The opportunistic origin of a new citrus pest

Left photo: Anise swallowtail larvae undergo dramatic color changes as they grow. The very small larvae are thought to mimic a bird dropping. Right: Young anise swallowtail larvae eat only tender leaves, but larger larvae can also damage mature citrus foliage.

Arthur M. Shapiro □ Kenneth K. Masuda

Where do new pests come from? Usually, somewhere else. But every once in a while a native species that had been considered innocuous is "suddenly" tranformed into an enemy of agriculture. The classic example is the Colorado potato beetle, which moved from weedy wild nightshades onto the related cultivated potato and marched from potato field to potato field across the continent.

Why should an insect move onto a new host? The answer is frequently chemical. Most insects are specialists on particular kinds of plants, which they recognize by means of distinctive chemical compounds peculiar to those plants. They also avoid plants containing repellent chemical stimuli, even if the proper attractants are also present. If man introduces a new plant in an area, and it is stimulatory but not repellent to an insect already there, a new pest may be born. Only about ten years ago such a process began to operate in citrus groves in the northern Sacramento Valley; for the first time growers had to pay attention to a pretty yellow and black butterfly named *Papilio zelicaon*.

In California *Papilio zelicaon* is usually called the anise swallowtail, reflecting its most common host plant; "anise" in California usually refers to sweet fennel, *Foeniculum vulgare*, an abundant perennial weed of the carrot family (Umbelliferae). The story of *P. zelicaon*, sweet fennel, and citrus growing is best told historically, as we have been able to reconstruct it.

Papilio zelicaon is apparently a native insect, found throughout western North America, feeding on various wild members of the carrot family. In California it occurs from sea level to above tree line. Over so wide a range, its life history is quite variable. In the bleak high mountain meadows it has only one generation during the short growing season. At sea level it may have four or five per year; it flies from March to October or November in the Sacramento Valley, and all year round in coastal San Diego County.

Yet this continuous breeding was apparently impossible before the white man came to California: all the native lowland host plants dry up during the long, rainless summers. Once sweet fennel was introduced by the Spaniards in the 18th century, the swallowtail could rear generation after generation in warm weather. As the plant spread to every vacant lot in the valleys, the butterfly followed it, so that by the second half of the 19th century the multiple-brooded insect was generally distributed in agricultural and urbanized California.

When we examine the physiology of these multiple-brooded *zelicaon*, it is clear that they differ profoundly from the single-brooded populations that still exist at low elevations in wild parts of the state where sweet fennel does not grow. In fact, there are physiological races, which we have shown in the lab to differ genetically in their propensity to enter and terminate dormancy. Single-brooded races persist particularly on serpentine soils and can sometimes be found close to multiple-brooded, fennel-feeding ones at the same elevation.

Dr. Steven R. Sims, working in our lab at Davis, found that artificial selection can rapidly alter the dormancy characteristics of a strain. We believe that natural selection accomplished the same thing on sweet fennel in the field. The advantages of multiple-broodedness are obvious; a shorter generation time means leaving more descendants per unit time. Where summer hosts are not available, selection would constantly weed out any deviant animals that failed to enter dormancy. In the high Sierra, encroaching cold weather would arrest development anyway, and in years of light snow pack a partial second generation can occur. Sims found that foothill, serpentine populations were the most obstinately single-brooded, whereas a population from 7,000 feet (Donner Pass) was intermediate, and Central Valley populations were strongly multiple-brooded under lab rearing regimes.

Orange (*Citrus sinensis*) belongs to the rue family (Rutaceae). Like fennel, it was introduced to California by the Spaniards. Commercial orange groves began near Los Angeles by 1841. By 1975 225,000 acres were in citrus production in California and Arizona. The anise swallowtail was not reported on citrus until about 1918. In 1922 J. R. Horton published a 10-page paper in the *Monthly Bulletin* on *P. zelicaon* as a citrus pest near Visalia. It has been a pest in southern California ever since, but it remained unknown as such in the citrus-growing areas near Chico for another 45 years or more.

In retrospect, the swallowtail's move onto citrus is hardly surprising. In the genus *Papilio* we find rue feeders, umbellifer feeders, and species that move back and forth between these (not closely related) plant families. A swallowtail is a major citrus pest in South Africa. Another, the orange dog (*P. cresphontes*), long common in the southeast, has expanded its range from Arizona into southern California. As early as 1941, Vincent G. Dethier, working with another swallowtail (*P. polyxenes* of the eastern United States, a close relative of *P. zelicaon*), showed that the rue and citrus families shared essential oils (anethole, methyl chavicol, anisic aldehyde, and the like) that were feeding stimuli to the insect: caterpillars will eat filter paper treated with them, but won't eat umbellifer foliage that lacks them. The chemistry provided a natural "bridge" to a new host plant.

We believe that *P. zelicaon* has crossed that chemical bridge at least twice—once in the south and a second time, more recently, in the north. (This is to be studied further by genetic analysis of crosses between the northern and southern citrus-feeding populations and crosses of both with tester stocks.) We wondered *why*, and whether it was evolving a citrus race just as it had evolved a sweet fennel race.

Sweet fennel is highly attractive to females from populations feeding on wild umbellifers. Sims also found in split-brood experiments that the insect has a lower propensity to dormancy when fed on fennel than on short-lived plants, even in the multiple-brooded strains. The shift onto fennel over a century ago might have been aided by the "Hopkins Host-Selection Principle" proposed by A. D. Hopkins in 1917, which holds that given a choice among acceptable hosts, a female insect will prefer to lay eggs on the one she herself ate. Once the species had made an initial breakthrough, the developmental-time advantages would assure a rapid spread of fennel preferences in the population. James Erickson found in research at Cornell that this "larval memory" occurred in *Papilio polyxenes*, but Christer Wiklund, working on a Swedish species of the same group, found it did not.

We wondered if something of the sort had happened on citrus. Fennel-feeding stock was obtained from Fairfield and Suisun City, Solano County. Citrus feeders were taken from the Bailey Ranch near Orland, Glenn County. The two strains were maintained in continuous lab culture, and egg-laying females were tested for plant preference. A completely unattractive control, the landscaping shrub *Escallonia* (Saxifrage family), was used with them in the experimental design. With scores of replicate tests, we found that *sweet fennel was the host preferred by females for egg-laying regardless of what they had eaten or what strain they represented.* The "Hopkins Host-Selection Principle" did not hold.

Evolution of a citrus race was still possible if citrus were intrinsically a better host than sweet fennel; we therefore compared growth, survivorship, and fecundity of both strains on both plants. Once again, we found *fennel was intrinsically superior to citrus on all counts.* The female lays her eggs on the young, growing shoot tips of citrus; young caterpillars can eat only tender, young leaves, although larger ones can handle mature foliage. This limits population levels, focuses the damage, and makes citrus trees a trickier host than fennel, all parts of which are available all year.

Why, then, is the anise swallowtail attacking citrus at all? The answer seems to be straightforward: it has nothing to lose. There is no fennel in the vicinity of the orange groves. By using citrus, the butterfly has expanded its range into areas it could not occupy before. There is nothing wrong with using a suboptimal host if that is the only host around.

Right now the U.C. recommendations for swallowtail control on citrus are Parathion, Phosdrin (mevinphos), or Guthion (azinphosmethyl). All are highly toxic, deadly to honey bees and beneficial parasites, and subject to many restrictions. The ecology of the situation suggested the possibility of trap-cropping with sweet fennel where the swallowtail becomes a significant problem. We carried out field tests with potted plants in citrus orchards, which showed the same female preference for fennel as had been found in the lab.

Because fennel regenerates quickly from its taproot, strips of it interplanted with citrus could be mowed regularly, after the egg-laying peak in each generation. We have found that regenerating sweet fennel is *more* attractive to females than uncut tops. Sweet fennel flowers are visited by many dipteran and hymenopteran natural enemies of a variety of pests, but not by the pests themselves. The plant is not known to harbor other potential citrus pests.

The most successful use of trap-cropping in California has been the interplanting of alfalfa and cotton to control lygus bugs. Perhaps one day sweet fennel will be a common sight in citrus orchards, and the anise swallowtail will once again be merely a pretty ornament to the landscape—not a pest.

Arthur M. Shapiro is Associate Professor of Zoology and Associate Research Zoologist in the University of California Agricultural Experiment Station, Davis. Kenneth K. Masuda is a graduate student in the Department of Zoology, U.C., Davis. *Field studies at Orland were conducted with the kind cooperation of the Bailey Ranch. This work was conducted under Agricultural Experiment Station Project CA-D*-BSC-3593.*

Spring planting is best for oilseed sunflower

Benjamin H. Beard ☐ Karl H. Ingebretsen

Non-oil (confectionery) sunflowers (*Helianthus annuus* L.) have been grown in the Sacramento Delta of California since the early 1930s. Production has varied from about 800 to 3,200 hectares (2,000 to 8,000 acres) per year with yields of 1,100 to 3,900 kilograms per hectare (1,000 to 3,500 pounds per acre). The larger seeds are used for direct human consumption, and the small seeds are fed to birds. The oil content of the whole seed ranges from 25 to 30 percent.

In the 1940s an oil-type sunflower with seeds containing 30 to 35 percent oil was introduced into the United States. These oilseed types had been developed by plant breeders in the U.S.S.R. Production of these types was on a limited scale until 1964, when new high-oil varieties representing a second major improvement abroad were introduced from Russia to Canada. These varieties produced seed containing 40 to 50 percent oil, had improved disease and pest resistance, and had a yield potential equal to previously grown varieties. They were grown commercially for the first time in the United States in 1967.

The first oilseed sunflowers were open-pollinated varieties. The plants were 1.8 to 2.4 meters tall, with small, thin-hulled seeds. Because the varieties were open-pollinated, there was extreme variation in plant height,