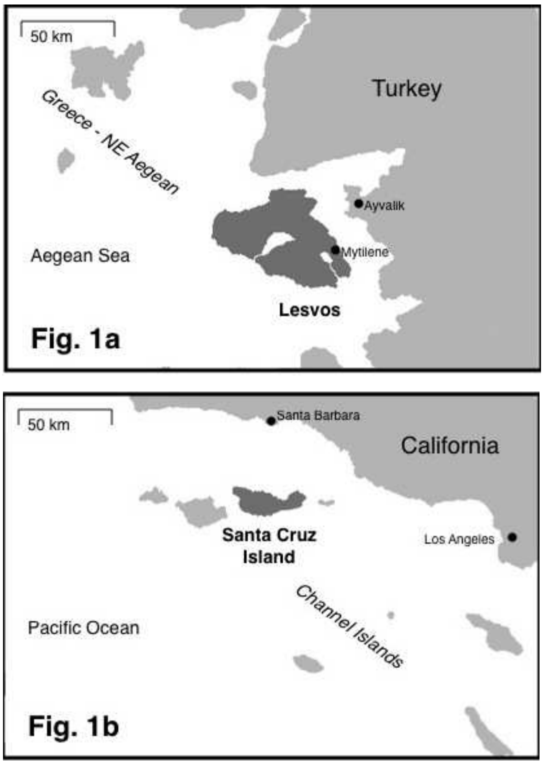

Figure 1. Maps showing Lesvos (a) and Santa Cruz Island (b) in relationship to the Turkish and US mainlands, respectively.

Santa Cruz Island, USA (Latitude 34^o N – Longitude 119^o W)

The largest of the eight Channel Islands, SCI is situated 30 km off the coast of southern California (Fig. 1b). The island is 249 square km in area and is 753 m at its highest point (Junak et al. 1995). SCI has an agricultural history that includes the introduction of several vertebrate species (pigs, sheep, cattle) and crops (grapes, hay, alfalfa, walnuts, almonds, vegetables) during 150 years of European settlement (Gherini 1997, 2005). Cattle ranching ceased in the 1980s and both sheep and pigs have been extirpated within the last decade. This agricultural period, however, is undoubtedly the source of several transported weed species, including *C. solstitialis* that was presumably carried onto the island with alfalfa seed, as in other areas of California (Hendry and Bellue 1936). The current study was carried out at the western edge of the Central Valley at the base of Portezuela grade.

MATERIALS AND METHODS

Nectar Flow and Standing Crop

In order to assess total nectar volumes available to nectarivores (including honey bees) during the day, nectar flow and standing crop levels were monitored at Lesvos on 16 June, 2007, and at SCI on 3 August of the same year. At each study locale, 15 plants were identified and tagged along a belt transect (≥ 1 m apart). Between 16:00 and 18:00, the evening prior to nectar collection, we marked and bagged two flower heads on each plant with a fine mesh bag that blocked visitors from accessing nectar. The following morning, the bag was removed from one of the flower heads to allow access by all visitors to its florets (“standing crop”), while the other bag was left on (“nectar flow”). The following day from 07:00 to 19:00 hours, we inserted 0.25µL capillary tubes into one floret on each flower head every two hours. After removing the nectar we measured the amount of nectar in the capillary tubes using digital, hand-held calipers. The readings were taken in millimeters and later converted into µL (Kearns and Inouye 1993). After nectar was removed from the bagged flowers, we immediately rebagged the flower head until the next collection time. After removing nectar we lightly marked the used florets with a Sharpie™ marker to ensure that a different floret was used during each collection period. The heights of all 15 transect plants (at each locale) were measured to the nearest cm to assess differences between populations at Lesvos and SCI.

Visitation Monitoring and Collections

Bee monitoring records were collected the day after nectar readings at both Lesvos (17 June) and SCI (4 August). As in previous studies (Barthell et al. 2000, Barthell et al. 2001, Barthell et al. 2005), monitoring was conducted by walking each transect (roundtrip) six consecutive times at a pace of five min for the entire transect (a total of 30 min per survey). Any visitors seen on flower heads were recorded according to family and genus, when possible. Each survey was repeated 4 times at the following start times: 09:00, 12:00, 15:00 and 18:00. The same 15 plants identified for nectar flow studies (above) were used in the visitation trials.

At Lesvos, collections of visitors were made (primarily) at adjoining patches of *C. solstitialis* (ca. 500 m from the visitation transect) near the study site at Pyrra. Additional collections were made on and near the campus of the University of the Aegean in Mytilene and in the vicinity of Kapi, near the northern apex of the island. These collections were compared with descriptions of existing collections for SCI (Rust et al. 1985, Thorp et al. 1994 and 2000), to determine the degree of overlap between *C. solstitialis*' pollinator guilds in its native and invaded habitats. At Pyrra, on 17 June, reciprocal collections were made by two of us (JFB and MLC) for concurrent 15 min intervals, with one person collecting from *C. solstitialis* and the other from the bush *Vitex agnus-castus* L. which was flowering among patches of *C. solstitialis*. These were conducted to assess if honey bees were in the area but demonstrating a preference for one species over the other one. Voucher specimens from our study are housed in the National Pollinating Insects Collections (USDA-ARS Bee Biology and Systematics Laboratory) in Logan, Utah, and in collections at the University of Central Oklahoma in Edmond, Oklahoma.

Nectar Quality

To assess nectar quality we used all 15 of our study plants and an additional five plants, bagging three flower heads per plant. We allowed them to build up their nectar supply throughout the last day (during monitoring of visitors) before cutting the stems below the flower heads and transporting them in Ziploc^{TM} bags to the laboratory. We kept the bags cool until we were able to begin removing the nectar. We did so by centrifuging flower heads in a 10 mL tube at 2500 rpm for five min per sample (Kearns and Inouye 1993). A sample was comprised of three inverted flower heads (wedged by their stems between the centrifuge tube opening and a rubber cork). A pipette was then used to transfer the resulting nectar from the tubes to a handheld refractometer for reading the concentration of sucrose equivalents using a BRIX scale (Kearns and Inouye 1993).

Analyses

Repeated measures MANOVAs were used to test for Island, Time of day, and Island x Time interaction effects on nectar flow and standing crop levels. Nectar flow and standing crop levels were tested for differences at sampling time intervals with two-tailed t-tests (see Fig. 2); the same test was used to differentiate plant heights. No statistical tests of nectar quality readings were conducted because the higher values of some samples could not be read due to the upper limit (50%) of our refractometer.

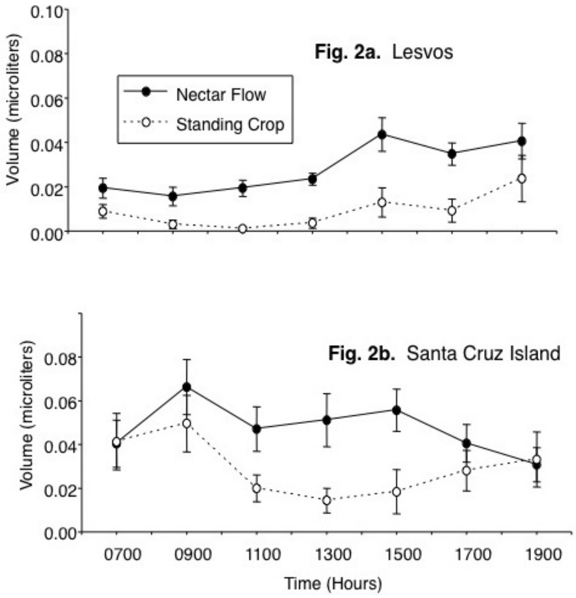

Figure 2. Nectar flow and standing crop of *Centaurea solstitialis* over 12 hour periods on Lesvos (a) and Santa Cruz Island (b).

RESULTS

Nectar Flow and Standing Crop

According to the repeated measures MANOVA, for nectar flow, there was a significant Island effect (F = 9.19; df = 1, 28; P = 0.005) and Island x Time interaction effect (F = 2.51; df = 6, 23; P = 0.051). Time by itself was not a significant factor (F = 1.41; df = 6, 23; P = 0.2538). For standing crop, there was only a significant Island effect (F = 7.19; df = 1, 28; P = 0.012). Neither the Time effect (F = 2.04; df = 6, 23; P = 0.101) nor Island x Time interaction effect was significant (F = 1.65; df = 6, 23; P = 0.178).

At Lesvos, nectar flow levels in *C. solstitialis* florets were significantly different from standing crop levels at each hourly interval except for the first (07:00) and last (19:00) ones according to two-tailed t-tests (Fig. 2a): 07:00 (t = -1.93, df = 28, P = 0.06), 09:00 (t = 2.75, df = 28, P = 0.01), 11:00 (t = 4.87, df = 28, P = 0.001), 13:00 (t = 5.64, df = 28, P = 0.001), 15:00 (t = 3.06, df = 28, P = 0.005), 17:00 (t = 3.55, df = 28, P = 0.001) and 19:00 (t = 1.28, df = 28, P = 0.21). The greatest difference between these treatments occurred at 15:00 (0.031 µL). An overall decrease in average nectar flow levels occurred between 15:00 and 19:00 while the converse is shown for standing crop during the same time period (Fig. 2a). Overall, nectar flow (as well as standing crop) never exceeded 0.050 µL during the 12 hr monitoring period and it exceeded 0.040 µL only twice (at 15:00 and 19:00).

Readings of flow and standing crop treatments on SCI were only significantly different during the three middle monitoring periods (11:00, 13:00 and 15:00): 07:00 (t = -0.06, df = 28, P = 0.95), 09:00 (t = 0.92, df = 28, P = 0.36), 11:00 (t = 2.29, df = 28, P = 0.03), 13:00 (t = 2.75, df = 28, P = 0.01), 15:00 (t = 2.67, df = 28, P = 0.013), 17:00 (t = 0.981, df = 28, P = 0.34) and 19:00 (t = -0.16, df = 28, P = 0.88). The largest difference between treatments was at 15:00 (0.037 µL). As at Lesvos, an overall decline in nectar flow levels occurred between 15:00 and 19:00 while standing crop levels increased during the same time period (Figure 2b). Average nectar flow levels exceeded 0.050 µL at three sampling periods (09:00, 13:00 and 15:00) and were above 0.040 µL on all occasions but one (19:00).

Nectar Quality

A total of 20 flower head samples from the Pyrra transect on Lesvos were centrifuged for nectar. Of these, nine gave an average reading of 45.44% (± 1 SE = 1.24). The remaining 11 did not yield usable readings. At least five of these clearly exceeded the upper limit of the refractometer scale (50%). On SCI, seven of the 20 plant samples yielded an average reading of 45.14 (± 2.56); the remaining 13 samples did not yield usable readings and, of these, at least nine had also exceeded the limit of the refractometer scale.

Visitation Patterns

Bee visitation remained between 10 and 20 individuals per 30 min monitoring period at both Lesvos and SCI until the final sampling period (18:00) when SCI declined to zero (Fig. 3). Bee numbers peaked at 15:00 for both locales when 19 individuals were recorded at Lesvos and 18 at SCI. Temperatures taken at the outset of transect monitoring periods for Lesvos include the following: 27° C (09:00), 36° C (12:00), 39° C (15:00) and 32° C (18:00); these high temperatures were accompanied by a regular breeze. For SCI, temperatures were 23° C, 25° C, 26° C and 24° C for the same times. At Lesvos the day was clear while at SCI fog was present (as is typical) during the initial monitoring period. By the last monitoring period at SCI, our study plants were beginning to be shaded by nearby canyon walls. In addition, plants used during our study on Lesvos were generally much larger in size (122.40 cm ± 6.27) than those on SCI (52.83 ± 3.83); this difference was significant according to a two-tailed t-test (P = 0.001; t = 9.47) and reflects our observation that *C. solstitialis* plants were generally smaller in stature (and less dense) on SCI in 2007.

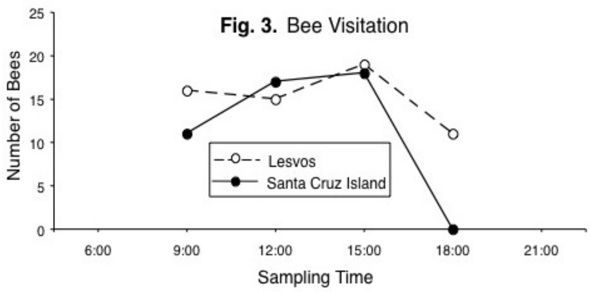

Figure 3. Total number of bees recorded on Lesvos and Santa Cruz Island at four sampling periods

Pollinator Guild (Lesvos Collections)

Table 1 shows that four families, 21 genera and 40 species are represented among our collections of bees at Lesvos: Andrenidae (one genus and two species), Apidae (six genera and 12 species), Halictidae (three genera and five species) and Megachilidae (11 genera and 21 species). Among the Apidae, the most commonly represented genus was *Eucera* (four species) but only one specimen of the honey bee (*Apis mellifera*) was collected at *C. solstitialis*. Two species of the genus *Lasioglossum* were identified within the family Halictidae. Among the Megachilidae, the most commonly represented genus was *Megachile* (eight species); no other genus was represented by more than three species.

Table 1. Yellow star-thistle bee guild composition based on collections from Lesvos, Greece, during June of 2007.

Bee Taxa		No.	%
Andrenidae			
	Andrena flavipes Panzer	1	0.5
	Andrena sp.	5	2.5
Apidae			
	Amegilla albigena (Lepeletier)	2	1.0
	Amegilla quadrifasciata (Villers)	1	0.5
	Apis mellifera L.	1	0.5
	Ceratina dallatorreana Friese	2	1.0
	C. aff. *chalybea* Chevrier	3	1.5
	C. chalcites Germar	1	0.5
	Eucera (*Hetereucera*) sp. #1	1	0.5
	Eucera (*Hetereucera*) sp. #2		1.0
	Eucera (*Synhalonia*) sp. #1	1	0.5
	Eucera (*Synhalonia*) sp. #2		1.0
	Pasites maculata Jurine	1	0.5
	Xylocopa iris (Christ)	1	0.5
Halictidae			
	Halictus resurgens Nurse	7	3.5
	Halictus aff. *polinosus* Sichel	3	1.5
	Lasioglossum ancillum Vachal	2	1.0
	Lasioglossum (*Evylaeus*) sp.	3	1.5
	Pseudapis bispinosa (Brullé)	1	0.5
Megachilidae			
	Afranthidium carduele (Morawitz)	2	1.0
	Coelioxys argentea Lepeletier	1	0.5
	Heriades crenulatus Lepeletier	1	0.5
	Hoplosmia bidentata (Morawitz)	46	23.0
	H. spinigera (Latreille)	2	1.0
	H. elegans Tkalcu	1	0.5
	Icteranthidium grohmanni (Spinola)	3	1.5
	Lithurgus chrysurus Fonscolombe	35	17.5
	Megachile albisecta (Klug)	4	2.0
	M. (*Eutricharaea*) *anatolica* Rebmann	4	2.0
	M. (*Eutricharaea) apicalis* Spinola	7	3.5
	M. (*Eutricharaea*) *pilidens* Alfken	1	0.5
	M. (*Eutricharaea*) sp.	1	0.5
	M. lefebvrei (Lepeletier)	16	8.0
	M. melanopyga Costa	1	0.5
	M. pilicrus Morawitz	22	11.0
	Osmia signata Erichson	2	1.0
	Pseudoanthidium lituratum (Panzer)	8	4.0
	P. reticulatum (Mocsary)	1	0.5
	Rhodanthidium septemdentatum (Latreille)	1	0.5
	Trachusa dumerlei (Warncke)	1	0.5
	Total: 40 species (21 genera and 4 families)	200	(-)

A total of 200 bee specimens were collected on *C. solstitialis* at Lesvos (Table 1). Of these, 160 (80.0%) were in the family Megachilidae; eighteen (9.0%) were in the Apidae, 16 (8%) in the Halictidae and six (3%) in the Andrenidae. Four species exceeded fifteen specimens during the collection period (all in the family Megachilidae): 1) *Hoplosmia bidentata* (Morawitz) (46 specimens), 2) *Lithurgus chrysurus* Fonscolombe (35), 3) *Megachile lefebvrei* (Lepeletier) (16), and 4) *Megachile pilicrus* Morawitz (22). Two species known to have occurred on SCI as non-native species, the honey bee (*Apis mellifera* L.) and the leafcutting bee *Megachile apicalis* Spinola, were both found on Lesvos; only one honey bee was collected, however, as opposed to seven specimens of *M. apicalis*.

During two, 15 min, reciprocal collections made on 17 June, MLC collected a single female *Megachile* sp. (no honey bees) on *C. solstitialis* while JFB collected five honey bees and one each of species in the genera *Megachile* (male), *Lasioglossum* (female) and *Xylocopa* (male) from 10:00 to 10:15 at *V. agnus-castus*. From 10:15 to 10:30, after exchanging species to monitor, JFB collected one each of a *Ceratina* species (male) and a *Hoplosmia* species (female) on *C. solstitialis* while MLC collected two honey bees and one specimen of a *Ceratina* species (female). In each case, honey bees were only collected on *V. agnus-castus*.

On several occasions we were able to observe an unidentified species of aphid (Homoptera) feeding in aggregations along stems of *C. solstitialis* plants near our study plot; the stems and associated flower buds were sometimes underdeveloped and/or discolored. Voucher specimens were collected for later identification and are currently being stored in the University of Central Oklahoma Invertebrate and Insect Collection in Edmond, Oklahoma.

DISCUSSION

Nectar Patterns

Significant differences between nectar flow and standing crop levels (during mid-day) on both Lesvos and SCI indicate that pollinators utilize substantial amounts of nectar during the warmer periods of the day. At both locales, the peak bee visitation time (15:00) corresponded to the greatest difference in nectar levels between nectar flow and standing crop. The lack of accumulated nectar volume at the outset of the day (07:00) on both Lesvos and SCI suggests that nectar reabsorption and/or variable secretion rates may be occurring during nocturnal and/or early morning periods. The congeneric *C. scabiosa* L. and *C. nigra* L., for example, are known to have reduced nectar production during periods of cool weather and overcast conditions (Lack 1982). Indeed, on SCI, where temperatures were relatively cool, a decline in nectar flow is revealed after 15:00 when the temperature was beginning to decline. It is also noteworthy that nectar levels were highest at both locales during the afternoon when the highest temperatures were recorded during our monitoring study (15:00); heat-induced nectar production has been described for at least one other Mediterranean plant species, *Thymus capitatus* Hoffmans (Petanidou and Smets 1996).

Perhaps the most conspicuous difference between the study locales is the higher overall nectar secretion levels at SCI relative to Lesvos. This pattern may reflect the effect of abiotic factors such as high temperature and wind that were both evident in the exposed, beachside location of our plant transect at Lesvos (through evaporative effects). The extremely high sucrose concentrations recorded for nectar at both Lesvos and SCI may also be an artifact of water loss from the nectar since concentrations taken earlier in the day were lower during an earlier study on SCI (Barthell et al., unpublished data). Such abiotic effects can influence plant nectar quality and, consequently, pollinator behavior (Peat and Goulson 2005). The occurrence of phloem-feeding aphids on these plants (absent in the western USA) may also be a contributor to reduced nectar volumes, and their influence should be examined in the future. Another factor may be the presence of seed head predators that are presumably quite common in the native range of *C. solstitialis*, including seven species introduced from Eurasia (including from Greece and Turkey) to the western USA (Turner et al. 1995, Rees et al. 1996, Balciunas and Villegas 2001). At least two species of fruit flies (in the genera *Urophora* and *Chaetorellia*) have been identified on SCI in recent years (Barthell et al. 2004). During the initial period of an invasion by *C. solstitialis*, the influence of such natural enemies is likely to be lessened and, consistent with this conjecture, *C. solstitialis* plant densities measured in nearby Turkey are substantially reduced relative to the western USA (Uygur et al. 2004).

Pollinator Guilds

Within one week we were able to accumulate 40 species of bees visiting *C. solstitialis* on Lesvos; this represents 1.6 times the number of species composing the SCI pollinator guild described by Thorp et al. (1994). At least two species were found in both locations, the honey bee (*Apis mellifera*) and the leafcutting bee *Megachile apicalis*, both of which are native to Eurasia and non-native to North America (Mitchell 1962, Michener 2000); we have also identified *M. apicalis* in western Turkey (Bursa), suggesting it is native to the Aegean region of Turkey as well. Overall bee diversity on Lesvos remains to be determined but is at least three-fold the 121 species currently recognized on SCI (R. W. Thorp, unpublished data). This is consistent with species-area predictions as substantiated for the Channel Islands (Rust et al. 1985, Thorp et al. 1994). The number of genera reported for SCI (21) is the same as that recorded for Lesvos (Thorp et al. 1994). The number of *Megachile* species on Lesvos was higher than for any other genus, a possible reflection of adaptations to *C. solstitialis* and other asteraceous species by some species of the genus *Megachile* and subgenus *Eutricharaea* (Müller and Bansac 2004).

Four bee families are recognized on both islands when guilds are compared with the findings of Thorp et al. (1994). However, the family Andrenidae was not detected at *C. solstitialis* on SCI, although species representing this genus do occur on the island. A species in the family Colletidae (genus *Hylaeus*) was collected on SCI but no representatives of this family were found during our collection period on Lesvos. The other three families are shared between locales: Apidae, Halictidae and Megachilidae. Of these, the highest proportion of species was in the family Megachilidae on Lesvos (at least 53% versus 28% on SCI) while on SCI the family Apidae was most common (40% versus 30% on Lesvos). The high representation of Megachilidae on Lesvos is consistent with the known diversity of the subgenus *Eutricharaea* in Eurasia (at least four species were detected on Lesvos during the current study). Observations indicate that a species in this subgenus, *Megachile apicalis*, is a frequent and important visitor of *C. solstitialis* in the western USA (Barthell et al. 2003, Stephen 2003, McIver et al. 2009), including on SCI (Thorp et al. 2000).

Yellow Star-thistle–Benefiting from New Circumstances?

Through the latter part of the 20th century and into the 21st, *C. solstitialis* has spread dramatically throughout the western USA (Maddox and Mayfield 1985, Pitcairn et al. 2006). Its requirement to be outcrossed contradicts classical assertions in the literature about how invasive plants succeed (Stebbins 1957, Baker 1965). Clearly, a mutualist (e.g., the ubiquitous honey bee) was required to facilitate the invasion of *C. solstitialis* into the western USA. Indeed, among the eight Channel Islands, the only islands with populations of *C. solstitialis* are those with a history of honey bee introductions: Santa Cruz Island and Santa Catalina Island. Santa Rosa Island, despite a long and intensive agricultural period (Allen 1996), remains without well-established populations of *C. solstitialis*. This observation is consistent with earlier work on SCI that shows a depression in reproductive capacity of *C. solstitialis* when honey bees are excluded from its flower heads (Barthell et al. 2000, Barthell et al. 2001). An exception is the self-compatible congener, *Centaurea melitensis*, which occurs in populations across Santa Rosa Island (as it does on SCI). The high levels of nectar in *Centaurea solstitialis* florets suggest that this species was able to draw honey bees away from competing plant species and this statement is corroborated by 1) our comparisons of honey bee visitation to *Grindelia camporum*, a native asteraceous species (Barthell et al. 2000), and 2) higher average nectar flow quantities and nectar (sucrose) quality (Barthell et al., unpublished data). Thus, the high nectar-producing environment at SCI, both in terms of flow and standing crop, was ideal for honey bees during the 1900s.

So why, in our preliminary observations on Lesvos, was *C. solstitialis* not attractive to honey bees to the same extent it is in the western USA? There appear to be at least two possible reasons as to why this is the case. First, another high nectar producing plant, *Vitex agnus-castus*, is effective in competing for other large-bodied, eusocial pollinators that may prefer (or require) larger nectar reserves (Schaffer et al. 1979); preliminary information from another study support this hypothesis both in terms of nectar volume and quality (Barthell et al., unpublished data). Secondly, the impact of native natural enemies (weevils, fruitflies, aphids, etc.) may compromise nectar production to such an extent that the plant becomes relatively unprofitable for foraging honey bees, even if a large and diverse set of smaller bodied bees persist in taking lower nectar levels from the plant as observed in the current study. These conjectures are not mutually exclusive, however, and probably influence one another at our study locale on Lesvos. Indeed, *C. solstitialis* and any other invasive plant that requires pollination may be the victim or beneficiary of its newly found circumstances when it arrives in a new habitat. In the case of *C. solstitialis*, it appears to have arrived in the right place at the right time since a surplus of mutualists (honey bees) and the absence of high nectar-secreting plant competitors and natural enemies may have ensured its success on SCI.

Implications for Conservation and Future Studies

Islands provide a special set of circumstances for the study of plant and animal invasions since, in mainland environments, the sheer diversity of species and number of individuals can make the progression of invasion events difficult to monitor (e.g., Roubik 1983). However, in our study locales the relatively low numbers of species (e.g., 121 species on SCI) allows one to more easily define plant-pollinator landscapes (Bronstein 1995); the mutualistic interactions in these landscapes would otherwise be especially difficult to ascertain, even though it is critical to identify these relationships in order to preserve them (Kearns et al. 1998). Understanding these interactions is also important because islands (with their reduced species diversity) may be especially vulnerable to biological invasions (Fritts and Rodda 1998). The willful spread of pollinators for real or perceived environmental benefits can have exceedingly important implications for both natural and agricultural systems and should be carefully evaluated for risks (Barthell et al. 2003). Growing evidence suggests that the cavalier spread of pollinator species such as the honey bee also negatively impacts native species (Goulson 2003, but see Butz Huryn 1997). The practice of globalizing the honey bee is an especially poignant case study wherein over-reliance on a single pollinator has led to a decline in pollinators for crops in the USA for the indefinite future (Barthell and Wells 2007).

We predict that the role of nectar (and other plant rewards) will be critical to understanding pollinator-plant mutualisms in both island and mainland locales; ecologists and conservation biologists have called for more significant efforts in this area for at least a decade (Kearns et al. 1998). Here, we have taken a preliminary step in testing this prediction by characterizing nectar flow and quality of an ubiquitous invasive plant species in the western USA, as well as establishing pollinator guild overlap between native and non-native environments where *C. solstitialis* occurs (islands in the USA and Greece). Future studies will focus more directly on the how nectar quantity and quality (and factors like handling time) determine foraging behavior of honey bees and solitary bees (e.g., Amaya-Márquez et al. 2008, Çakmak et al. 2009). This study has demonstrated that honey bees and solitary bee species (such as *Megachile apicalis*) represent model organisms for this effort. We will also try to understand the impact of negative interactions (e.g., insect phytophagy) on nectar production in *C. solstitialis* on both SCI and Lesvos. Indeed, plant-pollinator-herbivory interactions represent a growing area of interest among ecologists (e.g., Irwin et al. 2004). Finally, to our knowledge, this work is the first attempt to characterize and publish biogeographical data on nectar flow and quality in *C. solstitialis*, a model species for studies of mutualism-based interactions, including invasions (see Simberloff and Von Holle 1999, Richardson et al. 2000, Bruno et al. 2003).

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GENİŞLETİLMİŞ ÖZET

Amaç: Bu çalışmanın amacı *Centaurea solstitialis* (Güneşçiçeği) bitkisinin Santa Cruz adası (ABD) ve Ege Denizin'de bulunan Midilli adasında (Yunanistan) balözü akımı ve bu bitkiyi ziyaret eden arıların sayı ve çeşitliliğinin karşılaştırılmasıdır. Güneşçiçeği bitkisinin anavatanı Avrasya olup kendine döllenemeyen bir bitkidir. Yani döllenme ve tohumun oluşması için başka bir bitkiden çiçek özü veya polenin gelmesi gerekmektedir. Bu yüzden bu tip bitkiler gelecek nesillerinin devamı sağlayacak tohum oluşturulması için tozlayıcıları özellikle arıları

cezbetmek için balözü, çiçek özü ve yağ gibi maddeler salgılar.

Gereç ve Yöntem: Güneşçiçeği bitkisinin doğal alanı Avrasya olup batı Amerika'da yabancı bir bitki olarak oldukça istilacı bir yapıdadır. Balözü akımı çiçek tablaları arıların girmesi engelleyecek delikli kafes torbalar ile örtülerek çiçekçiklerdeki balözü miktarı ölçülmüştür. Balözü mevcut veya açık olan çiçek verileri ise delikli kafes torba ile kapatılmayan ve arılara açık olan çiçeklerden toplanmıştır. Her iki bölgede 15 bitki belirlenip 1m aralıklarla kafesle kapatılmıştır. Çalışmanın başlangıç gününden önce saat 16:00 ve 18:00 de her bitkiden iki çiçek tablası delikli kafes torba ile kapatılmıştır. Ertesi gün sabah delikli kafes torba çiçek tablalarından birinden çıkarılıp arıların girişine izin verilmiştir. Bu çiçeklere duran balözü denilmiş açık kalan çiçek tablalarına ise akan balözü denilmiştir. Ertesi gün saat 7:00 ve 19:00 arasında her 2 saatte bir 0.25 µl kapillari ince tüpler her çiçek tablasındaki çiçekçiğe sokularak balözü alınmış ve balözü miktarı ölçümleri yapılmıştır. Kapalı çiçeklerden balözü alındıktan sonra hemen tekrar delikli torba kafesler ile kapatılmıştır. Çiçekçikten balözü alındıktan sonda kalıcı Sharpie kalemle işaretlenip her toplamada farklı çiçekçiğin kullanılması sağlanmıştır. Arı kayıtları balözü kayıtlarının ilk gününden sonra başlamış ve balözü için kullanılan bitkiler kullanılmıştır. Bu bitkiler arasında 6 kez 5 dakika sürecek şekilde yürüyerek ziyaret eden arılar belirlenip kayıt edilmiştir. Her çalışma 30 dk sürmüş olup 9:00 ve 12:00 arasında günde 4 kez tekrar edilmiştir. Balözü kalitesi ise balözü biriktikten sonra bitkiler kesilip laboratuvara götürülmüş ve santrifüj edildikten sonar refraktometre ile ölçülmüştür.

Bulgu ve Sonuçlar: *Centaurea solstitialis* (Güneşçiçeği) bitkisini ziyaret eden arıların bu bitki ile birlikteliğini ve arı sayımlarını hem Midilli adası ve hemde Santa Cruz adasında karşılaştırma yapılabilecek zaman periyodlarında yapılmıştır. Her iki bölgede arıların en çok bu bitkiyi ziyaret ettiği zaman aralığı saat 15:00 aynı zamanda her iki bölgede bu bitkide balözü akımının en yüksek olduğu zaman aralığı olarak kaydedilmiştir. Bu zaman aralığı aynı zamanda duran ve akan balözü seviyesindeki en farklı durumun ortaya çıktığı zamandır. Balözü seviyesi konusunda iki bölgede delikli torba kafesler ile kapalı ve açık çiçeklerde özellikle tozlayıcıların çok yoğun olduğu dönemlerde önemli farklılıklar bulunmuştur. Akan balözü ve duran balözü miktarları Midilli adasında Santa Cruz adasındakilerden daha düşük olarak tespit edilmiştir. Arı bitki birlikteliğini sağlayan arı çeşitleri ise Midilli adasında Santa Cruz adasındakilerden daha yüksek olarak tespit edilmiştir. İlginç olarak Midilli adasında bu gözlem periyodlarında bal arıları kaydedilmemiştir.