Invasion and Colonization of Upper Elevations on East Maui (Hawaii) by *Vespula pensylvanica* (Hymenoptera: Vespidae)

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ABSTRACT The western yellowjacket *Vespula pensylvanica* (Saussure) has become established on the island of Maui since its initial appearance in 1978. On eastern Maui, colonies show a bimodal elevational distribution with peaks at 600–1,050 m and 2,400–2,700 m. At upper elevations (>2,000 m) nests occur at disproportionate frequencies beneath *Styphelia tameiameiae* (Chamisso and Sclechtendal) Mueller bushes. This plant also supports a honeydew-producing mealybug *Pseudococcus nudus* Ferris, which provides a dietary supplement for adult wasps. On Maui, *V. pensylvanica* retains its typical annual colony cycle, but in some years colonies overwinter and persist into a second year. Overwintered colonies are ≈20 times larger than annual colonies. Some overwintered colonies undergo at least two distinct episodes of queen cell construction. Evidence is provided in support of two distinct routes to requeening (a likely requirement for successful colony overwintering): outside queens join a colony late in the season, and queens produced within the colony at the end of the first season remain for the second season.

KEY WORDS Insecta, *Vespula pensylvanica,* biological invasion, *Pseudococcus nudus*

SOCIAL INSECTS are not native to the Hawaiian Islands (Perkins & Forel 1899). However, many social species have been inadvertently introduced, and some of these have become serious pests of humans and their activities (Chang 1988, Reimer et al. 1990). Less well documented, but of considerable importance, are their detrimental effects on native ecosystems (Williams 1927, Medeiros et al. 1986, Gambino et al. 1987, Reimer et al. 1990).

Several species of yellowjackets (*Vespula*) have experienced broad range expansions since 1900, invading regions devoid of a preexisting vespine fauna (Akre & MacDonald 1986) and even areas with well-established congeneric species (Donovan 1984, MacDonald & Akre 1984). Queens commonly hibernate in crevices in wood, facilitating passive long-range, human-assisted dispersal, and viable populations can apparently be derived from a single inseminated queen. *Vespula pensylvanica* (Saussure), native to western North America, is among the social insects unintentionally introduced into Hawaii. It was first recorded from Kauai in 1919 (Williams 1927); the first Maui record (of a single worker, elevation, 325 m) in March 1978 (Nakahara 1980) suggested that at least one colony had been established on the island during the previous year. Colonies detected at widely separated localities (12 km) on Haleakala volcano during 1979 indicated that upper elevations (>2,000 m) of East Maui were vulnerable to invasion. Subsequent persistence of the yellowjackets for >10 yr verified the successful establishment of a high-elevation population.

In this paper, we describe characteristics and adaptations of *V. pensylvanica* in its recently invaded habitat and focus on its reproductive cycles, nest site selection, and feeding activities. We compare these facets of basic biology on upper Haleakala volcano with what is known about the species in its native range in western North America, drawing from the studies of Duncan (1939), MacDonald et al. (1974), Akre et al. (1976), Roush & Akre (1978), and unpublished data collected by P.G.

Materials and Methods

Study Site. The main study site comprised ≈1,000 ha on the northwest slope of Haleakala volcano within Haleakala National Park (HALE), ranging from 2,050 to 3,050 m elevation. Haleakala is a dormant volcano comprising the eastern portion of the island of Maui. Volcanic bedrock in the study area is exposed in some places; in other places it is covered with a thin mantle of volcanic ash, eroded soil, and partly eroded volcanic rocks. Pasture vegetation immediately below the park boundary, composed mostly of introduced grasses, is replaced by subalpine shrubland vegetation within the park; vegetation becomes increasingly sparse at higher

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elevations and covers <5% of the ground above 2,900 m. Two groves of introduced trees (conifers and *Eucalyptus* spp.) at 2,050 and 2,600 m cover <20 ha.

Population Monitoring. *V. pensylvanica* forager populations were monitored at HALE from June 1981 to December 1988 using traps baited with the synthetic attractant, *n*-heptyl butyrate (Davis et al. 1969). A trap consisted of a clear 1.5-liter closed plastic cup containing 400 ml water and 5 ml vegetable oil. A glass vial attached to the lid contained a cotton wick charged with 1 ml of attractant. Four holes (diameter, 1 cm) near the top of the container walls allowed wasps to enter the trap. At ≈10-d intervals, the number of captured yellowjackets was counted and the fluids replaced. Ten traps were deployed on the northwest slope from 2,090 to 3,050 m elevation. To test for the effect of elevation on forager density, the total annual number of yellowjackets captured at each trap was analyzed in a randomized block analysis of variance (ANOVA) with elevation as the fixed variable; means were separated using Duncan's multiple range test, calculated using the GLM procedure of SAS Institute (1985, 183–260).

To discern seasonal patterns in foraging worker populations, the number of workers captured per week, pooled for all traps, was calculated for each month from 1982 to 1988 and analyzed in a randomized block ANOVA with month as the fixed variable; means were separated using Duncan's multiple range test. *V. pensylvanica* queens are also attracted to *n*-heptyl butyrate, and monthly trap capture data for queens were analyzed separately, using the same ANOVA procedures. In addition, flying queens were occasionally netted in the field; their reproductive status was evaluated as described below for queens captured from active nests.

Supplementary information useful in determining population trends was obtained from the Hawaii State Department of Health (DOH), the agency that responds to public reports of nuisance yellowjacket colonies. Data collected by the DOH from 1980 to 1988 regarding colony distribution included date, location, and elevation. Observations were also made in the field by the authors, National Park Service (NPS) and DOH staff, and by visiting scientists, with special attention to the flight activities of reproductives.

Nest Sites. During the summers and falls of 1986, 1987, and 1988, the study site was searched for active colonies. Seventeen of 30 nests were found in soil beneath the native shrub *Styphelia tameiameiae* (Chamisso and Schlechtendal) Mueller, the dominant ground cover species. To test if nests were preferentially associated with *S. tameiameiae*, nest distribution was compared with a vegetational ground cover analysis. One hundred points were sampled in a grid (2,700 m by 200 m) straddling the 2,620-m contour line, representative of habitat where yellowjacket foragers and nests were most abundant. At each sampling point a PVC-pipe square enclosing 400 cm^2 was randomly thrown into the air, and the spot where it landed was examined. The substrate within the frame was assigned to one of three categories: rock, if a 0.25-cm diameter aluminum nail could not be sunk to a depth of 3.0 cm anywhere within the sampling square; *Styphelia*, if live foliage of the plant was found anywhere within the square; other, if it fit neither the rock nor *Styphelia* category. Because the *Styphelia* category included some samples where *S. tameiameiae* foliage did not fill the square, this procedure likely overestimated the proportion of *S. tameiameiae* ground cover, thus providing a conservative test of *S. tameiameiae* nesting association, analyzed by a χ^2 test.

Colony Analysis. When an active colony was found, we attempted to collect the following data: elevation, date of first discovery, number of entrances, foraging rate (mean number of worker sorties per minute, measured over a 5-min period during fair weather), and characteristics of the ground directly above the subterranean nest. To assess the variability in numbers of nest entrances in different years, nests were categorized as having one or more than one entrance; observed frequencies were compared with frequencies expected based on the overall totals, using the *G* test (Sokal & Rohlf 1981).

A subset of nests was excavated and brought to the laboratory for analysis (1 in 1986, 5 in 1987, 11 in 1988). Data gathered from excavated nests included: date of excavation, nature of surrounding substrate, general shape of the nest, number of combs, estimated total number of cells, number and location of large (queen) cells, and approximate brood composition. When present, the sex was determined for subsets of pupae and mature larvae. Male pupae can be distinguished by their long antennae; male larvae can be determined by the presence of testes, visible through the dorsal abdominal integument (Marchal 1896).

Comb areas were computed by tracing outlines on heavy paper, weighing the cut-out shapes, and applying a conversion factor derived from the weights of paper pieces of known area. For 10 of the 1988 nests, direct cell counts were made on 46 of 55 possible combs. The mean conversion factor (4.9 cells/cm^2) was used to estimate the number of small cells for the remaining combs of nests from all three years. For nests containing large cells, a conversion factor (3.5 cells/cm^2) was derived from representative subsamples of three combs of nest 8601 and two combs of nest 8603. For some nests the paper of the lower combs had deteriorated before excavation; in these cases, comb numbers and areas were estimated from the distribution of meconial debris. Cell sizes could not be determined for these combs, and estimates of numbers of cells were calculated using the small cell conversion factor, a procedure that slightly underestimated numbers of large cells and overestimated numbers of small cells on combs containing large cells. The reproductive status of captured queens was determined by external signs of wear on the wings and gastral tergae (Spradbery 1973). For some queens, dissections were performed to provide additional data on internal development of ovaries and fat body, and presence or absence of sperm in the spermatheca.

Feeding Behavior. Carbohydrate foraging activities of males and workers were examined in the field. The number of yellowjacket landings (n = 1,042) on various plants in the study area was recorded, and yellowjacket activity on *S. tameiameiae* was examined more closely. The foliage of some plants was infested with the honeydew-producing mealybug *Pseudococcus nudus* Ferris; sprigs at the tips of growing branches were observed for yellowjacket visits. After a yellowjacket landed on a sprig, the total number of visits to that sprig in the next 10 min was recorded. The terminal 4 cm of the sprig was clipped, placed in a glass vial, and refrigerated in the laboratory until it could be dissected. Eighty sprigs (no more than 5 per plant) that had been visited at least once, and 40 randomly selected sprigs that had received no visits in a 20-min period, were collected. In the laboratory the number of mealybugs was counted and the honeydew accumulation scored (0, none; 1, trace; 2, light; 3, heavy). Data for honeydew rating versus number of mealybugs, and number of *V. pensylvanica* visits versus number of mealybugs, were analyzed by the Spearman rank correlation test (Dixon 1985).

Voucher specimens of *V. pensylvanica* and *P. nudus* are deposited in the collection of the Bernice P. Bishop Museum, Honolulu.

Results

Population Monitoring. Fluctuations in forager populations above 2,073 m, measured as pooled number of foragers captured weekly in all traps, are presented in Fig. 1. Males were rarely captured in monitoring traps. The strong seasonal character of the cycles, with highest worker populations occurring from August through October, and low populations occurring during the winter and early spring ($F = 5.34$; df = 11, 72; $P < 0.0001$) (Table 1) corresponds well with typical mainland activity cycles. However, worker activity on Maui does not drop to zero in all years. The exceptions (1981–1982, 1982–1983, 1983–1984, 1985–1986) indicate that activity at some colonies was sufficiently prolonged to overlap with the onset of worker activity from newly founded colonies.

There is also a seasonal pattern in the appearance of foraging queens, with most appearing from May through July ($F = 3.96$; df = 11, 72; $P < 0.0002$) (Table 1). However, 32 (14.0%) of 228 queens were captured after 1 August, and in 1984 queens were captured as late as October. Three foraging queens captured by net in late August 1987 had been inseminated and had moderately developed ovaries. A fourth queen, also inseminated, was captured on 1 September 1987 as she returned (without hesitation) to colony 8707. All four of these queens had frayed wings, but lacked the dorsal gastral markings that would indicate repeated oviposition.

The combined NPS (36 nests) and DOH (107 nests, including 3 in HALE) data on nest distribution according to elevation are presented in Fig. 2. Apparently, nests are unevenly distributed, with peaks of abundance at 750–900 m and 2,550–2,700 m. A sampling bias in the collection of these data must be noted: nests closer to areas of human activity are most likely to be discovered and reported, and most residences and human activities occur below 1,500 m. However, because workers usually forage close to the nest (Rogers 1972, Akre et al. 1975), the systematic sampling of foragers conducted within HALE corroborates the general shape of the higher elevation portion of Fig. 2, demonstrating an elevation effect above 2,000 m ($F = 7.18$; df = 9, 70; $P < 0.01$), with a peak at 2,591 m (Table 2).

Nest Sites. Of 100 grid substrate samples, 31 (31.0%) contained *S. tameiameiae;* 17 of 30 nests (56.7%) were located beneath *S. tameiameiae* bushes. Thus, there is a positive association with this plant ($n = 30$, $\chi^2 = 11.28$, df = 2, $P < 0.01$).

Colony Analysis. With regard to foraging rates and nest structures, colonies found in 1987 ($n = 9$) and 1988 ($n = 18$) resembled typical annual colonies. In contrast, the characteristics of colonies found in 1986 ($n = 6$) indicated much higher colony populations and suggested that they were already in their second year. Activity at these colonies ceased during the winter of 1986–1987. Of the six colonies monitored in September 1986, five had foraging rates consistently greater than 300 sorties/min. The highest foraging rate at colonies monitored during 1987 ($n = 7$) or 1988 ($n = 13$) was 53 sorties/min; the busiest of 11 annual colonies observed in California during 1985–1987 had 55 sorties/min.

The 1986 colonies also had more entrance holes (1, 2, 4, 4, 5, and 15, respectively) than those of subsequent years ($G = 13.20$, df = 2, $P < 0.01$). In 1987, 5 nests had one entrance and 1 nest had two; in 1988, 15 nests had one entrance and 1 nest had two. Some of the entrances of 1986 nests were highly modified, in contrast to the modest adjustments that can be expected in an annual colony (Duncan 1939, Spradbery 1973, Akre et al. 1980). Wasp paper had been extensively applied around some entrance holes, and a curious turret made of packed fine soil, ≈12.5 cm in diameter, was added to one entrance of nest 8602 (Fig. 3).

Data from excavated nests are summarized in Table 3. Nests of 1987 ($n = 3$) and 1988 ($n = 11$) were basically spherical in shape, and numbers of small cells ($n = 14$; $\bar{x} = 3{,}497$; range, 558–8,086) were within the ranges recorded from annual colonies in Washington (MacDonald et al. 1974) and

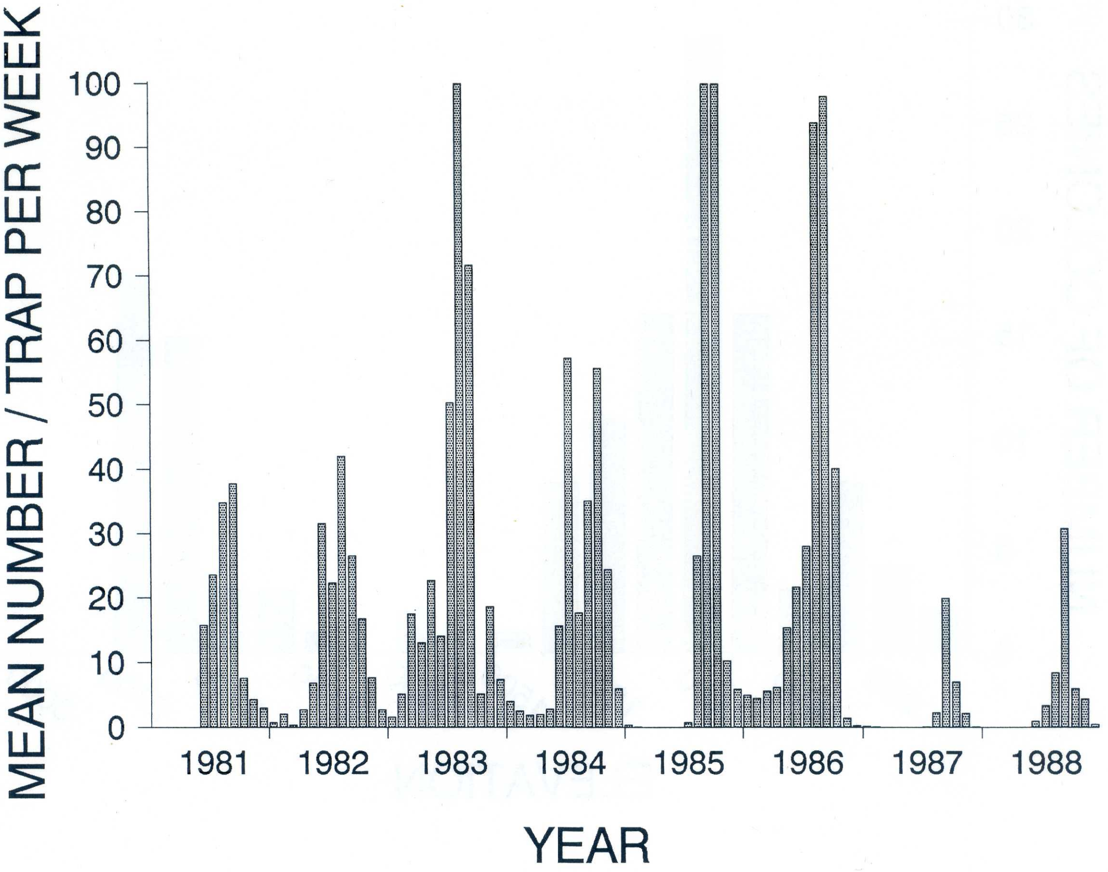

Fig. 1. Yellowjacket forager population trends at Haleakala National Park, 1981–1988.

Oregon (Roush & Akre 1978). None of these colonies had begun large cell construction. Overall colony health, as indicated by vigor of larvae and regular concentric distribution of immatures in combs, was variable. Of 11 colonies for which data are available, 9 (81.8%) had at least 10% male immatures. For four colonies, no queen was recovered; three of these showed symptoms of queen loss (irregular pattern of brood in combs, high percentage of male brood). In eight colonies, a single queen with frayed wings and extensive gastral markings (indicative of a laying or "mother" queen [Ross 1983]) was recovered. Two colonies had a single inseminated mother queen with gastral markings, as well as smaller queens that lacked gastral markings, but were inseminated and had well-developed ovaries (in colony 8804, $n = 2$, largest eggs = 2.0 and 1.6 mm; in colony 88816, $n = 1$, largest egg = 2.2 mm).

Table 1. Seasonal activity of *V. pensylvanica* workers and queens at Haleakala National Park

Month	No. workers trapped/wk	No. queens trapped/mo
Jan.	1.60a	0.00a
Feb.	2.07a	0.57a
March	3.63a	1.14a
April	3.43a	0.57a
May	6.81a	8.71bc
June	11.99ab	13.14c
July	23.17abc	4.29ab
Aug.	41.54cd	1.86a
Sept.	54.59d	1.86a
Oct.	32.97bcd	0.86a
Nov.	9.86a	0.00a
Dec.	3.27a	0.00a

Means within columns followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple range test [SAS Institute 1985]).

Nests found in 1986 differed strikingly from those of subsequent years. The number of small cells per nest was ≈20 times greater ($n = 3$; $\bar{x} = 65{,}737$; range, 58,289–80,508), and large (queen) cells were also constructed. In nest 8603 there were two distinct episodes of large cell construction, separated by three combs containing small cells exclusively. In nest 8606, only one episode of large cell construction was detected. The bottom two thirds of both of these nests were too deteriorated to accurately determine the composition of the bottom combs.

Nest 8601 showed many symptoms of decline (modest foraging rate, removal of dead larvae by workers, abundant males) when it was excavated in September 1986. It was composed of ≈20 comb

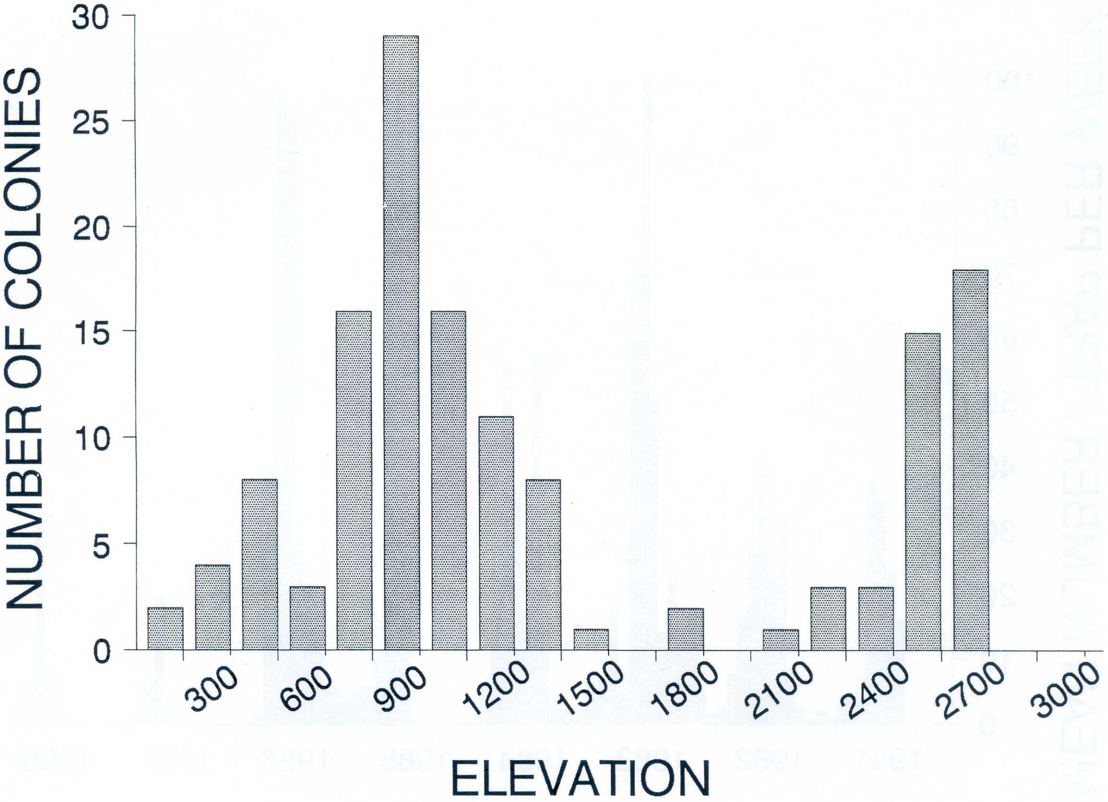

Fig. 2. Distribution of yellowjacket colonies on Maui according to elevation.

levels, with 2,107 large cells located in the centers of combs #7–9, completely surrounded by small cells. This arrangement, similar to that found in overwintered *V. germanica* (F.) nests in New Zealand (Thomas 1960), contrasts with the more typical peripheral location of large cells recorded elsewhere for annual *V. pensylvanica* colonies (MacDonald et al. 1974, Roush & Akre 1978).

Table 2. Mean annual numbers of *V. pensylvanica* foragers captured per *n*-heptyl butyrate trap at Haleakala National Park, 1982–1987

Elevation, m	$\bar{x}$ ± SD
2,073	79.88 ± 133.32a
2,134	198.50 ± 235.49a
2,256	313.88 ± 423.04ab
2,347	955.75 ± 810.79ab
2,438	631.25 ± 624.27ab
2,591	2,632.75 ± 1,614.39c
2,682	1,210.75 ± 1,150.06b
2,835	973.00 ± 948.08ab
2,957	353.75 ± 527.59ab
3,018	218.50 ± 304.72a

Means within a column followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple range test [SAS Institute 1985]).

Feeding Behavior. The plant *S. tameiameiae* was a favored destination of yellowjacket foragers, receiving 942 (90.4%) of 1,042 recorded visits. Honeydew on *S. tameiameiae* shoots was clearly associated with *P. nudus*, as indicated by the correlation between the numbers of *P. nudus* and the

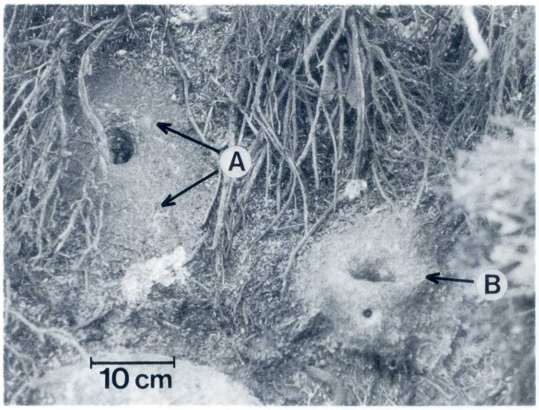

Fig. 3. Entrances to colony 8602. (A) Extensive papering of soil surrounding entrance. (B) Constructed turret containing two entry holes.

Table 3. Characteristics of *V. pensylvanica* nests excavated at Haleakala National Park

Excavation date	N	No. small cells		No. large cells	
		$\bar{x}$	Range	$\bar{x}$	Range
21 Sept. 1986	1	58,414		2,107	
31 May 1987[a]	2	69,399	58,289–80,508	1,220	936–1,503
1 Sept. 1987	3	2,795	1,792–4,150	0	
10 Sept. 1988	2	695	558–832	0	
6 Oct. 1988	5	4,739	2,423–7,644	0	
14 Nov. 1988	4	3,872	2,243–8,086	0	

[a] Numbers of cells estimated assuming that all cells in deteriorated lower combs were small cells. These nests were inactive when excavated, and belong to the same cohort as the nest excavated in 1986.

amount of honeydew present on the shoots (Spearman's $r_s = 0.621$, df = 118, $P < 0.001$ [Dixon 1985]). Yellowjacket attraction to heavily infested shoots is indicated by the correlation of number of visits per shoot and the number of mealybugs per shoot ($r_s = 0.394$, df = 118, $P < 0.001$). Workers and males of *V. pensylvanica* on *S. tameiameiae* sprigs probed and licked between leaves down to the stems (Fig. 4), where the mealybugs and their honeydew exudate were most concentrated.

Discussion

Vespula pensylvanica has colonized large areas of East Maui since its initial appearance in 1978, but with a nonuniform distribution. Yellowjacket nests are most abundant between 600 and 1,050 m elevation. The scarcity of nests below 600 m, a pattern found throughout the Hawaiian Islands (Nakahara & Lai 1981), indicates an inability to adapt to truly tropical conditions. In general, temperatures decrease with increasing altitude on Maui, and at upper elevations the annual temperature ranges resemble those of the temperate areas that constitute much of *V. pensylvanica*'s native range. However, there is a gap in nest distribution between 1,350 and 2,100 m elevation, with a second peak above 2,300 m. A physical factor that may account for the midelevation discontinuity is the Pacific trade wind inversion, which is strongest during the summer months (Mendonca & Iwaoka 1969). On Maui it is manifested as a cloud layer that frequently produces dense ground fog at elevations from 1,350 to 2,000 m, sometimes extending up to 2,300 m (Blumenstock & Price 1972); skies are generally clearer at higher and lower elevations. Decreased insolation and higher relative humidity just below the inversion layer might impair successful nest establishment there.

Fig. 4. *Vespula pensylvanica* male on *Styphelia tameiameiae* foliage. Arrow indicates aggregation of the honeydew-producing mealybug, *Pseudococcus nudus*.

In its native range, *V. pensylvanica* typically adheres to the temperate-adapted annual colony cycle characteristic of the Vespinae (Akre & MacDonald 1986). Although this basic annual pattern is retained on Maui, overwintering colonies are a significant component of *V. pensylvanica* populations at HALE in some years. Apparently, the entire cohort of nests found in 1986 had overwintered from 1985. In at least some cases, colonies may undergo two separate episodes of queen rearing.

Overwintered colonies do not differ from annual colonies merely in their duration; they also generate more yellowjackets. The number of small cells per nest is ≈20 times greater in overwintered colonies, and the larger populations of second-year colonies produce elevated foraging rates. The single entrance hole typical of annual nests is often inadequate to allow smooth passage of immense numbers of workers, and very large colonies may resolve this problem by constructing additional apertures. Multiple entrances might also facilitate air circulation through the nest.

The mechanisms involved in overwintering of *Vespula* colonies have not received detailed study. Climate may be the overriding extrinsic enabling factor. In its native range, *V. pensylvanica* colonies are known to overwinter only in coastal California (Duncan 1939; P.G., unpublished data) and in warm interior regions of southern California (R. Wagner, personal communication), where episodes of freezing temperatures are uncommon and brief. Except for the highest elevations, the East Maui temperature regime is also sufficiently mild to permit overwintering.

Intrinsic factors also influence the likelihood of a colony overwintering. Continuous presence and activity of workers would seem necessary. The concurrent construction of large and small cells in the overwintered Haleakala colonies indicate that a complete transition to the reproductive phase was avoided at the end of 1985; these colonies then reverted to a second (primarily) ergonomic stage (sensu Oster & Wilson 1978) in 1986.

Overwintering colonies are almost certainly polygynous (Duncan 1939, Spradbery 1973, Ross & Visscher 1983), indicating a need to requeen. Two distinct requeening mechanisms have been proposed for overwintering *Vespula* colonies: retention of daughter queens (Edwards 1980, Ross & Visscher 1983), and recruitment of "joiner" queens (Akre & Reed 1981, Ross & Matthews 1982). Because of the difficulty of determining the origin of post-callow queens, evidence for the retention of daughter queens is circumstantial at best. At HALE, the reversion from large- to small-cell construction (indicating the presence of new queens as the colonies entered their second ergonomic phase) is consistent with the retention of daughter queens. In contrast, joiner queens can be easily identified if they are present in polygynous colonies lacking large cells. Late-flying spring queens, which are seen in some years in mainland populations (Akre et al. 1976, Roush & Akre 1978) are likely joiner candidates. In most years at HALE, there is a pool of potential joiner queens present after colonies are well established; foraging queens are regularly captured in *n*-heptyl butyrate traps during August, and in some years as late as October (new queens dispersing from natal nests are not attracted [MacDonald et al. 1973]). Although it is unlikely that the two polygynous colonies discovered in the fall of 1988 would have successfully overwintered, they demonstrate the ability of colonies to requeen using joiners.

The evergreen plant *S. tameiameiae* may contribute strongly to the success of *V. pensylvanica* in HALE. The majority of nests were located in soil beneath *S. tameiameiae* shrubs, where accumulated organic matter from the plant itself likely provides insulation from wetting and harsh weather. Methods used in this study cannot determine if *S. tameiameiae* is a preferred site for queens starting nests, or if nests are started more randomly, with those beneath *S. tameiameiae* becoming more successful and more likely to be detected. *S. tameiameiae* also provides food resources for yellowjacket colonies. As a dominant plant species in the study area, its associated arthropod fauna is available to yellowjackets foraging for proteinaceous food. Also, it supports populations of *P. nudus*, which in turn generate honeydew, an attractive carbohydrate source.

As a predaceous alien species, *V. pensylvanica* poses a threat to the arthropod components of Maui's native ecosystems, which include many endemic species (Gambino et al. 1987). When colonies overwinter, this potentially disruptive effect is intensified by the elevated mass of prey arthropods collected to support colony populations and the extended time period over which predation occurs.

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