YELLOW STAR-THISTLE, GUMPLANT, AND FERAL HONEY BEES ON SANTA CRUZ ISLAND: A CASE OF INVADERS ASSISTING INVADERS

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ABSTRACT

Feral honey bees have populated Santa Cruz Island (SCI) for over a century; this circumstance has produced an ideal setting for testing the hypothesis that honey bees promote the reproductive success of introduced weeds on the island. Fully one quarter of the vascular plant species on SCI are introduced, many of them well-established in the island's Central Valley. To test our hypothesis we compared the native gumplant, *Grindelia camporum*, and the introduced yellow star-thistle, *Centaurea solstitialis*, for their attractiveness to honey bees and native bee species. Overall, numbers of honey bees observed at yellow star-thistle exceeded those of native bees by a ratio of at least 33 to 1 while native bee numbers exceeded those of honey bees at gumplant by at least 46 to 1. We also employed an exclusion experiment with three mesh bag treatments to separate the effects of honey bees and selected native pollinator groups on seed head development. Seed head weights obtained from plots of gumplant and yellow star-thistle demonstrate that, when honey bees were fully excluded (while allowing native bee visitation), average seed head weight of yellow star-thistle significantly declined while that of gumplant did not.

Keywords: *Apis mellifera*, *Centaurea solstitialis*, *Grindelia camporum*, honey bees, invasions, Santa Cruz Island.

INTRODUCTION

Feral honey bees (*Apis mellifera* L.) were introduced to the eastern United States over 250 years ago (Crosby 1986). As their westward migration (assisted by man) ensued, honey bees established thriving, feral populations. During the 1830s, Washington Irving (1956) noted an episode of "bee-hunting" in what is now Oklahoma, a practice common among Native Americans who had considered the bees an omen of advancing settlers. By 1853, colonies had been transported to and established in California (Watkins 1968) and have since adapted so well to the north-south length of the state as to reflect clines in both morphology and allozymes (Daly et al. 1991; Nielsen et al. 1994). Only recently, with the invasion of the ectoparasitic varroa mite, have feral honey bee populations begun to show a decline (Kraus and Page 1995). Despite the highly successful occupation of our native ecosystems by honey bees, their effects on native organisms have received little attention and experimental studies of their interactions with plant and native pollinator populations in North America are generally lacking in the literature (but see Butz Huryn 1997).

In the late 1980s, two of us (Robbin W. Thorp and Adrian M. Wenner) began investigating honey bee effects on Santa Cruz Island (SCI) with the ultimate goal of removing honey bees from the island (Wenner and Thorp 1994; Wenner et al. 1999, this volume). SCI is a relatively isolated island locale (several kilometers from the mainland) that has apparently supported feral honey bees for a century or more. This setting therefore provides an ideal venue for a classical "removal" study from which one can infer the historical consequences of the honey bee's presence there. In anticipation of the eventual removal of the honey bees from SCI, we began to design experimental exclusion studies that assess honey bee effects on plants.

With over 26% of the vascular plant species on Santa Cruz Island being nonnative (Junak et al. 1995), we hypothesized a relationship between honey bees and the high densities of introduced plant species, a relationship that may be mutualistic in nature. One such species is yellow star-thistle (*Centaurea solstitialis* L.) a European invader that now covers innumerable acres of land in the northwestern United States (Maddox and Mayfield 1985). In an earlier study (Barthell et al. unpublished manuscript-a) we examined the relationship between honey bee densities and seed set levels in this species. In the current study, however, we opted to compare the role of honey bees in the pollination of both yellow star-thistle and the native gumplant species, *Grindelia camporum* E. Greene, to test the hypothesis that the introduced species benefits more from honey bee pollination than the native species.

MATERIALS AND METHODS

Santa Cruz Island

Santa Cruz Island (SCI) is located off the southern California coast south of Santa Barbara. It is the largest of the eight Channel Islands, occupying 25,000 hectares. Its recent history (since 1800s) included heavy agricultural usage, including a vineyard and, most recently, a cattle ranch. In 1965 the University of California began managing aspects of research on the island and in 1987 The Nature Conservancy purchased the western 90% of the island and began managing it as a nature preserve. The National Park Service, which now owns the eastern 10% of the island, assists in its management. Despite its protected state, the Central Valley of the island still bears the remnants of its agricultural use, including considerable densities of introduced weed species (e.g., fennel, mustard, horehound, and yellow star-thistle).

The study was conducted among four study plots on the island (two per study plant species). Two of these were located in the Central Valley, one (containing gumplant) near the University of California Field Station and a second one (containing yellow star-thistle) alongside the main road just east of a large grove of eucalyptus trees dubbed “Sherwood Forest” by local researchers. The other two plots were located near the western edge of the Central Valley. One of these (containing yellow star-thistle) was alongside an abandoned section of road a short walking distance from the “Cascada” region (noted for its year-round spring). The remaining “Portezuela” plot was located at the top of the Portezuela grade (western edge of the Central Valley) and contained gumplant.

Monitoring Visitation

Twenty study plants were selected along a transect within each plot (about a meter separating plants). Flowers on the previously selected study plants in each plot were monitored for visitors simultaneously during four separate half-hour time periods on 12 July, 1994: 09:00-09:30, 12:00-12:30, 15:00-15:30, and 18:00-18:30. During each period, visiting bees were censused on the designated study plants during a 2.5 min walk along each transect, recording the number and types of visitors among the 20 study plants. This walk was reversed back to the starting point during another 2.5 min period. This process was repeated five additional times (producing a 30 min monitoring period).

Seed Head Weights

Four treatments were used in the study. The control was a flower bud without any obstruction to potential visitors while the remaining three used a mesh exclosure that prevented visitation by varying degrees. Exclosures were constructed from 20 cm-diameter circles of nylon mesh fitted with draw-strings. The largest mesh exclosure treatment contained 5 mm diameter openings which excluded large pollinators such as certain anthophorid bee species and bumble bees. A medium mesh treatment (3 mm openings) excluded honey bees but allowed visitation by small-bodied native pollinators (e.g., halictid bees). Finally, a fine diameter mesh (1 mm openings) excluded all bees.

The treatments were assigned by dividing each study plant into four quadrants, denoted as NE, SE, SW and NW. A single flower bud (of comparable developmental stage) was identified in each quadrant and marked with an identification tag. Treatments were randomly assigned to the selected buds. Since many flower heads were damaged during the study, alternate buds were sometimes selected to replace them.

All flower buds were allowed to develop and senesce before the flower heads were enclosed with a fine mesh bagging material that prevented the loss of any seeds. Fully senesced seed heads were later removed and stored in plastic bags.

In the laboratory, senesced seed heads were cut from their stems and weighed. The dense, viable seeds in successfully pollinated plants were assumed to contribute mostly to seed head weight, an assumption successfully employed in at least one other study on an unrelated plant species (Barthell and Knops 1997).

RESULTS

Visitation

Visitation data presented in Table 1 demonstrate that the two yellow star-thistle plots were predominantly visited by honey bees. At the Sherwood plot, for example, honey bees out-numbered native bees by a ratio of 34 to 1, while at the Cascada plot the ratio was 33 to 1. Native bees were mostly species in the family Halictidae (five observations) and the Anthophoridae (seven observations), with only one megachilid bee observed.

In contrast to study plots of yellow star-thistle, gumplant plots were seldom visited by honey bees (Table 1). The ratio of honey bees to native bees at the Field Station plot was 1 to 46 with no honey bee visitation at the Portezuela plot. The dominant native visitors were in the families Halictidae (61 total observations) and Anthophoridae (92 total observations).

Seed Head Weights

Treatment effects were observed for both yellow star-thistle ($P = .0002$; $F = 7.243$; $df = 3$) and gumplant ($P = .0001$; $F = 9.815$; $df = 3$) plot pairs according to a 2-way ANOVA. However, the yellow star-thistle plot at Cascada was so severely damaged from the chewing and tearing of treatment bags by the Channel Islands fox that we consider the analysis of data from that plot inconclusive. Only four control exclosure bags remained for analysis while many other bagged heads (though not completely removed from the plant) were compromised in their development. A comparison of the two yellow star-thistle plots in this study reveals the extent of this discrepency (Table 2).

Mean separation tests reveal that yellow star-thistle seed weights were significantly different between the large and medium mesh exclosure treatments (Fisher PLSD = .033) in the Sherwood yellow star-thistle plot (Table 2). There was no difference between these treatments, however, for the gumplant plots at the Field Station and Portezuela (Fisher PLSD = .109 and .122, respectively).

DISCUSSION

During simultaneous monitoring periods reported for this study, numbers of honey bees observed at yellow star-thistle far exceeded those of native bees and, conversely, native bees were far more abundant than honey bees at gumplant patches. These results are consistent with subsequent seed head weight patterns indicating that (for the study plots that escaped fox intrusion) yellow star-thistle seed heads from control and large-mesh treatments were significantly greater than the honey bee-excluding medium-mesh treatment in the Sherwood plot. No significant differences between these same treatments were observed in either gumplant plot. We find the results of the Cascada plot (containing yellow star-thistle) inconclusive given the high level of treatment damage caused by the Channel Islands fox, otherwise known as "demonic intrusion" (Hurlbert 1984). Our previous yellow star-thistle study that examined the same treatments in both island and mainland ecosystems but which used numbers and ratios of viable and non-viable seeds corroborate the results of the Sherwood plot (Barthell et al. unpublished manuscript-a). The visitation patterns described here for honey bees at yellow star-thistle are corroborated by Maddox et al. (1996) in California. Guilds of bees previously identified visiting our two plant species on SCI show considerable overlap, but honey bees seem to prefer yellow star-thistle (Thorp at al. 1994).

Although further comparisons are required (and are forthcoming), honey bees appear to demonstrate a propensity for visitation to and pollination of introduced European weeds such as yellow star-thistle. The disproportionate visitation (and resulting pollination) by honey bees to this introduced species demonstrates a discernible link between plant reproductive success and this widespread and long-term invasive pollinator. It is also realistic to consider the relationship between honey bees and yellow star-thistle, in the context of ecological invasion, as a "mutualism." The importance of such species interactions, when both interacting species benefit, are frequently underestimated in ecology (Bronstein 1994) and deserve special consideration in our understanding of invasion mechanisms.

Does the mutualistic interaction of honey bees with yellow star-thistle translate to range expansion for yellow star-thistle? Information from our study does not address this question directly. However, historical evidence indicates that

Table 1. Total numbers of bees (according to family) observed visiting each of four study plots on Santa Cruz Island (12 July 1994).

	Yellow Star-Thistle Plots		**Gumplant Plots**	
Taxa	Sherwood	Cascada	Field Station	Portezuela
Apidae (*Apis*)	135 (97)	300 (97)	2 (2)	0 (0)
Megachilidae	0 (0)	1 (<1)	2 (2)	5 (7)
Halictidae	1 (1)	4 (1)	26 (28)	35 (51)
Anthophoridae	3 (2)	4 (1)	63 (68)	29 (42)
Totals	139 (100)	309 (100)	93 (100)	69 (100)

Table 2. Mean ± S E and sample size (n) from seed head weights for study plots of yellow star-thistle and gumplant study plants according to four treatment categories.[1]

Study Plot	**No Mesh**	**Large Mesh**	**Medium Mesh**	**Small Mesh**
Star-thistle Plot I "Sherwood"	0.29 – 0.013 (19)[a]	0.28 – 0.013 (19)[a]	0.23 – 0.011 (17)[b]	0.21 – 0.009 (15)[c]
Star-thistle Plot II[2] "Cascada"	0.31 – 0.012 (15)[a]	0.31 – 0.011 (17)[a]	0.28 – 0.014 (16)[a]	0.28 – 0.013 (4)[a]
Gumplant Plot I "Field Station"	0.67 – 0.047 (20)[a]	0.61 – 0.028 (20)[a,b]	0.60 – 0.045 (20)[a,b]	0.42 – 0.030 (15)[b]
Gumplant Plot II "Portezuela"	0.65 – 0.042 (18)[a]	0.55 – 0.056 (13)[a]	0.57 – 0.040 (17)[a]	0.46 – 0.028 (18)[b]

[1] Protected Fisher's LSD results are denoted by letters; values followed by different letters (superscript) are significantly different from others in the same row.

[2] This plot received extensive damage by Channel Island foxes, particularly the small mesh treatment plants.

such a scenario is at least possible, as it appears that yellow star-thistle was introduced to the western United States (seeds of which appeared in building materials of homes) before the introduction of honey bees in the mid 1800s (Hendry and Bellue 1936). The later introduction of commercial hives and subsequent spread of feral honey bee populations in the state may, ultimately, have promoted the spread of yellow star-thistle.

Surprisingly few studies have endeavored to examine the extent of impact by honey bees on the native and introduced flora of North America. A recent review of the subject by Butz Huryn (1997) suggests that most evidence to date demonstrates visitor abundance shifts at flowers (perhaps an indication of interference competition) without direct linkage to the reproductive fate of native pollinators or plants. Roubik (1983), for example, did not find such evidence when measuring resource stores of native stingless bees in South America during invasion of the region by African honey bees. Many such studies may be limited, however, by the ability to adequately measure the variables in question. Frankie et al. (1998), for example, predict such difficulties in measuring invasion effects of honey bees in a study that monitored abundances of solitary, cavity nesting bees in California. However, under the right experimental circumstances, similar methods were used to detect other invader effects on solitary bees (Barthell et al. 1998). Indeed, as the number of invasive species increases within our native ecosystems, more efforts should be made to measure their effects before their negative consequences require us to learn about them *ex post facto*.

Elton (1958) concluded a certain inevitability to invasions, suggesting that invading species expand their ranges among continents just as diffusing particles expand in solution. Only recently have ecologists begun to examine the details of invasion mechanisms (e.g., Vivrette and Muller 1977; Vitousek and Walker 1989) which suggest that invasions, though not necessarily predictable in their onset, can eventually be understood in terms of the interactions of invaders with their new environments. One means by which invaders can exploit new environments is through a reunion with past ecological associates. The results of this study suggest that such an association exists between European-originating honey bees and yellow star-thistle populations in the western United States. Such associations are not likely to be uncommon. On SCI and elsewhere in California, for example, there is evidence of another mutualistic relationship between an invading solitary, leaf-cutter bee, *Megachile apicalis* Spinola and yellow star-thistle wherein the bee is using the extensive populations of this weed species as corridors of invasion throughout the state (Barthell et al. unpublished manuscript-b). This species was first recorded on SCI by one of us (Robbin W. Thorp) and its pattern of invasion appears to be dictated by the distribution of yellow star-thistle (Thorp et al. 1999, this volume). Similar associations, even entire communities of invading species, remain to be examined from this perspective on Santa Cruz Island and elsewhere.

Island ecosystems may be especially susceptible to invasion by introduced species (Fritts and Rodda 1998). In addition, endemic species and subspecies are commonly found on islands. There are eight endemic plant taxa on SCI, for example, and 37 that are endemic to the Channel Islands (Junak et al. 1995). Conserving these species will require an understanding of these taxa as mutualistic assemblages of plants and pollinators (Kearns et al. 1998). Ironically, the nonnative mutualisms that introduced honey bees contribute to may threaten their native counterparts through range expansion of noxious weed species. This scenario has unfolded on SCI between honey bees and yellow star-thistle and the same relationship may exist between honey bees and other introduced weed species there. Such relationships may place conservationists in the position of having to identify nonnative mutualisms (such as honey bees and yellow star-thistle) for elimination in order to preserve native ones. As difficult as such decisions may be, involving expertise from multiple disciplines, conservationists will need to resolve this paradox to effectively preserve native ecosystems.

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