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MARK-RECAPTURE STUDIES ON *VESPULA PENSYLVANICA* (SAUSSURE) QUEENS (HYMENOPTERA: VESPIDAE)

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Abstract.—A mark–recapture study of *Vespula pensylvanica* (Saussure) queens was conducted at two sites in California and one site in Hawaii. Queens flying during the spring returned repeatedly to specific locations. In the three years of the study, 21.6, 33.3, and 9.5% of marked queens were recaptured. A low return rate in 1989 may have been caused by a prolonged period of rainy weather that divided the spring queen flight period and perhaps increased mortality among early flying queens. The longest interval to recapture was 33 days, and some queens were recaptured on as many as three different days. Honeydew is attractive to spring queens, and they are able to return to the same gall repeatedly to feed.

Key Words.—Insecta, *Vespula pensylvanica,* mark–recapture, yellowjacket queen, honeydew

Knowledge of the extranidal behavior of yellowjacket (*Vespula*) queens is more limited than the corresponding body of knowledge for yellowjacket workers. This is to be expected, because workers vastly outnumber queens; successful colonies founded by a lone queen may generate hundreds or thousands of workers. Furthermore, flights of queens are usually restricted to periods of colony initiation in the spring and early summer, and mating and dispersal in the fall. The basic components of spring queen extranidal behavior, from the termination of dormancy to the rearing of the first worker adults, are well established (Akre et al. 1976, Ross 1983): after finding a nest site and initiating a nest, queens make trips to collect fiber, food, or water. Extranidal tasks are assumed by workers later in the colony cycle. Several studies have shown that marked workers will return to a specific location to make repeated collections of an abundant resource (Kalmus 1954, Broekhuizen & Hordijk 1968). Thus far, there is only scant evidence of the tendency of queens to return to previously visited areas. Palmer-Jones et al. (1949) reported that two marked *V. germanica* (Fabr.) queens returned repeatedly over 16 days to a vine sprayed with a glucose solution, and that a queen captured at another site (also sprayed with sugar) was marked, released a mile (1.4 km) away, and observed 9 days later at the capture site. In a laboratory study, Ross (1983) observed *Vespula* queens returning to the exact same site to gather plant fiber, but this was within an enclosed foraging chamber with a volume of only 1.7 liters. In the present study, a mark–recapture technique was employed to learn more about the behavior of spring queens of *V. pensylvanica* (Saussure).

MATERIALS AND METHODS

Studies were conducted at different localities for each of three years. From 15 Apr–2 Jun 1985, an area of approximately 0.65 hectare in Sunol Regional Wil-

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derness (140 m el.), Calaveras County, California, served as the study site. Nearly all captures (35 of 37) were made on foliage of a stand of *Quercus agrifolia* Née, oak trees. This species, common throughout the region, was the dominant plant within the restricted confines of the study area. Other plants present in substantial numbers in the understory and adjacent fields included wild oat (*Avena fatua* L.) and thistles (*Cirsium* spp.). From 27 Feb–15 Jul 1986, an area of approximately 0.18 hectare on the campus of the University of California, Berkeley (80 m el.), Alameda County, California, was studied. The site was fairly open, with a few *Q. agrifolia.* The ground cover where most queens were captured consisted mostly of Kikuyu grass (*Pennisetum clandestinum* Hochstetter ex Chiovenda), which was trimmed regularly to less than 4 cm high, and ivy (*Hedera helix* L.). From 24 Mar–15 Jul 1989, the study site consisted of six *Pinus* sp. trees in a clearing at Volcano (1175 m el.), Hawaii County, Hawaii. The trees were close enough to provide a continuous array of foliage, and the occupied ground surface area was equivalent to 8 square m.

In 1985, queens were netted by hand, anesthetized by placing them briefly in a chamber containing dry ice (solid CO_2), marked on the dorsum of the thorax with either Liquid Paper® or Testors enamel®, and released in a shaded spot to recover. Because accidental overexposure to dry ice caused some mortality, in subsequent years queens were removed from the net by firmly grasping the thorax with forceps, marked, and immediately released. All queens captured for the first time on any given day were marked with the same color; recaptured marked queens were marked with a second color, and so on, so that the capture history of any individual queen was recorded.

In 1985, observations were made during nine field trips to the study site; recapture data included queens recaptured and marked a second time ($n = 3$), and queens observed with sufficient clarity to determine the date of original capture ($n = 5$). In 1986 and 1989 the study sites were in areas that were checked several times daily; when queens were present a sampling session was initiated immediately. Only recaptured marked queens were included in the results for 1986 and 1989. The duration of sampling sessions was variable, ranging from a few minutes to several hours. The total time spent netting queens at each site was 40–50 h.

Results

In 1985, queens were captured from 15 Apr–30 May. However, the number of queens flying on the initial sampling date suggests that the queen flight period had begun earlier in the season. Eight (21.6%) of 37 marked queens were recaptured or sighted again (Fig. 1a). No individual queens were observed on more than two different days, and the longest interval between captures was 33 days. Queen extranidal activity apparently ceased by 2 Jun, when only workers were observed in the field.

Throughout the spring, *V. pensylvanica* queens, workers, and *Mischocyttarus flavitarsis* (Saussure) foragers were observed on *Q. agrifolia* bud galls of the cynipid *Callirhytis carmelensis* Weld. The gall, which produces sweet honeydew, was common on all *Q. agrifolia* in the study area. When vespid wasps landed on galls, they fed on honeydew by licking the gall surface. On 30 May a uniquely marked *V. pensylvanica* queen was observed to visit the same gall four separate times in two hours. Once, a *M. flavitarsis* forager approached and hovered within 2 cm

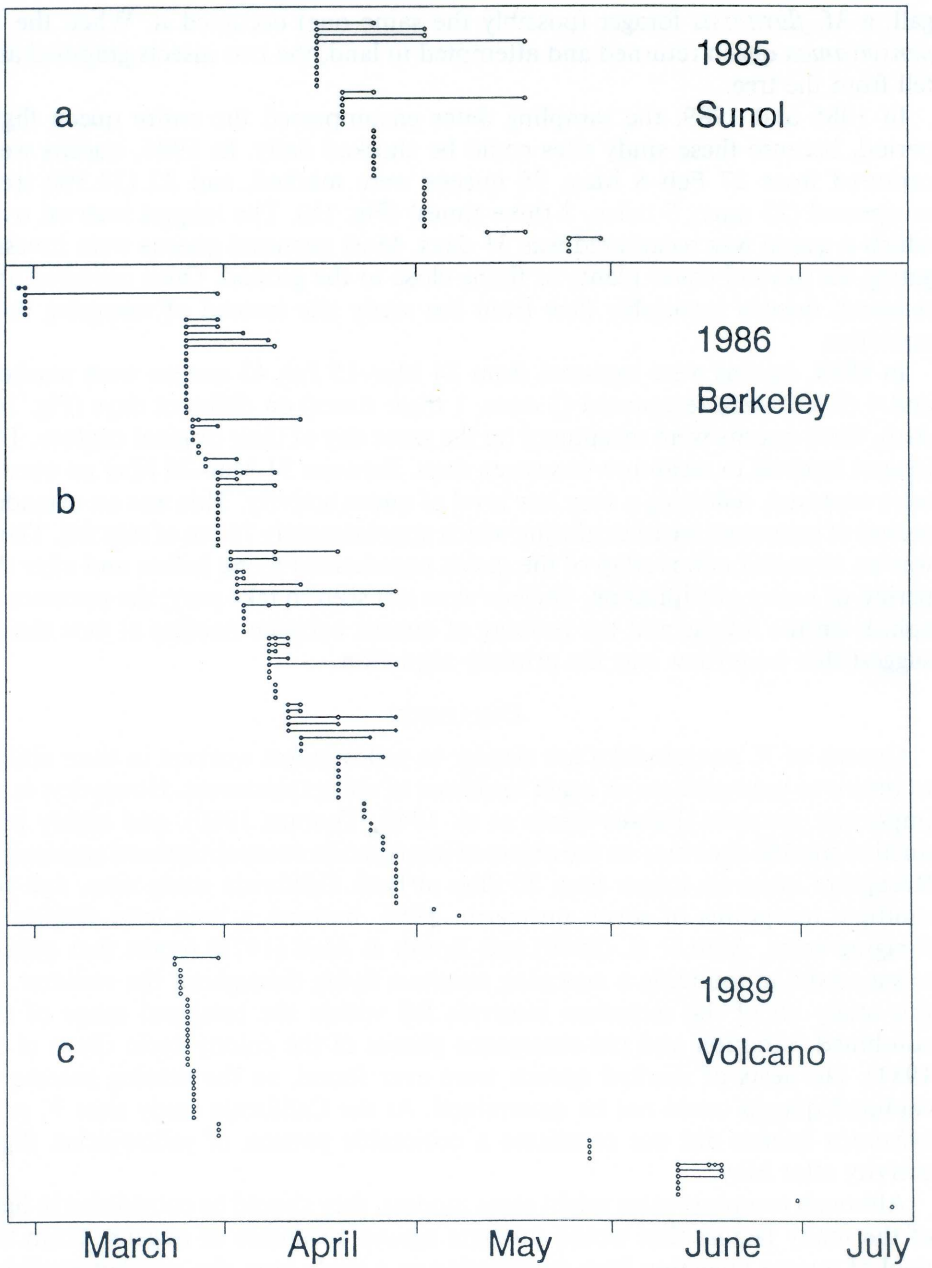

Figure 1. Mark–recaptures of *V. pensylvanica* queens; (a) Sunol, 1985; (b) Berkeley, 1986; (c) Volcano, 1989. Each horizontal row represents an individual queen; circles indicate capture dates; circles connected by a line indicate recaptured individuals.

when the marked yellowjacket queen was on the gall. In response, the *V. pensylvanica* queen interrupted her feeding to face the intruding wasp and raised her fore body and forelegs in an apparently agressive stance, causing the *M. flavitarsis* to retreat. Later, when the *V. pensylvanica* queen had temporarily vacated the

gall, a *M. flavitarsis* forager (possibly the same one) occupied it. When the *V. pensylvanica* queen returned and attempted to land, the two insects grappled and fell from the tree.

In 1986 and 1989, the sampling dates encompassed the entire queen flight period, because these study sites could be checked daily. In 1986, queens were captured from 27 Feb–8 May; 96 queens were marked, and 32 (33.3%) were recaptured (25 once, 5 twice, 2 three times) (Fig. 1b). The longest interval over which a queen was recaptured was 31 days. Most captured queens were investigating the ground cover plants or flying close to the ground. Once captured and released, queens invariably flew from the study site instead of resuming their activities.

In 1989, queens were captured from 24 Mar–15 Jul; 43 queens were marked, and 4 (9.3%) were recaptured (3 once, 1 three times) on different days (Fig. 1c). Also, three queens were recaptured on the same day of their original capture. The longest interval to recapture was seven days. Between 31 Mar–28 May no queens were captured, reflecting a very low level of queen activity. This was an extended period of inclement weather, during which approximately 76 cm of rain fell. There was an apparent nonoverlap of the queen populations flying before and after the period of heavy precipitation. Queens were not seen to take prey; the presence of aphids on the foliage and the probing of queens between needles at new shoots suggest that honeydew was the primary attraction.

Discussion

Queens of *V. pensylvanica* are similar to yellowjacket workers in their ability to return to approximate or exact locations to collect resources. Honeydew is an important resource (Palmer-Jones et al. 1949, Thomas 1960), and highly productive specific sites may be the object of interspecific competition and aggression. Recapture intervals longer than 30 days at both California study sites, and the multiple recaptures of seven queens in 1986, indicate a long term fidelity to foraging areas. Akre et al. (1976) and Roush & Akre (1978) report that queens unsuccessful at founding a nest may continue flying throughout the summer. In this study all of the recapture intervals fell within the temporal range of the combined initiation and pre-emergence phases of the colony cycle (Ross et al. 1981). No nests of marked queens were ever found, so the nesting success of captured queens could not be determined. At the California study sites *V. pensylvanica* queens did not constitute a noticeable portion of yellowjacket flight activity after May.

Although recapture rates might seem modest, they should be considered in light of the many factors that would mitigate against recapture of queens. From the pool of queens emerging from hibernation in a study area, the number available for recapture decreases progressively during the spring through mortality, emigration, and successful colony development. Immigration of queens into the study area increases the number of unmarked individuals that were not present on the initial sampling dates. The study areas presumably constituted small fractions of the total *V. pensylvanica* queen foraging ranges, the number of queens captured was only a fraction of those observed, and the time spent sampling was small compared to the total time available for queen foraging.

Several factors might have contributed to the low recapture rate (9.3%) in 1989.

The study site was by far the smallest of the three. None of the queens marked before the 58 day rainy period (n = 31) were recaptured after that time. This interval was longer than the entire period from nest initiation to extranidal worker foraging of a typical colony (Ross 1981). The absence of worker activity by 1 Jul and the very low forager population during the remainder of the year suggest that queens were unsuccessful in establishing colonies in 1989. Unfavorable spring weather has been associated with seasons of yellowjacket scarcity (presumably due to early nest failure) in the Pacific Northwest and elsewhere (Akre & Reed 1981).

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