

SEED SET IN A NON-NATIVE, SELF-COMPATIBLE THISTLE ON SANTA CRUZ ISLAND: IMPLICATIONS FOR THE INVASION OF AN ISLAND ECOSYSTEM

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Abstract—In two previous studies we demonstrated a positive association between honey bee visitation and seed set or seed head weight in the invasive yellow star-thistle, *Centaurea solstitialis*. However, as reported here, we were unable to find similar evidence for the congeneric tocalote, *Centaurea melitensis*. Both seed head weights and percent seed set levels obtained from two plots showed no significant differences among four treatments. Indeed, no significant differences occurred between controls (open) and bagged flower heads that excluded honey bees (but allowed native bee visitation). There were also no differences between controls and complete exclusion of bee-pollinators, confirming self-compatibility reported for this species elsewhere. Unlike *C. solstitialis*, *C. melitensis* attracts relatively low numbers of honey bees. In addition, *C. melitensis* is generally more widespread on the Channel Islands than *C. solstitialis*. We discuss these patterns with reference to the invasiveness of both species on Santa Cruz Island.

Keywords: *Apis mellifera*, *Centaurea solstitialis*, honey bee, invasive species, pollination, yellow star-thistle

INTRODUCTION

Honey bees (*Apis mellifera* L.) have been long-term, nonnative inhabitants of the North American continent. European-originating honey bees were in the eastern seaboard of the United States by the early 1600s (Crosby 1986) and were first imported into California by the mid-1800s (Watkins 1968). The African subspecies of the honey bee arrived in the United States by 1990, and as of 2003 has been found as far north along the California coast as the Santa Barbara/Ventura area and in the eastern and central portions of the state as far as Kings, Tulare and Inyo counties. Through their pollination services, the economic value of honey bees is undeniably important to the agricultural industry in the United States (Robinson et al. 1989). However, the effects of honey bees on non-agricultural

environments is subject to controversy, increasingly so during the last decade. One perspective is that honey bees have few or no effects in the native systems they inhabit (Butz Huryn 1997). Since Butz Huryn's assessment, however, additional experimental studies have emerged that produce conflicting evidence on this issue, prompting some to suggest that such a conclusion is premature (Richardson et al. 2000, Goulson 2003).

Honey bees have apparently resided in feral colonies on Santa Cruz Island (SCI), California, since the late 1800s (Wenner and Thorp 1994). Formal studies pertaining to honey bee effects on resident plants and pollinators have been ongoing on SCI since the late 1980s (Wenner and Thorp 1994, Thorp et al. 2000, Wenner et al. 2000). During 1993 and 1994, several of us (JFB, JMR,

RWT and AMW) used exclusion methods to identify and measure honey bee effects on seed set in the noxious weed yellow star-thistle (*Centaurea solstitialis* L.). In our initial study (1993), we excluded honey bees from flower heads while allowing the dominant native bees (family Halictidae) to visit the same flower heads (Barthell et al. 2001). When compared with unbagged (control) flower heads, we found significant differences in resulting seed set levels from these flower heads. Overall honey bee (*Apis*) visitation rates recorded among plots on SCI were much higher than for native bees: 6.6 times the number of all non-*Apis* bee records. Significant honey bee effects on seed set were also recorded on two mainland sites (University of California, Davis, CA and Cosumnes River Preserve near Sacramento, CA).

In 1994, we conducted a comparative study on SCI in which we found clear differences in numbers of honey bees and native bees on *C. solstitialis* and the native gumplant (*Grindelia camporum* Greene); honey bees outnumbered native bees 30 to 35 fold at plots containing the star-thistle while, reciprocally, natives outnumbered honey bees by at least 46 to 1 in gumplant plots (no honey bees visited plants in a second plot). These visitation data are consistent with foraging patterns observed by Thorp et al. (2000) on SCI. Seed head weights resulting from flower heads treated with exclosures as described above revealed that while no significant differences occurred among treatments for the native gumplant, significant differences were evident for *C. solstitialis*. Thus, for these two species that overlap spatially and temporally on SCI, it appears that honey bees provided relatively higher reproductive assistance through pollination to the non-native species (*C. solstitialis*), despite the fact that both species require pollinators and are largely self-incompatible.

Yellow star-thistle is known to be an obligate outcrossing species (Sun and Ritland 1997). As such, an ubiquitous, large-bodied and strong-flying vector like the honey bee is an ideal candidate for pollinating its flowers. If honey bees are promoting seed set in *C. solstitialis*, it would stand to reason that a self-compatible flowering plant species should not accrue the same benefits from honey bee pollination. Using a closely related (congeneric)

species that does not require such a pollinator can serve as a null condition for comparison against our previous results for *C. solstitialis* (Barthell et al. 2000, Barthell et al. 2001). In 1994, during a period of high honey bee densities and coincident with our other SCI studies, we treated plots of tocalote, *Centaurea melitensis*, with the same exclusion method as described above. We knew this species had lower visitation rates by honey bees than *C. solstitialis* while appearing to maintain stable or expanding population densities (Thorp et al. 1994, pers. observ.). We therefore hypothesized that seed set values in this species would not show the same treatment differences as those recorded for *C. solstitialis*, perhaps because of differing breeding system characteristics.

MATERIALS AND METHODS

Study Site

The largest of the eight Channel Islands, SCI supports over 100 bee species (Thorp et al. 2000), but is sufficiently insulated from other land masses to dampen exogenous effects (e.g., invasions and human impacts). The island's preserve status also ensures that human-induced perturbations remain at a minimum. It is currently owned by The Nature Conservancy and the National Park Service; the Central Valley and western portion of the island (where this study was conducted) are managed through the University of California Natural Reserve System. SCI is recovering from a history of heavy agricultural usage, including farming (vineyards) and cattle ranching which tapered off and finally ended in the late 1980s. Artifacts of previous agricultural use can be found in the presence of several introduced weed species (e.g., fennel and yellow star-thistle) that are particularly abundant in former agricultural sites.

Two plots were established for the study. One of these was located ca. 1.5 km east of the Christy airfield along a road that bisects the island and that connects the Central Valley with the western end of the island. The second plot was located at the base of Islay Canyon near the University of California Field Station. We refer to these locations as "West Plot" and "East Plot", respectively. Although *C. melitensis* can be found at several locations on SCI (Junak et al. 1995), we

Table 1. Results of a two-factor ANOVA testing effects of enclosure treatments and plot location on the weight (g) of *C. melitensis* seed heads on Santa Cruz Island.

Source of variation	<i>F</i>	SS	MS	df	<i>P</i>
Enclosures (E)	1.19	0.01	0.004	3	0.3160
Location (L)	164.21	0.52	0.524	1	0.0001
E × L	1.51	0.14	0.005	3	0.2151
Error	-	0.36	0.003	112	-

chose two distinct locations separated by several km in order to ensure that any experimental effects we observed were not site-specific.

Assessing Pollination/Reproduction

As in previous studies (Barthell et al. 2000, Barthell et al. 2001), four treatments were used in the experiment. Enclosures were created by cutting 18 cm diameter mesh circles and threading a string around their perimeters so they could be drawn “closed” into bags that envelop the unopened inflorescences. Three such treatments with varying mesh opening diameters were used for the study: (1) a large-mesh enclosure treatment (5-mm diameter openings) that excluded large-bodied pollinators including anthophorid bees, (2) a medium-mesh treatment (3-mm openings) designed to exclude honey bees but allow visitation by small-bodied native pollinators (e.g., halictid bees) and (3) a fine-mesh treatment (1-mm openings) that served to exclude all bee-pollinators as a check for self-compatibility; flower heads without enclosures served as controls.

The four treatments (including the control) were randomly assigned to unopened flower heads on each of 15 plants on 14 June 1994 along a belt transect (ca. 1 m separating treated plants). Only peripheral flower heads of approximately the same developmental stage were used to avoid age-related effects. An identification tag was attached to each study plant to identify the plot, along with individual plant and treatment sequences that were applied within the plant crown. Several weeks later, after treatment and control flower heads had opened, flowered and begun to senesce, the flower heads were enclosed with a fine mesh bagging

material to prevent the loss of dispersing seeds. Seed heads were removed on 6 September 1994, and stored in bags until they were weighed and dissected in the laboratory. Weights were taken after first removing the stem from each seed head at the base of the receptacle. All parts of the seed head were then weighed (receptacle, all seeds and residual floral components). After recording its weight, each seed head was dissected and a seed set ratio (viable to viable and non-viable seeds) was calculated for it. (These latter values were arcsin transformed for statistical analyses.) Seed head weights and seed set ratios were tested with a two-factor analysis of variance (ANOVA; treatment and plot location). A simple linear regression was used to compare seed head weights with numbers of seeds (viable, non-viable and a combination of these) per seed head to test the validity of seed head weights as an estimate of pollination success. Plant heights measured on 26 July 1994 were compared between plots using an unpaired, two-tailed *t*-test.

RESULTS

Seed Head Weights

A two-factor ANOVA detected no significant treatment differences among seed head weights (Table 1). Although plot differences were significant for the same variable, no interaction effect was revealed in the same ANOVA. Seed head weights were higher for all treatments in the West Plot relative to the East Plot (Table 2). These plot differences among treatments varied from 0.10 (control) to 0.17 g (large mesh).

Table 2. Mean (± 1 SE) seed head weights (g) for study plots of *C. melitensis* plants ($n = 15$) according to four treatment categories.

Study Plot	No Mesh (Control)	Large Mesh	Medium Mesh	Small Mesh
East Plot	0.17 (± 0.01)	0.11 (± 0.02)	0.14 (± 0.02)	0.14 (± 0.02)
West Plot	0.27 (± 0.01)	0.28 (± 0.02)	0.26 (± 0.01)	0.28 (± 0.02)

Table 3. Results of a two-factor ANOVA testing effects of enclosure treatments and plot location on the seed set percentages (arc-sin transformed) of *C. melitensis* seed heads on Santa Cruz Island.

Source of variation	<i>F</i>	SS	MS	df	<i>P</i>
Enclosures (E)	1.03	349.97	116.66	3	0.3824
Location (L)	1.60	180.71	180.71	1	0.2093
E × L	0.55	185.15	61.72	3	0.6527
Error	-	12,690.68	113.31	112	-

Seed Set

No significant treatment differences among the seed set arc-sin transformed percentages were observed in our two-factor ANOVA (Table 3). Unlike the weight data, however, no plot differences were observed in seed set (Table 4). When the total number of seeds (viable and non-viable) per seed head was compared between plots, the average value for the West Plot (69.53 ± 1.45) was significantly greater than the East Plot (44.83 ± 2.80) according to a two-tailed *t*-test ($P = 0.0001$; $t = 7.84$).

Seed Head Weights vs. Seed Numbers

Regressions of viable, non-viable and combined (viable and non-viable) seed numbers against seed head weights showed that only viable

seed and combined seed numbers predicted seed head weight well. Significant regressions using viable seed numbers occurred within both the East ($P = 0.0001$; $F = 650.28$; $df = 59$) and West ($P = 0.0001$; $F = 118.12$; $df = 59$) Plots with 0.92 and 0.67 R^2 values, respectively. Greater variation in numbers of viable seeds was evident in the East Plot (Fig. 1a) relative to the West Plot (Fig. 1b), and this fact is consistent with the lower mean seed head weights for the same plot, as described above. In the East Plot, a significant relationship also existed between the total number of seeds per seed head and the weight of those seed heads ($P = 0.0001$; $F = 335.83$; $df = 59$) with an R^2 value of 0.85. However, the relationship between non-viable seeds and seed head weight was not significant ($P = 0.9345$; $F = 0.01$; $df = 59$) with an R^2 value of 0.01. Within the West Plot, the relationship between total number of seeds and seed head weight was significant ($P = 0.0001$; $F = 113.51$; $df = 59$), with an R^2 value of 0.66. As in the East Plot, the relationship between non-viable seeds and seed head weight was not significant ($P = 0.2663$; $F = 1.26$; $df = 59$) with an R^2 value of 0.02. The slopes of lines formed from seed head weights vs. viable and vs. total seed numbers were significant within both plots but this was not the case for slopes formed from the regression of non-viable seed numbers per seed head and seed head weights.

Plant Height

Plants in the West Plot ($98.07 \text{ cm} \pm 3.42$) and East Plot (67.20 ± 2.02) were significantly different in height according to a two-tailed *t*-test ($P = 0.0001$; $t = 7.77$).

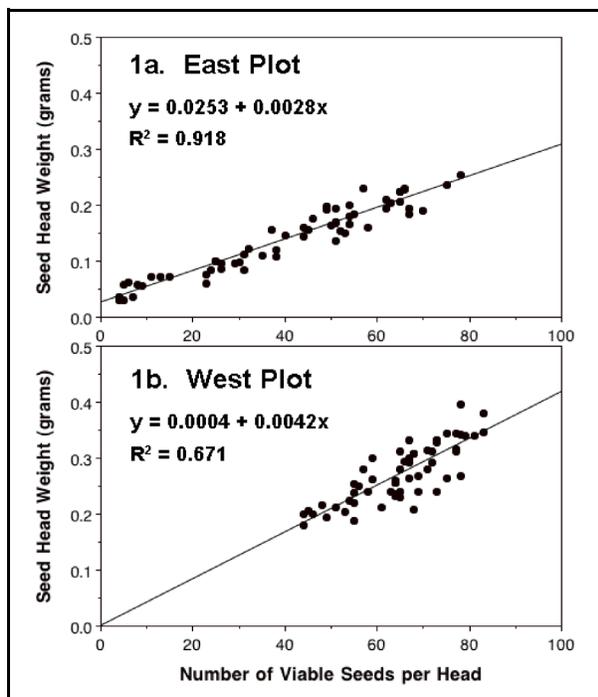


Figure 1. Simple linear regression results for East (a) and West (b) plots on Santa Cruz Island showing the relationship between number of viable seeds per seed head and seed head weight.

DISCUSSION

Centaurea melitensis produced high seed set levels when treated with small-mesh bagging in

Table 4. Mean (± 1 SE) seed set percentages (arc-sin transformed) for study plots of *C. melitensis* plants ($n = 15$).

Study Plot	No Mesh (Control)	Large Mesh	Medium Mesh	Small Mesh
East Plot	76.93 (± 3.57)	81.99 (± 3.25)	79.25 (± 2.19)	75.69 (± 4.31)
West Plot	83.25 (± 1.57)	81.59 (± 2.13)	80.47 (± 2.00)	78.37 (± 1.63)

our study, values that were statistically indistinguishable from the other treatments or the control. This finding is consistent with other studies that demonstrate self-compatibility in this species (Porrás and Álvarez 1999, Porrás and Muñoz 2000, Gerlach and Rice 2003). The plots we chose for the study produced distinct plant types that differed significantly in seed head weights, total number of seeds per head and plant height. Despite these differences that suggest environmental (e.g., nutrient or pollinator limitation) and/or genetic variation between plots, we detected no interaction effects with our treatments. These results therefore indicate that seed head weights are sufficient to estimate pollination success in our study plants as reflected in number of numbers of viable seeds. Although we have no visitation data for these plots, our results were obtained at a time when SCI was still dense with feral honey bee colonies and when honey bees dominated visitation records at plots of yellow star-thistle (Barthell et al. 2000; Thorp et al. 2000; Wenner et al. 2000). Previous work shows that honey bees do visit *C. melitensis*, but at a lower frequency than they visit *C. solstitialis* (Thorp et al. 2000).

Our findings for *C. melitensis* contrast with our other studies of the congeneric *C. solstitialis* on SCI. Breeding system and genetic studies of *C. solstitialis* indicate it is a largely self-incompatible species (Maddox et al. 1996, Sun and Ritland 1997). Our own work on SCI corroborated these findings, with seed set of *C. solstitialis* never exceeding five percent in small-mesh treatments during 1993, although higher levels were detected at two mainland locales (Barthell et al. 2001). *Centaurea melitensis*, on the other hand, had high levels of seed set among all treatments during our study. Gerlach and Rice (2003) also described self-compatibility in this species but also found increased seed set after supplemental pollination, suggesting *C. melitensis* reproduction may be enhanced by high pollinator activity at its flower heads. We were not able to shed additional light on

this question, however, given our experimental design. Although honey bees provide a valuable service as pollinators to the obligate out-crossing *C. solstitialis*, a self-compatible (and closely related) species such as *C. melitensis* should have less dependence on honey bees. Our study results are consistent with this conclusion and serve to bolster our earlier conclusions about the importance of honey bees to *C. solstitialis*.

One enigmatic point that emerges from this study is the relative success of *C. melitensis* and *C. solstitialis* as invasive species. Baker's hypothesis (1965) that self-compatibility enhances invasiveness in weeds suggests that *C. melitensis* would be a more successful invader than *C. solstitialis*. However, distributions and range expansion rates of *C. solstitialis* suggest it is the better invader (Maddox and Mayfield 1985). At least two factors seem to explain this paradox. First, *C. solstitialis* was "lucky" to have invaded environments in the western USA where high densities of both commercial and feral honey bees developed after the mid-1800s (Hendry and Bellue 1936, Watkins 1968). Secondly, a recent comparative study of three *Centaurea* species in California shows that *C. solstitialis*' invasion success also relates to its ability to avoid competition for water by extending its flowering period into the summer when other plant species minimize their growth (Gerlach and Rice 2003).

Invasion success may also be perception. *Centaurea melitensis* is actually noted on all Channel Islands, whereas conspicuous populations of *C. solstitialis* are only described for Santa Cruz and Santa Catalina (Junak et al. 1995), both of which have a history of habitation by honey bees. Furthermore, *C. melitensis* is more widespread on Santa Cruz Island than is *C. solstitialis* (L. Laughrin pers. comm.). These latter observations suggest that Baker's hypothesis (1965) is valid with respect to *C. melitensis* on the Channel Islands; and although less conspicuous, *C. melitensis* is also widespread in mainland California (Hickman 1993, DiTomaso and Gerlach 2000).

Nonnative plants are a conspicuous and enlarging component of our ecosystems; alien species account for 20 to 48% of vascular plant taxa among the Channel Islands, including over one-quarter of the vascular plant taxa on SCI (Junak et al. 1995). As empirical evidence continues to demonstrate the ubiquity of invasive species, understanding how these organisms invade new environments is an increasingly important consideration if we are to restore native systems. Nonnative pollinators such as honey bees should be evaluated for their direct and indirect influences on non-native flowering plant species. Evidence from this study (albeit indirect) further clarifies our understanding of the mutualistic relationships among honey bees and invasive plant species such as *C. solstitialis*. Indeed, the role of “positive” interactions (such as mutualism) during invasion are receiving increased attention and may even represent a novel paradigm for understanding ecosystem function (Simberloff and Von Holle 1999, Richardson et al. 2000).

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