

BIOLOGICAL CONTROL AND ERADICATION OF FERAL HONEY BEE COLONIES ON SANTA CRUZ ISLAND, CALIFORNIA: A SUMMARY

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Abstract—After 1880, feral colonies of European honey bees (*Apis mellifera*) spread over all of Santa Cruz Island, though never invading any of the other northern Channel Islands. In line with other exotic animal removal programs (e.g., cattle, sheep, pigs), we outlined a program in October 1987 to eradicate all honey bee colonies on that island. That project evolved through four phases: 1) mapping and eradication of many colonies on the eastern half of the island (1988–1993), 2) introduction of a parasitic mite as a biological control (1994–1998), 3) monitoring residual honey bee activity (1999–2004), and 4) continued monitoring and certification of honey bee absence (2005–2008). We located the last known feral colony at the top of the Matanza grade on August 6, 2002 and found that same colony dead on March 31, 2003. The number of target foraging sites visited by honey bees declined steadily through the years, with the last visitors seen on rosemary plants at the ranch headquarters in August of 2004. We conclude that the introduced exotic European honey bees no longer exist on Santa Cruz Island.

INTRODUCTION

In the 1880s a beekeeper introduced European honey bees (*Apis mellifera*) to Santa Cruz Island and abandoned the project. Those bees then spread over all of Santa Cruz Island but never reached any of the other northern Channel Islands (Wenner and Thorp 1993). Although honey bees have an enviable reputation as a beneficial insect, any introduction of a non-native species can have a devastating effect on native plants and animals (Wenner and Thorp 1994). For example, honey bees may have played a major role in the extinction of the Carolina parakeet, due to bee swarms usurping tree cavities that the parakeets used for nesting (Rosen 2008). Honey bee effects have also been investigated by examining their impact on the nests of both social and solitary bees (Roubik 1983; Sugden and Pyke 1991).

Several reviews exist on the impact of honey bees on natural systems, with a variety of conclusions about this invasive species' overall impact on ecosystems (Sugden et al. 1996; Butz Huryn 1997; Goulson 2003). Our work on Santa Cruz Island began out of concern for the role of honey bees in competing with native pollinators for island plant resources (Wenner and Thorp 1994;

Thorp et al. 1994). On various trips to the northern Channel Islands in the 1960s and 1970s, one of us (AMW) had noticed a marked difference in pollinator visitation on flowering plants. For example, manzanita blossoms on Santa Rosa Island had an entire suite of native insects of various families, while those same plant species on Santa Cruz Island had honey bee visitation almost exclusively. Those observations led to the question of how much honey bees had altered the ecological balance on Santa Cruz Island and whether honey bee colony removal might shift the balance in favor of native bees and native plants pollinated by those bees (Wenner and Thorp 1994; Thorp et al. 1994).

During favorable seasons, native species might coexist quite well with honey bees. However, during unfavorable seasons when resources are limited, competition between honey bees and native bees is expected to be more severe (Thorp 1996). For example, during years of drought honey bees have a major competitive advantage in that they have nectar and pollen stores they can rely upon. Many native species, by contrast, have annual life cycles and therefore have no such stores and cannot successfully compete with the introduced honey bees. The native bee species and the plants that rely

on them for pollination then suffer. Consequently, intense scramble and interference competition likely occurs between honey bees and native bees during these drought periods (Wenner and Thorp 1994). We therefore reasoned that removing honey bee colonies from Santa Cruz Island would restore balance between native plants and their pollinators.

The honey bee removal project was initiated in October 1987, when we obtained permission from the island's owner, Dr. Carey Stanton, to begin removal of the exotic honey bee colonies. This effort later became part of The Nature Conservancy's overall goal to remove various European invasive species from the island. In previous publications (Wenner and Thorp 1994; Wenner et al. 2000), we described rationale, goals, scope, and earlier progress in our long-term feral honey bee removal project on Santa Cruz Island in greater detail; below we outline the major points.

Initially we envisioned several benefits from the eradication of honey bees on Santa Cruz Island. The first was to eliminate competition with native bee species on the island. The second was to reduce pollination of weed species, especially those that had co-evolved with honey bees. The third was to facilitate recovery of native plants that rely on pollination by native bee species. The fourth was to provide a field laboratory free of exotic honey bees that would permit unique comparative pollination studies among regions in the United States, as well as elsewhere in the world, including in the native range of honey bees (Eurasia). Later, there was concern that Africanized honey bees, a recent introduction into Santa Barbara County, might colonize Santa Cruz Island. We were not concerned that swarms could cross the Santa Barbara Channel intact on their own, but that drones might be swept across from the mainland by Santa Ana winds. Since Africanized drones aggressively mate with European honey bee queens and their genes are dominant for defensive behavior and absconding, an influx of drones could lead to genetic contamination. This could result in introgression of African honey bee genes into the island population(s), a phenomenon that is difficult to stem in mainland environments (Page and Erickson 1985). Removal of all honey bees would forestall that eventuality and make Santa Cruz Island a safe place for visitors. Although similar attempts failed in mainland venues (Tew et al. 1988), we felt the

likelihood of success would increase in an insular island ecosystem. This contribution summarizes the four phases of this honey bee removal project as it evolved through two decades.

METHODS AND RESULTS: FOUR PHASES

First Phase (1988–1993)—Locating and Eliminating Feral Colonies

During the first three years we located colonies by improved bee hunt techniques (Wenner et al. 2000) and mapped those locations. We also gathered background data on floral resource use by honey bees and native bees (e.g., Wenner and Thorp 1994; Thorp et al. 1994, 2000). This early period of the study was designed to develop baseline information on the ecological conditions that characterized Santa Cruz Island before the removal of honey bees.

At the end of the 1990 season we began to eliminate colonies on the eastern half of the island. (See Figure 1 in Wenner and Thorp 1994.) To kill most colonies, we sprayed an aerosol mist of methyl chloroform into the cavities containing them. That mist immediately anesthetized all bees, after which we blocked up all entrances so that bees in that cavity would die. In some cases we had to treat more than once. For colonies that we could not access, we used a remote baiting system employed earlier in the eradication of Africanized honey bee colonies (Williams et al. 1989; Danka et al. 1991).

Following the eradication of colonies, we routinely surveyed the island for the presence of honey bee swarms both in natural (e.g., tree, ground) cavities that had been previously occupied by colonies we had exterminated, and in traps equipped with chemical lures (Schmidt and Thoenes 1990). Swarms are groups of workers with individual queens, which bud off from existing colonies, seek appropriate cavities, and start new colonies. When new swarms were detected, they were exterminated following the methods described above. These efforts to seek out and eradicate new swarms were continued throughout the duration of our project.

By January of 1992, honey bee visitation on plants had declined markedly on the eastern half of the island, while native bee presence increased (see

Wenner and Thorp 1994 for details). By the end of the 1993 season, we had documented the existence of more than 200 colonies and eliminated 153 of them (Wenner et al. 2000). Those totals included swarms caught in traps equipped with chemical lures.

Second Phase (1994–1997)—Biological Control and Colony Demise

From 1994 to 1997 we used biological control to eradicate honey bee colonies. In 1993, heavy rains in January washed out most roads, severely restricting travel around Santa Cruz Island. Fennel thickets had also become impenetrable in many areas following the removal of cattle from the island in 1989 (L. Laughrin, personal communication; A. Wenner, personal observation). Many colonies became inaccessible, rendering our bee hunt techniques (Wenner et al. 1992) ineffective. Therefore, in 1994 we implemented the use of varroa mites (*Varroa destructor*) as an alternative technique for eradicating colonies.

Varroa mites are parasitic on honey bees but apparently not on any other bee or wasp species (Kevan et al. 1991; Wenner et al. 2000). Thus, mites posed no threat to Santa Cruz Island native bees. Previous studies indicated that, even though the European honey bee was not the original host for the mite, it was still very effective in lowering population levels of honey bees (Kraus and Page 1995). These characteristics (high host specificity and the potential for density dependent parasite-host population interactions) suggested an opportunity to use biological control to reduce honey bee levels on Santa Cruz Island. In addition, the use of varroa mites met all 14 requirements for release of biological control agents in Nature Conservancy preserves, as described in a February 15, 1994 memorandum (“Policy on Intentional Release of Non-Indigenous Biocontrol Agents on Preserves Owned or Managed by The Nature Conservancy”) forwarded to the authors by Diane Devine of The Nature Conservancy.

In December 1993 and January 1994, we introduced varroa mites to the eastern half of Santa Cruz Island. To introduce mites, we captured 85 honey bees with a net, one at a time, and placed a single mite on each bee. The bees were then released. We continued to routinely monitor the island for the presence of colonies, including new

colonies found and new swarms trapped after January 1994 in both natural and artificial cavities. The monitoring involved an average of six visits per year for a total of 25 trips to the island during that four-year period.

During the first two years after varroa mite introduction, the number of swarms observed remained relatively unchanged. However, swarm numbers declined dramatically in 1996, and we did not observe any new swarms in swarm traps thereafter (Fig. 1).

Third Phase (1998–2004)—Monitoring Residual Honey Bee Activity

Despite an absence of demonstrable swarming, we could still find a few individual foraging honey bees at various places and at various times on the island. Accordingly, we traveled about the island several times each year for seven years, documenting the presence of individual foraging honey bees and native bee species (e.g., Thorp et al. 1994, 2000). Nineteen foraging sites were recognized as most likely to have honey bee visitation, due to the existence therein of plants preferred by honey bees. Each year from 1998–2004, we visited a subset of these sites. Timing of site visits followed no set schedule, since visits depended upon the time of year that plants of interest flowered, as noted in Table 1 of Wenner and

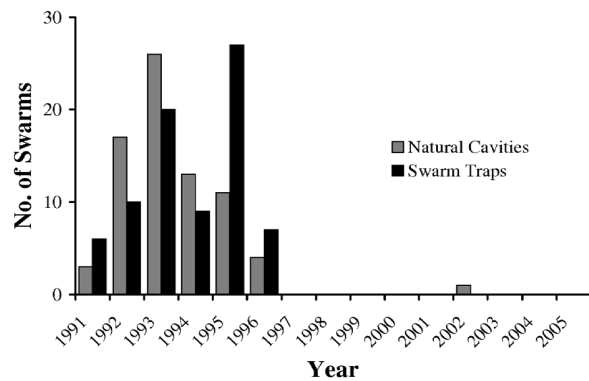


Figure 1. Numbers of new honey bee swarms observed each year on Santa Cruz Island from 1991–2005. Gray bars denote swarms observed in natural cavities that had been previously occupied by colonies we had exterminated. Black bars denote swarms caught in swarm traps.

Thorp (1994). Through time, even though we could still find a few honey bees foraging at a few sites, the numbers present were not sufficient to determine colony location by bee hunt techniques (Wenner et al. 1992).

In addition to visiting foraging sites, we continued to inspect installed swarm traps and insert fresh chemical lures each year in swarm traps located in those regions where honey bees had recently visited target plants. No swarms occupied those swarm traps, though, and the number of sites with honey bee foragers declined steadily year by year.

From our tallies of honey bee foraging distributions and flight lines, it appears that three colonies had survived until 2001. By inference, based on flight line observations, we determined that one colony existed in the lower Laguna Canyon region, one near the Main Ranch complex, and one in the Matanza area to the northwest of the main airstrip.

We located a feral colony at the top of the Matanza grade on August 6, 2002 but found that same colony dead by March 31, 2003. Ten years after a 1993 study in which Barthell et al. (2001) tallied 1,681 foraging honey bees among three plots during one day, we found only three honey bees in just one of the original plots in July of 2003 (Barthell et al. 2004). Another colony must have

existed on the island, because a few honey bees were seen on rosemary plants at the Ranch headquarters in July of 2004. By September of that year, though, honey bees were no longer observed foraging at that remaining site.

Fourth Phase (2005–2007)—Confirmation of Honey Bee Absence

For a total of six trips (two each year) during the final three seasons of our project we continued to check swarm traps and inspect 19 foraging sites, although we did not replace lures in the swarm traps. During this period, we did not detect any honey bees. All trips were planned to take advantage of times that target plants would be in optimal bloom. During the final three-year period, Lyndal Laughrin (UC Reserve manager) and David Dewey (TNC Island manager) did not observe honey bees in their extensive travel about the island in the course of their duties (personal communication).

In addition to our consistent revisitations of “hot spots” where honey bees had last been seen, and checking for them foraging at target flowers known to be preferred by honey bees, we also searched additional areas as we traversed the island looking for native bees. Overall, our search efforts were intensified in the last three years, compared to those years when honey bees were present. This search effort at flowers attractive to bees should have

Table 1. Data from 19 target sites monitored for *Apis mellifera* during each of the last eight years.

Season	a) Total # of 19 sites monitored	b) Total # of our visits to those sites	c) Sites that had honey bee foragers	d) Total # of times bees seen	e) # of fresh swarm lures installed	f) # of times trap hives checked	g) # of swarms caught
2000	15	27	9	11	43	122	0
2001	15	24	7	9	27	71	0
2002	11	16	4	5	27	57	0
2003	9	13	2	4	30	41	0
2004	15	24	1	1	28	46	0
2005	10	15	0	0	*	*	0
2006	11	15	0	0	*	*	0
2007	8	13	0	0	*	*	0

* We neither saw nor caught swarms after 1996, so we ceased putting lures in those hives after 2004.

revealed any rare visitation by honey bees, since bees can forage up to more than two miles from their colonies.

SUMMARY OF LAST EIGHT YEARS

In accordance with the limitations described above, during the last eight years of our project we concentrated our observations on the sites where we last saw honey bees foraging (Table 1, column a). Depending on weather and road conditions, as well as time of bloom for target plant species, we had a total of 147 visits to all those sites during the eight-year period (Table 1, column b). The number of sites with foraging bees declined steadily each year during the first five years (Table 1, column c), and the total number of times that we saw bees at any one site also declined at those sites (Table 1, column d). No bees were seen during the final three years at any of the sites we inspected.

During the first five of the last eight years we continued to insert lures into swarm traps (Table 1, column e; 155 lures total) but ceased doing so during the last three years (fourth phase), since we no longer saw any bees foraging at any of the target sites. Neither did we find any swarm traps (both those with new lures and those that had swarm lures inserted earlier) occupied during the 337 times we checked them in this last phase (Table 1, column f). The absence of swarms in column g of Table 1 corresponds with the fact that we saw no swarms after 1996.

DISCUSSION

Since bees are capable of foraging more than two miles from their colonies, and since we found no bees foraging at the “hot spots” we had monitored, we consider it likely, after 20 years of effort, that introduced feral (European) honey bees no longer exist on Santa Cruz Island. While removing the honey bees we eliminated a major competitor for native bee species (Sugden et al. 1996; Butz Huryn 1997; Thomson 2004), gained a more complete survey of native bee species diversity (Thorp et al. 1994, 2000), documented bee species visitation on both native and exotic plants (Wenner and Thorp 1994; Thorp et al. 1994, 2000;

Barthell et al. 2000), studied native bee and honey bee pollination of native and exotic plants (Barthell et al. 2000, 2001, 2005), contributed to biogeographical understanding by documenting the composition of the bee communities on islands compared to somewhat equivalent mainland areas (Thorp et al. 1994, 2000), enhanced our knowledge of honey bee foraging behavior and colony distribution (Wenner et al. 1992; Wenner and Thorp 1994; Thorp et al. 1994, 2000), reduced or eliminated the threat of island colonization by Africanized honey bees (Wenner and Thorp 1994), tested the effectiveness of varroa mites as a biological control against honey bees (Wenner et al. 2000; Wenner and Thorp 2002), and documented the rate at which varroa mites could eliminate honey bee colonies in a region (Wenner and Thorp 2002).

In retrospect, our success is due to several factors. First, Santa Cruz Island is a closed ecosystem, with the long distance over water providing a barrier to unaided invasion by honey bees. Second, there was little opportunity for honey bees to evolve resistance to the varroa mites, since honey bees on the island had essentially no genetic variability (Wenner and Thorp 1993). The relatively short duration of our project also permitted no time for mite and honey bee coevolution, and the European honey bee is not the original host of the mite. Third, varroa mites can survive only in honey bee colonies (warm conditions, with live bees and/or brood year round), making them a good biological control agent that is unlikely to adversely affect native bee species.

We eliminated a known total of 300 colonies by the use of physical and biological controls, while parasitic mites (our biological control agent) likely eliminated a number of other honey bee colonies that we had not previously detected on Santa Cruz Island. Our accomplishment may be a rare case, where an introduced exotic biological control agent has apparently completely eliminated another introduced exotic species, although cases of virtually complete “control” have been recorded, including the case of the cottony cushion scale, *Icerya purchasi* Maskell, in southern California citrus orchards (Caltagirone and Doult 1989). Santa Cruz Island itself is the venue of the often cited case of the cochineal insect *Dactylopius opuntiae* (Cockerell) reducing cactus (*Opuntia* spp.) populations (Goeden and Ricker 1981). However,

even that major biological control (cochineal) success had less dramatic results than the case of varroa impacting honey bee colonies on the island. Indeed, one might consider this current case as one of “biological eradication” rather than one of classical biological control *per se*. The use of varroa mites also differs from classical biological control because the European honey bee was not the coevolved host of the control agent: rather, the Asian honey bee *Apis cerana* Fabr. served in that role. In addition, we did not travel to the native range of the host to collect the control agent, as is the practice in classical biological control programs.

Aside from elimination of an exotic species, our adverse impact on the island ecology has been minimal. Extensive observations of native bee abundance and diversity both before and after varroa introduction indicate that no other species of Hymenoptera on Santa Cruz Island have been negatively impacted (Thorp et al. 1994, 2000). Also, varroa mites are known to be very specific to the non-native honey bee genus *Apis* for their reproduction—although those mites can be dispersed by non-*Apis* species (Kevan et al. 1991). The only potential drawback to our operation may be the monitoring materials we used during the last 20 years. At the peak of our study, we had 134 swarm traps installed about the island, with an additional 15 installed during the last several years. These asphalt/paper pulp hives, formed in a flowerpot mold and fitted with a lid (Schmidt and Thoenes 1990), were very durable when first installed. Over time, however, the asphalt vaporizes. We replaced traps whenever they became too fragile to hold the weight of a bee colony or removed them when bees no longer foraged in given areas. Also, since we caught no swarms anywhere on the island after 1996, the reduced number of swarm traps mattered little.

During our October 2006 visit to the island, we removed most of the remainder of the intact traps and brought them back to the mainland. Exceptions were as follows: 17 swarm traps were missing from their original installation sites, perhaps blown down by wind and moved about by pigs; five swarm traps had become so thoroughly engulfed by the vegetation around them that they could not be removed; we abandoned 14 swarm traps located in brush too dense for retrieval or in terrain too dangerous for safe retrieval; and one swarm trap had

become occupied by a yellow jacket colony during the 2006 season, and was not removed. In time, any remaining swarm traps will reach the ground, become wet with rain, and disintegrate.

Ongoing Studies

Monitoring of native bees on Santa Cruz Island continues. As of April 2007, the number of bee species that have been found on Santa Cruz Island stands at 121 species in 5 families and 35 genera (R. Thorp, unpublished data). This increase of seven species since our last report of 114 (Thorp et al. 2000) is mainly due to refinements in identifications of previous specimens. At least one of these, *Megachile apicalis* Spinola, is a non-native species that we have recently detected in its native Eurasian habitats in association with the invasive weed yellow star-thistle (J. Barthell, unpublished data). This species continues to spread across the island in correlation with the spread of yellow star-thistle (Thorp et al. 2000).

Honey bees have not been detected by any sampling method since July 2004 and have not been major players in the island bee fauna since 1996 (e.g., no more swarms caught in swarm traps), when the introduced varroa mites began to rapidly decimate the European honey bee populations (Wenner and Thorp 2002). However, dramatic increases in populations of native bees have not yet been observed, perhaps for several reasons (Thorp 1996). Any changes are likely to be small and subtle, since most native bees are K-strategists (relative to honey bees) that emphasize considerable maternal investment in provisioning for a few young and often have a single generation per year, rather than r-strategists that produce large numbers of eggs and are multivoltine. Indeed, other environmental changes may have more noticeable impacts on native bee population fluctuations (e.g., drought, excess rains, displacement of native flora by invasive weeds such as fennel and yellow star-thistle, diseases, and other natural enemies) than the effects of sporadic competition for limited food resources.

Although our understanding of resource competition among honey bees and solitary bees on Santa Cruz Island is still in its infancy, a few observations deserve consideration. The presence of the honey bee has been demonstrated to increase the reproductive capacity of highly invasive plants,

including yellow star-thistle on Santa Cruz Island (Barthell et al. 2000, 2001). We also know that this same plant species is a strong competitor with other plant species in the California grasslands and has been expanding its range at a remarkable rate during the last several decades (Pitcairn et al. 2006). Although many native bee species also utilize yellow star-thistle as a source of nectar and/or pollen (Thorp et al. 1994), the loss of native plant habitat is due, at least in part, to honey bee effects; oligolectic bee species, surviving on less common native plant species that compete with yellow star-thistle, may therefore be at risk. Furthermore, when given a choice, we have found that many native species will leave their primary native host plants (e.g., gumplant or *Grindelia camporum* E. Greene) to visit yellow star-thistle. There may be many other cases of host plant overlap between native bees and honey bees (see Thorp et al. 1994, 2000).

One possible increase in population abundance of a native bee that may be related to decline in honey bee populations seems evident. *Halictus farinosus* has been more apparent in recent years (R. Thorp, unpublished data). This sweat bee is a solitary ground nesting species with females slightly smaller than honey bee workers and is broadly polylectic in its choice of pollen plants. Due to its similar size and wide floral resource use, this species overlaps greatly with honey bees for food and may be showing release from competition for floral resources. Indeed, this species was recorded for the first time on yellow star-thistle only after the decline of honey bees (Barthell et al. 2004). As an annual species it would never have the same impact on island pollination as honey bees.

Recently, we have begun comparative investigations between Santa Cruz Island and the island of Lesbos in Greece to investigate the roles of mutualists (bees) and competitors (plants) that influence the success of yellow star-thistle in the western USA, including Santa Cruz Island. Lesbos is the largest of the Northeast Aegean Islands off the western coast of Turkey; both honey bees and yellow star-thistle are native to this location. Like Santa Cruz Island, Lesbos has an increasingly well-characterized bee pollinator community (Petanidou and Lamborn 2005). Our efforts have already begun to characterize the native pollinator guild of yellow star-thistle. We hope our findings will shed light on competitive effects among pollinators and plants as

described above, including the role that nectar plays in the success of invasive plant species like yellow star-thistle.

It should be noted that yellow star-thistle requires outcrossing by pollinators to reproduce (Sun and Ritland 1997). Thus, with the honey bees now gone from Santa Cruz Island, the exotic yellow star-thistle (with its primary exotic pollinator) could now decline in abundance on Santa Cruz Island. The seed bank of that species should become depleted, a process that could take years or even decades to complete (Joley et al. 1992; Callihan et al. 1993). This issue is further complicated by the fact that at least two phytophagous fruit fly species have also reached the island since 1993 (J. Barthell, unpublished data), and could further negatively impact yellow star-thistle abundance. Regardless, we predict that several such manifestations of the extinction of the non-native honey bee in the future will result in a return to a more natural ecological balance on Santa Cruz Island.

ACKNOWLEDGMENTS

The University of California's Natural Reserve System, The Nature Conservancy, and the National Park Service greatly assisted our efforts on Santa Cruz Island. We especially thank Lyndal Laughrin, Brian Guerro, Chris Spohrer, David Dewey, Kate Faulkner, Sarah Chaney, and the scores of volunteer assistants during the two decades of our study. We also thank the diligence exerted by Christine Damiani during the editing process.

REFERENCES

- Barthell, J.F., R.W. Thorp, A.M. Wenner, and J.M. Randall. 2000. Yellow star-thistle, gumplant, and feral honey bees on Santa Cruz Island: A case of invaders assisting invaders. Pages 269–273. *In*: Browne, D.R., K.L. Mitchell and H.W. Chaney (eds.), Fifth California Islands Symposium. MBC Applied Environmental Sciences, Costa Mesa, CA.
- Barthell, J.F., J.M. Randall, R.W. Thorp, and A.M. Wenner. 2001. Promotion of seed set in yellow star-thistle by honey bees: Evidence of an

- invasive mutualism. *Ecological Applications* 11(6):1870–1883.
- Barthell, J.F., J.M. Randall, R.W. Thorp, and A.M. Wenner. 2004. Measuring Recovery of an Island Ecosystem after Removal of Honey Bees. Report to the National Geographic Society.
- Barthell, J.F., R.W. Thorp, A.M. Wenner, J.M. Randall, and D.S. Mitchell. 2005. Seed set in a non-native, self-compatible thistle on Santa Cruz Island: Implications for the invasion of an island ecosystem. Pages 269–273. *In*: Garcelon, D.K., and C.A. Schwemm (eds.), *Proceedings of the Sixth California Islands Symposium*, Institute for Wildlife Studies, Arcata, CA.
- Butz Huryn, V.M. 1997. Ecological impacts of introduced honey bees. *Quarterly Review of Biology* 69:31–51.
- Callihan, R.H., T.S. Prather, and F.E. Northam. 1993. Longevity of yellow starthistle (*Centaurea solstitialis*) achenes in soil. *Weed Technology* 7:33–35.
- Caltagirone, L.E., and R.L. Doutt. 1989. The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology* 34:1–16.
- Danka, R.G., J.L. Williams, C.W. Harmon, T.E. Rinderer, and H.F. Morris. 1991. Doses and residues of acephate baits used to eradicate undesirable honey bees: A hazard assessment. *Bulletin of Environmental Contamination and Toxicology* 47:422–427.
- Goeden, R.D., and D.W. Ricker. 1981. Santa Cruz Island—Revisited. Sequential photography records the causation, rates of progress, and lasting benefits of successful biological weed control. Pages 355–365. *In*: E.S. Delfosse (ed.), *Proceedings of the V International Symposium on the Biocontrol of Weeds*. July 22–27, 1980, Brisbane, Australia. CSIRO, Melbourne.
- Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 34:1–26.
- Joley, D.B., D.M. Maddox, D.M. Supkoff, and A. Mayfield. 1992. Dynamics of yellow starthistle (*Centaurea solstitialis*) achenes in field and laboratory. *Weed Science* 40:190–194.
- Kevan, P.G., T.W. Lavery, and H.A. Denmark. 1991. Association of *Varroa jacobsoni* with organisms other than honey bees and implications for its dispersal. *Bee World* 71:119–121.
- Kraus, B., and R.E. Page. 1995. Effect of *Varroa jacobsoni* (Mesostigmata, Varroidae) on feral *Apis mellifera* (Hymenoptera, Apidae) in California. *Environmental Entomology* 24:1473–1480.
- Page, R.E., and E.H. Erickson. 1985. Identification and certification of Africanized honey bees. *Annals of the Entomological Society of America* 78:149–158.
- Petanidou, T., and E. Lamborn. 2005. A land for flowers and bees: Studying pollination ecology in Mediterranean communities. *Plant Biosystems* 139: 279–294.
- Pitcairn, M.J., S. Schoenig, R. Yacoub, and J. Gendron. 2006. Yellow starthistle continues its spread in California. *California Agriculture* 60:83–90.
- Rosen, J. 2008. What a little bird told us. *Los Angeles Times*, February 24, <http://www.latimes.com/news/opinion/commentary/la-op-rosen24feb24,0,6033118.story>.
- Roubik, D.W. 1983. Experimental community studies: Time-series tests of competition between African and neotropical bees. *Ecology* 64:971–978.
- Schmidt, J.O., and S.C. Thoenes. 1990. The efficiency of swarm traps: What percent of swarms are captured and at what distance from the hive. *American Bee Journal* 130:811.
- Sugden, E.A., and G.H. Pyke. 1991. Effects of honeybees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* 16:171–181.
- Sugden, E.A., R.W. Thorp, and S.L. Buchmann. 1996. Honey bee—Native bee competition: Focal point for environmental change and apicultural response in Australia. *Bee World* 77:26–44.
- Sun, M., and K. Ritland. 1997. Mating system of yellow starthistle (*Centaurea solstitialis*), a successful colonizer in North America. *Heredity* 46:20–23.
- Tew, J.E., C.H. Bare, and J.D. Villa. 1988. The honey bee regulated zone in Mexico. *American Bee Journal* 128:673–675.

- Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85(2):458–470.
- Thorp, R.W. 1996. Resource overlap among native and introduced bees in California. Pages 143–151. *In*: A.S. Matheson, S.L. Buchmann, C.O. O'Toole, P. Westrich, and I.H. Williams (eds.), *The Conservation of Bees*. Linnean Society Symposium Series Number 18. Academic Press, London, UK.
- Thorp, R.W., A.M. Wenner, and J.F. Barthell. 1994. Flowers visited by honey bees and native bees on Santa Cruz Island. Pages 351–365. *In*: Halverson, W.L., and G.J. Meander (eds.), *Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Thorp, R.W., A.M. Wenner, and J.F. Barthell. 2000. Pollen and nectar resource overlap among bees on Santa Cruz Island. Pages 261–268. *In*: D.R. Browne, K.L. Mitchell, and H.W. Chaney (eds.), *Fifth California Islands Symposium*. MBC Applied Environmental Sciences, Costa Mesa, CA.
- Wenner, A.M., J.E. Alcock, and D.E. Meade. 1992. Efficient hunting of feral colonies. *Bee Science* 2:64–70.
- Wenner, A.M., and R.W. Thorp. 1993. The honey bees of Santa Cruz Island. *Bee Culture*. 121:272–275.
- Wenner, A.M., and R.W. Thorp. 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. Pages 513–522. *In*: Halverson, W.L. and G.J. Meander (eds.), *Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Wenner, A.M., and R.W. Thorp. 2002. Collapse and resurgence of feral colonies after varroa arrival. Pages 159–166. *In*: E.H. Erickson, Jr., R.E. Page, Jr., and A.A. Hanna (eds.), *Proceedings of the 2nd International Conference on Africanized Honey Bees and Bee Mites*. The A.I. Root Co., Medina, OH.
- Wenner, A.M., R.W. Thorp, and J.F. Barthell. 2000. Removal of European honey bees from the Santa Cruz Island ecosystem. Pages 256–268. *In*: D.R. Browne, K.L. Mitchell, and H.W. Chaney (eds.), *Fifth California Islands Symposium*. MBC Applied Environmental Sciences, Costa Mesa, CA.
- Williams, J.L., R.G. Danka, and R.E. Rinderer. 1989. Baiting system for selective abatement of undesirable honey bees. *Apidologie* 20:175–179.