Technical Report 86
Yellowjacket (Vespula pensylvanica)
Biology and Abatement in the National Parks of Hawaii

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The western yellowjacket *Vespula pensylvanica* (Saussure) has become widely established in the Hawaiian Islands, where it exhibits a high degree of reproductive plasticity. Although most colonies in Hawaii Volcanoes and Haleakala National Parks adhere to the basic annual cycle dominant throughout this wasp’s native range in western North America, overwintered colonies were detected in some years. Polygyny, achieved by adding queens to an established colony, is a likely prerequisite for successful overwintering. The large size of overwintered colonies and some annual colonies (with more than 300 worker sorties per minute from the nest) results in very heavy predation on local arthropod biota. Workers of *Vespula pensylvanica* take a wide variety of prey at or near plant and soil surfaces. Populations of highly precitive endemic arthropods may in some instances be unable to recover from such intense predation pressure. Although even local eradication of *V. pensylvanica* is not feasible, toxic baiting trials using Knoxout 2FM in canned chicken bait, with enhancement of bait acceptance with heptyl butyrate, were in many instances effective in drastically reducing yellowjacket forager populations. Toxic baiting was most consistently effective in high-elevation shrubland and least effective in forest situations. A protocol is presented for use by resource managers in dealing with yellowjacket threats to native biota and to visitors.
PREFACE

The invasion of the Hawaiian Islands by non-native species has been to the overall detriment of native Hawaiian ecosystems. The damage caused by large mammals such as pigs and goats is on a scale readily apparent to the human eye; perhaps for this reason, the effects of feral mammals, and ecosystem recoveries after reductions in their populations, are fairly well documented. In contrast, the effects of alien insects occur on a much finer scale, and are more easily overlooked. While our understanding of the roles of invertebrates in native Hawaiian ecosystems lags behind that for plants and larger animals, native and alien insects are no less worthy of investigation.

The western yellowjacket *Vespula pensylvanica* (Saussure) was first recorded from the Hawaiian Islands in 1919. This wasp species is troublesome for several reasons. First, it interferes with human activities. The sting, which has evolved as an anti-vertebrate defense mechanism, is painful. For the small percentage of humans allergic to yellowjacket venom, a sting can cause severe medical problems such as anaphylactic shock. Estimates of the number of sting-related fatalities in the United States range from several dozen to several hundred per year, but only one, an O'ahu construction worker in the mid-1980s (G. Komatsu, pers. comm.), has been recorded from Hawai'i. Most people are familiar with the yellowjacket's stinging ability, and dense populations can interfere with people's outdoor activities through intimidation. Foraging yellowjackets are attracted to many of the foods that people eat, and by perfumes and other fragrances. The higher the yellowjacket population, the more likely they are to sting or otherwise disturb people. However, even at low population levels, there can be unfavorable encounters with wasps if a nest is accidentally disturbed. Yellowjackets are sensitive to vibrations, and subterranean nests are not easy to detect and avoid. Recreational, research, or resource management activities may disturb nests sufficiently to induce stinging behavior; unfortunately, many nests are discovered this way.

The second category of yellowjacket problems concerns their interactions with other organisms, mostly arthropods, and applies only in areas where yellowjackets are established as alien species. Yellowjackets are predators, feeding on a wide range of arthropod taxa, with great potential for negative impact on the native fauna. This is especially significant in the Hawaiian Islands, which have a high degree of endemism, and where arthropods that have evolved in the absence of social insects may lack the anti-predator defensive mechanisms selected for elsewhere. Native insects play important roles in the functioning of Hawaiian ecosystems, be it as pollinators, predators keeping herbivores in check, detritivores, or food for vertebrates. Depletion of local populations of certain species through yellowjacket predation may disrupt the overall system in unpredictable ways. Thus, yellowjacket abatement in the Hawaiian National Parks is an important component of the National Park Service's overall strategy of enhancing biodiversity through the preservation of natural ecosystems.

This report has several objectives: 1) to document the invasion of Maui and Hawai'i by VP, and identify factors influencing its successful establishment; 2) to describe VP's impact on the native Hawaiian arthropod fauna, to provide justification for a VP pest management program; and, 3) to furnish information on practical and logistical successes and problems encountered in VP abatement research, to be taken into consideration by park resource managers in designing and implementing overall pest management activities for the parks. The report is divided into three sections, each summarizing investigations of different aspects of *V. pensylvanica* biology in the Hawaiian Islands: I. Yellowjacket natural history, including significant adaptations to the Hawaiian environment; II. Yellowjacket predation on arthropods; and III. Yellowjacket abatement.
SECTION I
YELLOWJACKET NATURAL HISTORY

INTRODUCTION

Yellowjackets (Vespula vulgaris [L.], Vespula pensylvanica [Saussure]) are among the non-native insects introduced into the Hawaiian Islands in historical times. Both species are native to western Hawaiian populations (Miller 1961). Vespula vulgaris was recorded only from the island of Maui during the 1970's; populations were not widespread, and the lack of collection or other records after 1980 suggest a temporary infestation and failure to become established. In contrast, V. pensylvanica has been present on the islands since the early twentieth century, and may now be considered to be permanently established. The first state record of V. pensylvanica was on Kaua‘i in 1919 (Nakahara 1980); there have been continuous, but sporadic records from that island up until the present. In 1936 it was recorded from Oahu, and the islands of Maui, Lana‘i, Moloka‘i, and Hawai‘i were invaded in the late 1970’s (Nakahara 1980). The persistence of populations on Hawai‘i and Maui through 1990 are clearly documented (Gambino 1991); informal oral communications suggest that V. pensylvanica is also still present on Oahu, Lana‘i, Moloka‘i, and Kahoolawe; there are no known reports from Niihau.

The genus Vespula Thomson can be subdivided into a number of species groups; V. pensylvanica belongs to the Vespula vulgaris group, with whose members it shares many biological characteristics (Carpenter 1987). The Vespula life history is quite complex, as might be expected of a highly social species. General accounts of yellowjacket biology are provided by Duncan (1939), Spradbery (1973), Akre et al. (1976), Roush & Akre (1978), Edwards (1980), and Akre & MacDonald (1986). Numerous aspects of V. pensylvanica biology, though worthy of additional research, are not pertinent to the present study, and are omitted from consideration here.

The development of an effective V. pensylvanica abatement strategy in Hawai‘i requires a good understanding of relevant aspects of its biology, such as nesting activities and colony cycle. This section presents a generalized account of these, based on typical behavior in the native range as outlined in the references listed in the previous paragraph and from unpublished observations from California, and provides a basis for analysis and comparison of V. pensylvanica’s biology in Hawai‘i.

Typical colonies undergo an annual cycle characteristic of the subfamily Vespinae. Inseminated queens hibernate in protected places during the winter and begin flying in the spring at the onset of fair weather. A colony is founded by a single queen (haplometrosis). She chooses a sheltered location to initiate the nest, usually underground, but sometimes in hollow spaces in buildings or tree trunks. Exposed aerial nests are rare. The queen engages in many tasks during the early stages of colony development; she collects plant fibers to make paper used to build the nest, lays eggs, collects food to feed herself and the developing larvae, defends the nest against intruders if necessary, and may actively warm the immatures during cold weather. The period from nest initiation to the emergence of the first clutch of workers is a time of great vulnerability for the colony. Once the first workers are reared and begin foraging, they assume most of the work duties of the colony, and the queen does little more than feed, lay eggs, and regulate worker behavior through the actions of her pheromones. The colony enters a period of rapid growth. The nest, built of wasp paper, consists of a series of horizontally oriented combs surrounded by an envelope with one or several small entrance holes. It expands downwards and laterally as new combs are first added at the bottom and then enlarged by the construction of new cells at the periphery. Nests built in an easily excavated substrate have a general spherical or ovoid shape, but when the substrate cannot be removed by workers, the nest conforms to the shape of the cavity they are able to create, which may be highly irregular. Small plant roots can be chewed through and removed, but larger roots are incorporated into the nest architecture and may strengthen the nest by providing support.

Genetically, females arise from fertilized (diploid) eggs, while males develop from unfertilized (haploid) eggs. Early in the colony cycle, only small
cells suitable for rearing workers (which are sterile females) are built. Later in the season large cells are constructed; these are used to rear new queens. The difference in cell size is the only known basis for the differentiation of female immatures into workers or queens. The non-overlap of sizes of females reared in small and large cells enables them to be easily identified as workers or queens, respectively. Males can be reared in either size cell, yielding a bimodal size distribution; however, in typical queenright colonies most males are reared in small cells, and most large cells are used for rearing queens. Newly emerged queens normally do not participate cooperatively in colony activities; they feed while maturing in the nest, mate, and disperse to seek out hibernation sites. Males also perform little or no work to benefit the colony; their function is to mate with new queens. When they leave the nest they engage in stereotypical “patrolling” flights, thought to be a component of mating behavior.

The colony passes through a decline phase at the end of its cycle. Once colony resources have been channelled into reproductives, fewer workers are produced, and the cohesive social organization characteristic of the early phases of the colony cycle breaks down. Many aspects of behavior, such as brood care, nest maintenance, foraging, and defense become erratic. As a result, the nest physically deteriorates and the population drops. New queens and males disperse, and colonies that are able to linger through the fall are usually eventually shut down completely by cold weather.

Although a successful colony may rear thousands of new queens, the chances of any individual queen successfully producing queen offspring the next year are very small. Few queens are able to survive to establish colonies, and the majority of colonies fail before rearing any queens. Premature colony decline may result from the death of the queen, or from a queen unable to exert effective pheromonal control of her workers. In these cases, the ovaries of some workers, which are normally vestigial, may develop and produce viable eggs. Since workers do not mate, eggs laid by them invariably develop into males. A colony may continue to be active for some time without its queen, and may produce some male offspring, but will eventually die out when the workers are lost through attrition.

**MATERIALS & METHODS**

Similar methods were used to investigate *V. pensylvanica* biology at Haleakala (HALE) and Hawai‘i Volcanoes (HAVO) National Parks. Four basic aspects were studied: 1) fluctuations of worker populations; 2) nest sites; 3) colony analysis (structure and occupants); 4) queen physiology and behavior.

**Population Monitoring**

Worker adults are the direct cause of nearly the entire negative impact of *V. pensylvanica*, both the stinging of people and the predation of native arthropods. A monitoring system to quantify worker populations is an important tool for identifying temporal and geographical variations, and to assess the effectiveness of control measures. This section describes the use of monitoring to elucidate population trends; its use in the context of evaluation of abatement efforts will be discussed in Section III. Heptyl butyrate, a synthetic chemical to which *V. pensylvanica* workers are attracted (Davis et al. 1969), was used in traps deployed to monitor worker populations. The basis for *V. pensylvanica* attraction to heptyl butyrate is unknown; it is neither a food substance nor a pheromone naturally produced by the insects. *V. pensylvanica* queens are also attracted to heptyl butyrate, and separate records of queen captures were kept; these will be discussed in the section on reproductive plasticity.

Yellowjacket monitoring programs were conducted at Haleakala National Park on Maui (HALE) from 1981-1990, and Hawai‘i Volcanoes National Park on Hawai‘i (HAVO) from 1984-1990 (Table 1). Several sponsoring agencies operated these programs, using different techniques; consequently, quantitative comparisons of population levels between systems are not valid. Nonetheless, some qualitative population trends are evident regardless of the monitoring system. Two types of traps were used: a wet trap containing vegetable oil, water, and a wick of attractant (Gambino et al. 1990), and a dry
Table 1. Yellowjacket population monitoring programs on Maui and Hawaii.

<table>
<thead>
<tr>
<th>Location</th>
<th>Elevation (m)</th>
<th>Dates</th>
<th>Agency</th>
<th>Type of Trap</th>
<th>No. of Traps</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAUI</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haleakala Nat.</td>
<td>2050-3050</td>
<td>June 1980-December 1988</td>
<td>NPS Resources Management Division</td>
<td>Wet</td>
<td>10</td>
</tr>
<tr>
<td>Park</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HAWAII</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kipuka Kulalio</td>
<td>2165</td>
<td>May 1984-December 1986</td>
<td>Hawaii Dept. of Health</td>
<td>Wet</td>
<td>1</td>
</tr>
<tr>
<td>Kipuka Kulalio</td>
<td>1890</td>
<td>May 1988-December 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Kipuka Maumalu</td>
<td>1890</td>
<td>June 1988-November 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Kipuka Ki</td>
<td>1320</td>
<td>May 1984-December 1986</td>
<td>Hawaii Dept. of Health</td>
<td>Wet</td>
<td>1</td>
</tr>
<tr>
<td>Kipuka Ki</td>
<td>1320</td>
<td>June 1988-November 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Kipuka Puuulu</td>
<td>1230</td>
<td>May 1984-December 1986</td>
<td>Hawaii Dept. of Health</td>
<td>Wet</td>
<td>1</td>
</tr>
<tr>
<td>Kipuka Puuulu</td>
<td>1230</td>
<td>June 1988-December 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Kilauea</td>
<td>1200</td>
<td>May 1984-December 1986</td>
<td>Hawaii Dept. of Health</td>
<td>Wet</td>
<td>1</td>
</tr>
<tr>
<td>(Park HQ)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kilauea</td>
<td>1200</td>
<td>December 1988-December 1990</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>(Park HQ)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kilauea</td>
<td>1170</td>
<td>December 1988-December 1990</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>(Research)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ola’a</td>
<td>1170</td>
<td>August 1988-October 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Ka’u Desert</td>
<td>935</td>
<td>October 1988-December 1989</td>
<td>NPS Research Division</td>
<td>Dry</td>
<td>5</td>
</tr>
<tr>
<td>Kipuka Nene</td>
<td>900</td>
<td>May 1984-December 1986</td>
<td>Hawaii Dept. of Health</td>
<td>Wet</td>
<td>1</td>
</tr>
</tbody>
</table>

The main study site at HALE consisted of approximately 1000 hectares on the northwest slope of Haleakula Volcano, ranging from 2050-3050 m elevation (Gambino et al. 1990). From 1981 to 1988, ten traps were maintained by the HALE Resources Management Division. To discern seasonal patterns in foraging worker populations at HALE, the number of workers captured per week, pooled for all traps, was calculated for each month from 1982-1988 and analyzed in a randomized block ANOVA with month as the fixed variable; means were separated using Duncan’s multiple range test, calculated using the GLM procedure of SAS Institute, Inc. (1985). 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.

At HAVO, a much larger and more diverse area was sampled, ranging from 900 to 2165 m elevation. Monitoring was not continuous at all sites, and was suspended when the availability of staff time was limited or when wasp populations approached zero for extended periods during the winter or spring.
months. HAVO monitoring data were not analyzed statistically.

Nest Sites

A total of 101 active nests were discovered from 1986-1990: 41 at HALE and 74 in or close to HAVO. For each nest, a brief description of the nest site was recorded. Unless the nest was excavated, only the surface features surrounding the opening(s) of the entrance tunnel could be described. For excavated nests, certain subterranean features associated with the nest were discovered only after digging.

At HALE there seemed to be an association with the native shrub Stypheila tameiameiae (Chamisso & Schlechtendal) Mueller, the dominant ground cover species. To test if nests were preferentially associated with S. tameiameiae, distribution of 34 nests was compared with a vegetation ground cover analysis. One hundred points were sampled in a grid (2700 m by 200 m) straddling the 2620 m contour line, representative of habitat where yellowjacket foragers and nests were most abundant. At each sampling point a PVC-pipe square enclosing 400 cm² was randomly thrown into the air, and the spot where it landed was examined. The substrate within the frame was assigned to one of two categories: Stypheila, if live foliage of the plant was found anywhere within the square; other, if it lacked Stypheila foliage. Because the Stypheila 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 chi-square test.

Nests at HAVO occurred in a number of different habitats; no obvious nest site trends were noticed when all nests were pooled. To clarify trends in different areas, nests were grouped into the following geographical categories (represented by at least 5 colonies each): Kipuka Paiau, Puhiamau, Ola’a Tract, Keauhou, Namakani Paio, Ka’u Desert, and Kilauea.

Colony Analysis

The most complete picture of yellowjacket biology can be obtained by making observations at active colonies. Thirty seven nests were excavated and brought to the laboratory for analysis. Data gathered from excavated nests included: date of excavation, general shape of the nest, number of combs, estimated total number of cells, number and location of large (queen) cells, approximate brood composition, and population of adult reproductives. We attempted to extract as much information as possible from each nest; however, given the time constraints of the project, it was not practical to collect complete data from all nests. Thus, the various data presented in the results section are from subsets of the total number of nests.

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 some nests, direct cell counts (number of cells in 10 cm²) were made for representative sections of combs containing small cells and, if present, large cells. In nests where cells were measured on only some combs, the mean cells/cm² value of measured cells was used to calculate numbers of cells on combs whose cells were not measured. For colonies where no cells were measured, the mean cells/cm² value of measured cells for all nests from that island and year were used to calculate cell numbers. For some nests the paper of some combs had deteriorated prior to 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.

Nests types were classified according to the following criteria: typical immature (TI) colonies were colonies collected before 1 October, prior to the initiation of large cell construction; queen cell (QC) colonies were annual colonies that underwent a single episode of queen rearing, deduced from the presence in the nest of large cells containing meconia; no large cell (NLC) colonies were annual colonies that remained active after 1 October, but had not initiated large cell construction; no large cell, queens (NLCQ)
colonies were the same as NLC’s except that there was evidence of polygyny; overwintered (OW) colonies were colonies that underwent at least one episode of queen rearing, and persisted at least into a second summer.

**Queen Physiology and Behavior**

When present, subsets of pupae and mature larvae from excavated nests were sexed. 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). In some cases adult queens and large workers were collected from nests; these were stored frozen until they could be dissected under Heinz’s diluent solution and examined for wing wear, gastric discoloration, size of largest egg, fat body development, and presence of sperm in the spermatheca. A total of 143 queens from 23 nests were examined. Queens were designated “hibernation-ready” if they contained extensively developed fat body and undeveloped ovaries; “oviposition-ready” if they were inseminated, had reduced fat body, and had developed ovaries with an egg at least 1.5 mm long; “mothers” if they were the only oviposition-ready female in the colony or were clearly the most worn (wing wear and gastric pigment loss) of a polygynous assemblage. Dissections sometimes gave inconclusive or intermediate results, so that some queens could not be placed in any of these categories.

Extranidal behavior of queens falls into two basic categories. Hibernation-ready queens disperse from their natal nest to mate or to seek hibernation sites. Collections of these queens outside of nests is rare because they neither engage in conspicuous flight activities nor are attracted to heptyl butyrate. In contrast, post-hibernation queens (referred to here as spring queens, regardless of the date of capture) are attracted to heptyl butyrate and were collected in monitoring traps; they may have an extended flight period associated with the various tasks involved in establishing (or joining) a nest. Temporal occurrence of queens trapped at HALE (during 1982-1988, the years for which data are available for the entire calendar year) was analyzed using the same methods as for workers collected in the monitoring program.

At HAVO, the trapping regime was more irregular than at HALE. To reduce the sampling bias, trap captures of queens were included for analysis only if the particular site was sampled for an entire calendar year. To supplement the data on trap captures of queens at HAVO, flying queens not associated with any known nest were captured by net. Whereas the trap monitoring program consisted of a standardized sampling regime, aerial queens were captured opportunistically throughout 1989 in the course of frequent but irregular field trips taken while conducting this and other studies (Gambino 1990) in the vicinity of HAVO. A subset of netted queens was dissected to evaluate their physiological status. Queens were designated as typical spring queens if they were inseminated and had greatly reduced fat body deposits. Ovarian status was evaluated, but not considered in assigning them to the typical spring queen category, because for queens coming out of hibernation, ovaries and eggs normally develop gradually over several months during the colony initiation and pre-emergence phases. Again, the status of some queens was ambiguous, particularly if they were un inseminated but lacked extensive fat body; most likely these were queens that had not mated prior to hibernating, and are more closely aligned with typical spring queens, though their ability to successfully initiate colonies is questionable. At HAVO, queens collected by both methods were pooled for analysis of temporal patterns.

**RESULTS**

The study sites (HALE and HAVO) differ in a number of physical characteristics, and gave considerably varied results. In this subsection, results from the two parks are presented separately.

**Population Monitoring**

HALE: Fluctuations in forager populations above 2073 m, measured as pooled numbers of foragers captured weekly in all traps, are presented in Figure 1. Males were only rarely captured in monitoring traps. The strong seasonal character of the cycles, with highest worker populations occurring
Table 2. Seasonal activity of *Vespula pensylvanica* workers at Haleakala National Park, 1982-1987.

<table>
<thead>
<tr>
<th>Month</th>
<th>No. workers trapped per wk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan.</td>
<td>1.60 a</td>
</tr>
<tr>
<td>Feb.</td>
<td>2.07 a</td>
</tr>
<tr>
<td>Mar.</td>
<td>3.63 a</td>
</tr>
<tr>
<td>Apr.</td>
<td>3.43 a</td>
</tr>
<tr>
<td>May</td>
<td>6.81 a</td>
</tr>
<tr>
<td>June</td>
<td>11.99 ab</td>
</tr>
<tr>
<td>July</td>
<td>23.17 abc</td>
</tr>
<tr>
<td>Aug.</td>
<td>41.54 cd</td>
</tr>
<tr>
<td>Sept.</td>
<td>54.59 d</td>
</tr>
<tr>
<td>Oct.</td>
<td>32.97 bcd</td>
</tr>
<tr>
<td>Nov.</td>
<td>9.86 a</td>
</tr>
<tr>
<td>Dec.</td>
<td>3.27 a</td>
</tr>
</tbody>
</table>

Means within columns followed by the same letter are not significantly different (P = 0.05; Duncan’s multiple range test).

Table 3. Elevation effects on *V. pensylvanica* forager populations at Haleakala National Park. Values are mean annual numbers of foragers captured per heptyl butyrate trap, 1982-1987.

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>Mean (± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2073</td>
<td>79.88 ± 133.32 a</td>
</tr>
<tr>
<td>2134</td>
<td>198.50 ± 235.49 a</td>
</tr>
<tr>
<td>2256</td>
<td>313.88 ± 423.04 ab</td>
</tr>
<tr>
<td>2347</td>
<td>955.75 ± 810.79 ab</td>
</tr>
<tr>
<td>2438</td>
<td>631.25 ± 624.27 ab</td>
</tr>
<tr>
<td>2591</td>
<td>2632.75 ± 1614.39 c</td>
</tr>
<tr>
<td>2682</td>
<td>1210.75 ± 1150.06 b</td>
</tr>
<tr>
<td>2835</td>
<td>973.00 ± 948.08 ab</td>
</tr>
<tr>
<td>2957</td>
<td>353.75 ± 527.59 ab</td>
</tr>
<tr>
<td>3018</td>
<td>218.50 ± 304.72 a</td>
</tr>
</tbody>
</table>

Means (± SD) within a column followed by the same letter are not significantly different (P = 0.05; Duncan’s multiple range test).

from August through October, and low populations occurring during the winter and early spring (*F* = 5.34; df = 11.72; *p* = 0.0001) (Table 2) corresponds well with typical mainland activity cycles. However, forager activity did not drop to zero in all years, revealing the presence of overwintering colonies from 1981-82, 1982-83, 1983-84, and 1985-86. Yellowjacket distributions across elevations were non-uniform (*F* = 7.18; df = 9.70; *p* = 0.01), with a distinct peak at 2591 m (Table 3). Exclusion of yellowjackets from the lower elevations of the study area may be due to weather conditions associated with the characteristic temperature inversion that occurs on East Maui (Blumenstock & Price, 1972). It generates a cloud layer that frequently produces dense ground fog at elevations from 1350 to 2000 m, sometimes extending up to 2300 m. The amount of insolation may be an important physical factor affecting *V. pensylvanica* distribution.

HAYO: As was true on Maui, worker populations were generally highest during the late summer and autumn. Colonies overwintered during some years, with evidence of this phenomenon in 1983-84 (Kipuka Kulailo, K. Ki, K. Puaulu), 1985-86 (K.
Table 4. Nest Sites of *V. pensylvanica* on mainland North America and Hawaii. Figures indicate the percentage of N nests in each site type.

<table>
<thead>
<tr>
<th>Region*</th>
<th>OR</th>
<th>WA</th>
<th>CA1</th>
<th>CA2</th>
<th>HALE</th>
<th>HAVO</th>
</tr>
</thead>
<tbody>
<tr>
<td>N Overwinter</td>
<td>33</td>
<td>61</td>
<td>56</td>
<td>37</td>
<td>34</td>
<td>74</td>
</tr>
<tr>
<td>Soil Cavity</td>
<td>57.6</td>
<td>95.1</td>
<td>87.5</td>
<td>100</td>
<td>100</td>
<td>77.0</td>
</tr>
<tr>
<td>Roots/Log</td>
<td>0</td>
<td>6.6</td>
<td>8.9</td>
<td>2.7</td>
<td>0</td>
<td>23.0</td>
</tr>
<tr>
<td>Under Rock</td>
<td>0</td>
<td>0</td>
<td>1.8</td>
<td>2.7</td>
<td>26.5</td>
<td>12.2</td>
</tr>
<tr>
<td>Under Building</td>
<td>0</td>
<td>0</td>
<td>7.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>On Ground</td>
<td>42.3</td>
<td>4.9</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>17.6</td>
</tr>
<tr>
<td>Log/Stump</td>
<td>33.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>17.6</td>
</tr>
<tr>
<td>Duff/Sand/Sod Pile</td>
<td>9.0</td>
<td>4.9</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aerial</td>
<td>0</td>
<td>0</td>
<td>12.5</td>
<td>0</td>
<td>0</td>
<td>5.4</td>
</tr>
<tr>
<td>Building Walls</td>
<td>0</td>
<td>0</td>
<td>8.9</td>
<td>0</td>
<td>0</td>
<td>1.4</td>
</tr>
<tr>
<td>Tree Cavity</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4.0</td>
</tr>
<tr>
<td>Tree/Exposed</td>
<td>0</td>
<td>0</td>
<td>3.6</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*Key to regions and sources:
OR: Oregon forest, Roush & Akre 1978
WA: Washington State, MacDonald et al. 1974
CA1: Coastal central California, Gambino unpublished
CA2: Inland central California, Gambino unpublished
HALE: Haleakala National Park, Maui
HAVO: Hawaii Volcanoes National Park & Vicinity, Hawaii

Kulalio), and 1988-89 (K. Puaulu, Ka’u Desert) (Figure 2). Continuous observations of wasp activity, or analysis of colony architecture, also gave evidence of overwintering at K. Kulalio from 1987-88, and at Keauhou from 1989-1990.

Populations on Hawai’i were not tightly synchronized, and phenologies varied according to location. At a number of sites there were extended periods (3 months) of irregular population fluctuation, without clearly defined peaks. Although the large variance inherent in using a single monitoring trap per site (DOH program: K. Kulalio 1986, K. Nene 1985 and 1986, K. Ki 1984 and 1986) may account for some of these irregularities, they were also apparent when five traps per site were used (K. Puaulu 1989, K. Nene 1989, Ka’u Desert 1989).

**Nest Sites**

Table 4 provides a comparison of nest site data from mainland North American and Hawaiian populations of *V. pensylvanica*. In all populations, most nests occurred in subterranean situations. The incidence of nests at or above ground level generally increased with the availability of cavities in these locations, mostly as hollow tree stumps (Oregon, HAVO) or voids in buildings (coastal California).

**HALE**: Cavities at or above ground level are extremely rare, accounting for the totally subterranean nature of nests. Of 100 grid samples, 31 (31.0%) contained *S. tameiameiae*, while 19 of 34 (55.9%) nests were located beneath *S. tameiameiae* bushes. Thus, there is a positive association with this plant (chi-square = 9.84; df = 1; P 0.005). However, it was not determined whether *S. tameiameiae* is a preferred site for queens initiating nests, or if nests are initiated more randomly, with those beneath *S. tameiameiae* becoming more successful and more likely to be detected. Accumulated organic matter from the plant itself is easily excavated, and likely provides insulation from wetting and harsh weather.
Table 5. Nest sites of *V. pensylvanica* at Hawaii Volcanoes National Park and vicinity.

<table>
<thead>
<tr>
<th>Sitea</th>
<th>PUA</th>
<th>PMA</th>
<th>OLA</th>
<th>KIL</th>
<th>KHO</th>
<th>NPA</th>
<th>KAU</th>
<th>OTH</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>21</td>
<td>10</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>Subterranean Soil Cavity</td>
<td>7</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Roots/Log</td>
<td>8</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Under Rock</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>On Ground, Log/Stump</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>aerial Building Walls</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tree Cavity</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Key to Sites:
PUA: Kipuka Puaulu (Bird Park)
PMA: Puhimau
OLA: Ola’a, Large Tract (HAVO) and State Forest Reserve
KIL: Kilauea Vicinity
KHO: Keauhou Ranch
NPA: Namakani Paio
KAU: Ka’u Desert
OTH: Other

Furthermore, incorporation of *S. tameiameiae* roots into the nest architecture may enhance structural stability.

**HAVO:** Among the various HAVO habitats there was considerable diversity in nesting sites (Table 5). The Ka’u Desert, with terrain most similar to the HALE study site, also had exclusively subterranean nests; the majority were under large rocks. At the other end of the spectrum, the Ola’a rain forest, with a moist and densely packed soil substrate, had only one of seven nests beneath the ground. The abundant hollow interiors of old *Cibotium* tree ferns provided cavities that were the most common nest site. In vegetationally complex, partly forested Kipuka Puaulu, most nests were associated with old logs or stumps, whether below, at, or above ground level.

**Colony Analysis**

**HALE:** A total of 17 colonies were excavated (Table 6). Nests found in 1987 (n = 3) and 1988 (n = 11) resembled typical prereproductive annual nests of mainland *V. pensylvanica* populations, and are considered together here. They were basically spherical in shape, with numbers of small cells (x = 3497; range = 558-8086) similar to the ranges recorded in Washington (MacDonald et al. 1974) and Oregon (Roush & Akre 1978). None of these colonies had initiated large cell construction, which would not be unusual for colonies collected during the summer (TIL’s, n = 5), but atypical for colonies that remained active into the autumn (NLC’s, n = 7; NLCQ’s, n = 2).

Nests found in 1986 (two of these were excavated during the spring of 1987, long after activity had ceased during the previous winter) differed strikingly from those of subsequent years. The number of small cells per nest was approximately 20 times greater (n = 3; x = 65737; range = 58289-80508), and large (queen) cells were also constructed. In nest HAL8603 there were two distinct episodes of large cell construction, separated by 3 combs containing small cells exclusively. In nest HAL8606 only one episode of large cell construction was detected. The bottom two thirds of both of these nests were too deteriorated to provide an accurate record of cell construction during late 1986 and early 1987.
Table 6. Characteristics of *Vespula pensylvanica* colonies from Haleakala National Park.

<table>
<thead>
<tr>
<th>Nest</th>
<th>Date of Excavation</th>
<th>Type</th>
<th>No. of cells</th>
<th>Queens Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAL8601</td>
<td>21-Sep-86</td>
<td>OW</td>
<td>58414</td>
<td>2107</td>
</tr>
<tr>
<td>HAL8603</td>
<td>30-May-87</td>
<td>OW</td>
<td>58289</td>
<td>936</td>
</tr>
<tr>
<td>HAL8606</td>
<td>01-Jun-87</td>
<td>OW</td>
<td>80508</td>
<td>1503</td>
</tr>
<tr>
<td>HAL8701</td>
<td>30-Aug-87</td>
<td>TI</td>
<td>4150</td>
<td>0</td>
</tr>
<tr>
<td>HAL8706</td>
<td>31-Aug-87</td>
<td>TI</td>
<td>1792</td>
<td>0</td>
</tr>
<tr>
<td>HAL8708</td>
<td>31-Aug-87</td>
<td>TI</td>
<td>2442</td>
<td>0</td>
</tr>
<tr>
<td>HAL8801</td>
<td>10-Sep-88</td>
<td>TI</td>
<td>558</td>
<td>0</td>
</tr>
<tr>
<td>HAL8802</td>
<td>10-Sep-88</td>
<td>TI</td>
<td>832</td>
<td>0</td>
</tr>
<tr>
<td>HAL8812</td>
<td>05-Oct-88</td>
<td>NLC</td>
<td>2423</td>
<td>0</td>
</tr>
<tr>
<td>HAL8813</td>
<td>05-Oct-88</td>
<td>NLC</td>
<td>4479</td>
<td>0</td>
</tr>
<tr>
<td>HAL8804</td>
<td>06-Oct-88</td>
<td>NLCQ</td>
<td>4452</td>
<td>0</td>
</tr>
<tr>
<td>HAL8810</td>
<td>06-Oct-88</td>
<td>NLC</td>
<td>4699</td>
<td>0</td>
</tr>
<tr>
<td>HAL8811</td>
<td>06-Oct-88</td>
<td>NLC</td>
<td>7644</td>
<td>0</td>
</tr>
<tr>
<td>HAL8807</td>
<td>14-Nov-88</td>
<td>NLC</td>
<td>2243</td>
<td>0</td>
</tr>
<tr>
<td>HAL8808</td>
<td>14-Nov-88</td>
<td>NLC</td>
<td>2776</td>
<td>0</td>
</tr>
<tr>
<td>HAL8814</td>
<td>14-Nov-88</td>
<td>NLC</td>
<td>2382</td>
<td>0</td>
</tr>
<tr>
<td>HAL8816</td>
<td>14-Nov-88</td>
<td>NLCQ</td>
<td>8086</td>
<td>0</td>
</tr>
</tbody>
</table>

*a* Nest Types:
- **TI** - Typical immature
- **QC** - Queen cell
- **NLC** - No large cells
- **NLCQ** - No large cells, queens
- **OW** - Overwintered

*b* Queen Types (see text for full descriptions)
- **Ovip** - Oviposition-ready
- **Hiber** - Hibernation-ready

Nest HAL8601 was retrieved in excellent condition, and its architecture received more detailed study. Prior to excavation this colony showed many symptoms of decline. Dead larvae were being removed from the nest, the colony contained an abundant male population, and colony defense was not vigorous. The nest was bell-shaped with a globular top turret (diameter = 20 cm) that fanned out in the lower portions to a diameter of 50 cm. The top combs (down to the ninth) were discrete units. Starting with comb #10 the comb structure became more irregular; lower combs were apparently initiated at several distinct loci and engulfed obstacles such as rocks as they were extended. Combs initiated separately were sometimes fused together, as revealed by irregularities of cell pattern along the fused margins. Some combs were even continuous, along a circuitous route, with the combs below them. The irregularities of the lower comb structure were compounded by the substrate; by expanding downward the nest had contacted irregularly surfaced bedrock, and further downward excavation by the wasps was impossible. In all three queen-cell combs (#7-9), large cells were clustered in the center, surrounded by small cells. This arrangement, similar to that found in overwintered *V. germanica* (F.) nests in
### Table 7. Characteristics of *Vespula pensylvanica* colonies from Hawaii.

<table>
<thead>
<tr>
<th>Nest</th>
<th>Date of Excavation</th>
<th>Type(^a)</th>
<th>No. of cells</th>
<th>Queens Present(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>small</td>
<td>large</td>
<td>Mother</td>
</tr>
<tr>
<td>HVO8810</td>
<td>17-Aug-88</td>
<td>TI</td>
<td>15266</td>
<td>0</td>
</tr>
<tr>
<td>HVO8819</td>
<td>18-Aug-88</td>
<td>TI</td>
<td>9959</td>
<td>0</td>
</tr>
<tr>
<td>HVO8815</td>
<td>15-Oct-88</td>
<td>NLC</td>
<td>5418</td>
<td>0</td>
</tr>
<tr>
<td>HVO8816</td>
<td>26-Oct-88</td>
<td>OW</td>
<td>43221</td>
<td>2341</td>
</tr>
<tr>
<td>HVO8828</td>
<td>27-Oct-88</td>
<td>QC</td>
<td>15769</td>
<td>73</td>
</tr>
<tr>
<td>HVO8823</td>
<td>10-Nov-88</td>
<td>QC</td>
<td>8227</td>
<td>356</td>
</tr>
<tr>
<td>HVO8826</td>
<td>10-Nov-88</td>
<td>NLC</td>
<td>31246</td>
<td>0</td>
</tr>
<tr>
<td>OLA8801</td>
<td>16-Dec-88</td>
<td>QC</td>
<td>22720</td>
<td>806</td>
</tr>
<tr>
<td>HVO8817</td>
<td>18-Jan-89</td>
<td>QC</td>
<td>6282</td>
<td>829</td>
</tr>
<tr>
<td>HVO8814</td>
<td>19-Jan-89</td>
<td>QC</td>
<td>22967</td>
<td>5060</td>
</tr>
<tr>
<td>HVO8822</td>
<td>19-Jan-89</td>
<td>QC</td>
<td>10155</td>
<td>1821</td>
</tr>
<tr>
<td>HVO8831</td>
<td>24-Jan-89</td>
<td>QC</td>
<td>4344</td>
<td>668</td>
</tr>
<tr>
<td>HVO8902</td>
<td>16-Oct-89</td>
<td>NLCQ</td>
<td>835</td>
<td>0</td>
</tr>
<tr>
<td>KAU8901</td>
<td>25-Oct-89</td>
<td>NLC</td>
<td>4309</td>
<td>0</td>
</tr>
<tr>
<td>HVO8908</td>
<td>20-Nov-89</td>
<td>NLCQ</td>
<td>4896</td>
<td>0</td>
</tr>
<tr>
<td>HVO8907</td>
<td>25-Nov-89</td>
<td>QC</td>
<td>14857</td>
<td>645</td>
</tr>
<tr>
<td>HVO8906</td>
<td>11-Jan-90</td>
<td>NLCQ</td>
<td>27821</td>
<td>0</td>
</tr>
<tr>
<td>HVO8904</td>
<td>17-Jan-90</td>
<td>NLC</td>
<td>26263</td>
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</tr>
<tr>
<td>HVO9001</td>
<td>26-Jan-90</td>
<td>QC</td>
<td>14999</td>
<td>5271</td>
</tr>
<tr>
<td>HVO8903</td>
<td>10-Feb-90</td>
<td>OW</td>
<td>546260</td>
<td>47229</td>
</tr>
</tbody>
</table>

\(^a\)Nest Types:
- TI - Typical immature
- QC - Queen cell
- NLC - No large cells
- NLCQ - No large cells, queens
- OW - Overwintered

\(^b\)Queen Types (see text for full descriptions)
- Ovip - Oviposition-ready
- Hiber - Hibernation-ready

New Zealand (Thomas 1960), contrasts with the more typical peripheral location of large cells on mixed-cell combs recorded elsewhere for annual *V. pensylvanica* colonies (MacDonald et al 1974; Roush & Akre 1978).

The synchrony of forager populations at HALE, noted earlier, is matched by the apparent synchrony of nest development. In 1986, only six colonies were found; all had apparently overwintered from 1985. In subsequent years, no overwintering colonies were located and most colonies were more modest in size. In 1988, none of the excavated colonies (n = 11) had initiated large cell construction, even though 7 of 9 taken after September were queenright.

**HAVQ:** Of 20 excavated nests, only 11 had structures that might be considered typical (2 TI's, 9 QC's) (Table 7). A common feature of the atypical nests was the failure to construct large cells before October (4 NLC's, 3 NLCQ's). Five annual nests contained more than 20,000 small cells; of 88 nests...
recorded from Washington (MacDonald et al. 1974) or Oregon (Roush & Akre 1978), the greatest number of small cells was 7397.

Two overwintered nests were excavated. HVO 8816 was poisoned with insecticide on 1 September 1988 and dug up approximately two months later. Its architecture was irregular due to the shallowness of the soil; expansion along the contours of the rock surface had produced uneven lateral sections. This, and the partial deterioration of some combs, made it impossible to determine which had been most recently active. All large cells were present on four mixed large cell/small cell combs.

Colony HVO8903 was discovered in September 1989; its peak traffic rate was estimated to be 1200 per minute. The nest, which had several irregularly shaped entrances, was within and beneath a large downed tree trunk; to facilitate observations, the entrances were closed or modified with structures of soil, cardboard, and wood. Males were often found in the vicinity of the modified nest entrances. The colony was not excavated until its traffic rate declined to zero on 10 February 1990.

The nest had been initiated within the hollow tree trunk, filled the cavity within, and expanded beyond into the soil in irregular lobes. It consisted of approximately 35 comb layers containing about 546,000 small cells and 43,000 large cells. The topmost comb contained 138 small cells; the second comb contained 459 small cells and 145 large cells, and the third comb contained 229 small cells and 48 large cells. If these were the first combs built they represent an extremely early switch to large cell construction in the life of this colony. Combs #4-7 contained small cells exclusively, followed by a series of 12 combs containing cells of both sizes. Many lower combs contained both small and large cells. Most large cells were spread in vertically aligned peripheral portions of up to eight combs. Many large cells were capped; the contents of 10 large cells from each of 8 combs were examined, and contained 77 queens and 3 males; all were dead and partly desiccated.

A small "bud" nest was constructed in a cavity adjacent to, but not connected to, the main nest. It had a separate entrance tunnel, and contained 1516 large cells in 5 combs.

**Queen Physiology and Behavior**

**HALE**: There was a seasonal pattern in the appearance of spring queens (Figure 3A), with most appearing from May through July ($F = 3.96; df = 11,72; p = 0.0002$). 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 (Ross ref).

Regarding excavated colonies, at four no queen was recovered; three of these showed symptoms of queen loss (irregular pattern of brood in combs, high percentage of male brood). A single mother queen was recovered from eight colonies, including 5 NLC's. Two colonies (NLCQ's) had a single inseminated mother queen and smaller queens (nest HAL8804, $n = 2$; nest HAL8816, $n = 1$) that lacked external signs of wear, were inseminated, and had well developed ovaries (size of their largest eggs: in nest HAL8804, 2.0 and 1.6 mm; in nest HAL8816, 2.2 mm).

**HAVO**: Data for trap captures of 160 queens pooled from 1985, 1986, and 1989 are presented in Figure 3B. Most captures occurred from April to June, but there were a fair number of outliers, including some in November and December. Seventy-five queens were captured by net during 1989 (Figure 3C), with a peak in March. Twenty-four net-captured queens were dissected, and all but two were typical spring queens; the exceptions were uniseminated, but still lacked the fat body deposits indicative of queens seeking hibernation sites.

Of the 7 QC colonies in which queens (at least 10 per colony) were examined, hibernation-ready queens were detected at only 4, whereas oviposition-ready queens were present in all 7. This contrasts sharply with the typical situation, where autumn
queen production yields hibernation-ready queens exclusively. Multiple oviposition-ready queens were found in all three NLCQ colonies. Queens in NLCQ colonies, as well as some of the oviposition-ready queens from QC colonies and the auxiliary queens of the polygynous HALE colonies, appeared smaller than typical queens.

At the large overwintered colony HV08903 queens were first observed outside the nest on 26 January 1990. Their behavior was indistinguishable from foraging workers; i.e., they flew in and out without hesitation (at a rate of about 0.5 per minute). Three returning queens were captured, and all were oviposition-ready. During 30 minutes of observation, 12 clumps of wasps were noticed in the vicinity of one of the modified nest entrances. Clumps, consisting of 3-10 males clustered around a single queen, seemed to be related to mating behavior (Ono et al. 1985), although no actual copulations were observed. There were fewer than 150 live workers present when the nest was excavated on 10 February, and approximately 400 live queens. Twelve queens were captured and dissected. Four were oviposition-ready and inseminated, two were oviposition-ready but uninseminated, three were hibernation-ready but uninseminated, and three were intermediate regarding fat body and ovarian development, and were inseminated.

DISCUSSION

Fundamental to any effective pest management program is an understanding of the biology of the pest. For insects whose biology varies significantly under different environmental regimes, the need for on-site studies is essential. Data describing where and when the pest occurs, and characteristics that render it vulnerable, need to be incorporated into the program to permit fine tuning of control strategies. Research on *V. pensylvanica* in the Hawaiian Islands illustrates this point well.

An aspect of *V. pensylvanica* biology particularly relevant to its pest management in Hawai‘i might be described in general terms as reproductive plasticity; the most spectacular manifestation is the overwintered colony. Potential for plasticity likely resides in all *V. pensylvanica* populations, but is not expressed unless certain constraints are relaxed. On the North American mainland, most *V. pensylvanica* colonies follow the strict annual colony cycle pattern. Although peak numbers of foragers may fluctuate widely between years for reasons that are not well understood, the degree of variation among colonies within a population is somewhat restricted. Thus, while it is difficult to predict the magnitude of the forager population in any given year, the peak will occur at a fairly predictable time, and appropriate preventative or abatement measures can be scheduled accordingly.

The portion of *V. pensylvanica*’s mainland range where reproductive plasticity is most fully expressed is coastal California (*V. vulgaris* colonies also overwinter in the region), whose Mediterranean climate is characterized by nearly frost-free winters. Considering the distribution of overwintered *Vespa* colonies worldwide (Duncan 1939; Tissot & Robinson 1954; Thomas 1960; Vuillaume et al. 1969; Spradbery 1973; Akre et al. 1980; Jeanne 1980; Nakahara 1980; Nakahara & Lai 1981; Ross & Matthews 1982; Ross & Visscher 1983; Gambino 1986; Plunkett et al. 1989; Gambio et al. 1990), a mild winter is clearly prerequisite for overwintering. Winters at middle elevations of the Hawaiian Islands are also without sustained periods of freezing temperatures, and it is hardly surprising to find considerable plasticity here as well. Although *V. pensylvanica* might be expected to thrive at sea level, this has not proven to be the case in the Hawaiian Islands. Perhaps the wasp has been unable to adapt to certain aspects of the sub-tropical climate; alternatively, they may be excluded by the abundance of ants at lower elevations. Interestingly, on the mainland, the only recorded colony at a latitude as far south as Hawai‘i was at Tancitaro, Mexico, elevation 2000 m (Miller 1961).

Colony cycles in Hawaiian *V. pensylvanica* populations range from the predictable annual type to erratic but massively productive two year nests, with many intermediate variants. Overwintering colonies occur irregularly, with frequency varying among years and localities. Though comprising a small fraction of total colonies, they can contribute disproportionate numbers of workers (Plunkett et al.,
1989) and reproductives to the overall population; in some nests, many thousands of queens are produced over extended intervals.

No two overwintering colonies are alike, but they appear to share some characteristics. Requeening seems to be a prerequisite. At least one episode of large cell construction occurs, but only a fraction of colony resources are diverted to queen rearing, and immatures are reared concurrently in large and small cells. A reversion to small cell construction follows, presumably in the spring and summer of the second year. If the colony remains healthy, there may be a second round of large cell construction. These criteria exclude late developing annual colonies that fail to construct large cells, or to revert to rearing workers, regardless of whether their decline phase extends into the following spring. No three-year colonies (that is, active during three consecutive summers) have been verified.

Overwintered colonies are inextricably linked to the formation of polygynous assemblages within them; these in turn arise from adjustments of queen physiology and behavior. There are two proposed routes to polygyny: retention of daughter queens, and addition of joiner queens. The first has never been unambiguously documented, though it is widely accepted among researchers familiar with overwintering Vespula colonies (Duncan 1939; Thomas 1960; Spradbery 1973; Edwards 1980; Ross & Visscher 1983; Akre & MacDonald 1986; Gambino et al. 1990; Gambino 1991). Among the 7 late-season QC colonies excavated at HAVO, the composition of queen populations is telling; hibernation-ready queens made up only 19.0% (15 of 79) of those examined, and these were distributed among only 4 of the colonies. The majority of queens were already oviposition-ready, and were found in all of the colonies. It may be that hibernation is not required for successful reproductive development of new queens, though it has not been abandoned altogether. Although hibernation-ready queens were not found in some QC colonies, they may have dispersed or transformed before the nests were excavated. Apparently, some new queens mate, fail to disperse, develop their ovaries, and commence laying eggs. It is not clear whether the accumulation and subsequent depletion of fat body reserves remain essential components of development, or are sometimes bypassed.

Joiner queens can be easily determined by their presence in colonies lacking the large cells necessary to rear them (the NLCQ colonies found on both islands). In the native temperate range, the pool of potential nest joiners includes only post-hibernation typical spring queens (Akre & Reed 1981). Where colonies overwinter, and especially where extended queen rearing occurs, the pool is enlarged by a set of queens with an alternate phenology (Figure 3). The phenomenon of joiner queens may be even more common than the few cases documented here. Some of the oviposition-ready queens at QC colonies may well have been joiners rather than retained daughters. Also, the large size and high activity rates at some first year colonies at HAVO suggest that polygyny may have preceded the opportunity for them to rear their own new queens.

Yellowjacket colonies were consistently concentrated in only a portion of the HALE study area (centered at 2591 m). Thus, colonies experience relatively uniform environmental conditions and are well-synchronized in their development. From 1987-1991, in the absence of overwintering colonies, forager populations peaked regularly from late August through September, providing a coherent window of opportunity for abatement measures. The failure of any 1988 colonies to even initiate large cell construction supports the tantalizing suggestion that no new queens at all were produced in the study site that year, and that recolonization the following year resulted from spring queens immigrating from considerable distances.

Vespula pensylvanica also occurs elsewhere in HALE (within the crater) outside of the study area. Clearly, conditions on the northwest slope are not representative of the entire park, and a greater diversity of yellowjacket behavior is likely to be discovered by a more comprehensive investigation of V. pensylvanica throughout the park.

Vespula pensylvanica biology at the HAVO study site was much more variable than at HALE. Populations in different regions were not synchronized; the general pattern was for earlier population buildups in drier regions such as Ka‘u and Kipuka
Nene. Some populations declined swiftly, while others lingered on erratically for several months. However, even within a region, colonies sometimes showed diverse patterns of development. The irregular occurrence of overwintered colonies made it difficult to predict population trends with accuracy comparable to that possible at HALE.

To understand the extreme variability of V. pensylvanica biology at HAVO, the physical conditions of the study area must be considered. HAVO is composed of a highly diverse mosaic of habitat types resulting from often steep gradients of elevation, annual insolation, rainfall, and temperature, overlaying a variety of soil and vegetation substrates. Given such extreme environmental variation, different reproductive strategies may achieve varying degrees of success at different times and places; as a result, no single pattern of colony development is fixed in the overall population. If there are genetic determinants of the reproductive mode, and the males and queens can disperse between different habitat types (as would seem likely given the strong flying abilities of reproductives of both genders), then extreme reproductive plasticity may be adaptive for the species in Hawai‘i. Colony variants that would seem to be reproductive dead ends may even acquire adaptive value under this scheme. For example, colonies that grow large (20,000 cells) without constructing large cells may instead contribute only males as input to the genetic pool, or may postpone production of new queens until assertive outside joiner queens can be recruited.

Compared to HALE, a yellowjacket management program at HAVO would require a more comprehensive monitoring system and greater flexibility in responding to asynchronously developing populations, with diffuse forager peaks and the occasional unpredictable overwintered colony. Thus, the partitioning of the park into Special Ecological Areas is an important management technique facilitating appropriate local responses to V. pensylvanica populations as they develop.

The dispersal and migration of yellowjacket queens are among the least well known aspects of their biology. Pertinent questions about movements of V. pensylvanica queens at both parks remain unanswered, and a better understanding might provide insights for adjusting management strategies. This would be a challenging, though potentially rewarding, avenue for future research.

SECTION II
YELLOWJACKET PREDATION

INTRODUCTION

Like other species in the V. vulgaris species group, V. pensylvanica obtains proteinaceous food through predation and scavenging (Akre et al. 1980). Of the two food collection strategies, scavenging most often brings wasps in contact with humans, and may account for some overestimation of the importance of dead animal flesh in the nutrition of V. pensylvanica colonies. In California V. pensylvanica can build to outbreak populations while relying almost exclusively on arthropods as food (unpublished data).

To justify abatement research in Hawaii and elsewhere, it is important to provide evidence of V. pensylvanica’s impact on native organisms. Two approaches were employed to investigate this. First, a qualitative study was conducted at HALE and HAVO to determine the identity of arthropods upon which V. pensylvanica successfully preys. Direct field observations of wasp predation, while helpful in elucidating behaviors used to locate, capture, and transport prey (Duncan 1939; Heinrich 1984), yield limited information on the identity of the prey species. Furthermore, such studies of prey selection are biased in favor of easily observed wasp activities. Prey items in the yellowjacket diet can be objectively sampled by intercepting foragers carrying prey as they return to the nest (Kleinouth 1958; Broekhuizen & Hordijk 1968; Archer 1977; Gambino 1986; Harris 1989, although this method also has its drawbacks. In the present study the forager interception strategy was used to collect and identify V. pensylvanica prey items from Maui and Hawaii.

An additional study designed to quantitatively assess the impact of V. pensylvanica predation was conducted near Puhimau in HAVO. This was the site of high V. pensylvanica forager density during the summer and fall of 1989. The short-term prey intake
of several active colonies was measured. Observa-
tions away from colonies were also made, using
objective measures of yellowjacket forager popula-
tions, and abundance of ohia (*Metrosideros polymor-
pha*) foliage arthropods (potential prey).

**MATERIAL & METHODS**

**Qualitative Studies**

Two basic techniques were used to sample prey
collected by *V. pensylvanica* workers. The simplest
was to use a hand-held insect net to collect workers
as they returned to the nest. At moderate sized typical
colonies, it was easiest to briefly inspect returning
foragers as they approached, and to capture only
those carrying visible prey items. By partially ob-
structing the nest entrance, returning workers could
be induced to hesitate before entering, increasing the
opportunity for inspection and capture. At very ac-
tive large colonies, an alternate strategy was to
make numerous sweeps with the net in the vicinity of the
nest entrance and to retreat some distance once 40-60
workers had been captured. In either case, yellowjackets were separated from their prey items in
the net bag. Wasps were allowed to escape; prey
items were retained and processed.

In the second collection method a trap made of
5.1 cm (2") PVC pipe fixtures was placed over the
entrance of the tunnel leading to the subterranean
nest. The trap consisted of a flat wooden base, a
T-shaped fixture set into a hole at the center of the
base, a plug, and a laterally oriented removable el-
bow (Figure 4). The trap was placed over the tunnel
entrance at night and anchored with spikes driven
through the corners of the base; the base edges were
covered with packed soil. During subsequent days,
foraging workers learned to pass through the unob-
structed pipes to exit and return. Wasps sometimes
constructed new tunnels around the trap base to
bypass the modified entrance; this behavior was dis-
couraged by covering the holes with soil. Once a
regular traffic pattern through the trap was estab-
lished, daytime sampling was initiated. To conduct
a prey sampling session the elbow was replaced with
a similarly shaped unit that had a closed inner end
and a distal inwardly directed screen funnel open to
the outside. At the same time, a plug covering the
upward facing aperture of the T was removed, allow-
ing wasps exiting the nest to leave. Sampling ses-
sions lasted about 20 minutes, when an equilibrium
between wasps entering and escaping from the trap
was reached. The trap was removed, and wasps were
anaesthetized with CO2 gas and dumped into a sort-
ing tray. Prey items were collected with forceps into
a vial; wasps recovering from anaesthesia were re-
leased on the ground near the nest entrance.

In several instances yellowjackets not associated
with any nest were observed engaged in attacks on
disabled arthropods, or carrying pieces of prey. Prey
items recovered from these encounters are also in-
cluded in the analysis.

Collected prey items were preserved by first
steeping them for one minute in just-boiled water,
and then transferring to vials of 70% ethanol. Indi-
vidual prey items were examined for identification in
the laboratory using a binocular dissecting scope.
Because handling of prey by *Vespula* workers prior
to returning to the nest commonly includes removing
appendages and other body parts, and chewing to
form a bolus (Duncan 1939), the level of taxonomic
determination was highly variable. Specimens with
clear diagnostic characters in good condition could
be assigned to species, while some mutilated pieces
could not be identified below phylum. Items were
considered identified if they could be determined to
order; comparisons between geographic regions
were made at this level.

Study areas included Haleakala National Park
(HALE) on Maui and Hawaii Volcanoes National
Park (HAVO) on Hawaii. *Vespuia pensylvanica*
colonies sampled at HALE occurred within a fairly
uniform habitat on the northwest slope of Haleakala
volcano (Gambino et al. 1990) and are considered as
a single geographic unit. The area sampled at HAVO
was larger and more diverse; for comparative analy-
sis of yellowjacket diets, HAVO nests were grouped
into the following geographic units: Kipuka Puaulu,
Ola’a Tract + Ola’a Forest Reserve, and Puhimau.

**Quantitative Studies**

As part of the quantitative evaluation of *V. pens-
ylvania* predation, prey recovery traps were at-
tached to 3 colonies (HVO8904, HVO8905, and HVO8906) in the Puhipau area. On 24 November 1989, activity counts and prey samples were taken on a rotating basis from 0636 until 1746. During each sampling interval the number of yellowjacket sorties per 2 minutes was counted; then the trap was inserted and left in place for ten minutes. The numbers of yellowjacket captured, and the numbers of prey items they collected, were counted. For each interval, the following parameters were estimated: wasp trips per minute, total trips during the interval, prey items per returning wasp, and total prey captured during the interval. For each colony, these quantities were summed to give a total for the day (Table 8). Data from these trap captures were also included in the qualitative prey sampling program.

The study site for the evaluation of Y. pensylvanica predation was a section of land southeast of Kilauea Crater, 2.5 km long and 125 m wide, bisected by Chain of Craters Road, which descends gradually in a fairly straight line from 1120 m to 1055 m elevation. Four sampling plots were established, centered at 810 m intervals along the road. Vegetation at each of the plots was comparable, consisting of an open ohia forest with an understory of Myrica faya, interspersed with more open areas vegetated by native shrubs (Dodonaea viscosa, Dubautia ciliolata, and Styphelia tamaiaeae), alien grasses (Schizachyrium condensatum and Andropogon virginicus), and native ferns (Dieranopteris linearis and Nephrolepis spp.).

Yellowjacket forager populations were sampled using the Yellowjacket Inn trap, baited with a wick containing 0.4 ml of heptyl butyrate. At each plot 5 traps were suspended from tree limbs bordering the road, separated by at least 25 meters. After 24 hours, numbers of captured Y. pensylvanica workers (no queens or males were taken) were tallied. Forager densities were sampled in the fall on 29 November and 4 December 1989, and again on 4 June and 28 June 1990 for the early summer period. Numbers were pooled to give mean estimates of forager density (predation pressure) at each site for both late fall and early summer.

A beating sheet technique was used to sample arthropods from foliage-bearing limbs of ohia trees; twenty trees were sampled at each plot. One limb per tree was struck 10 times with a standard striker, and arthropods landing on a square white sheet (area = 0.5 m) held directly beneath the limb were dumped into a 15-l plastic tub and collected with an aspirator. Limbs were selected so that approximately the same amount of foliage was directly over the sheet for each sampling. Collembola numbers were estimated to the nearest five, but since this taxon was composed of arthropods believed to be below the size threshold for Y. pensylvanica predation, Collembola were not included in the quantitative analyses. All other arthropods were transferred to plastic 1.7 ml tubules and held in a cooler at approximately 5°C.

In the laboratory, samples were held in the closed tubules for up to two days at -10°C. For each sample the total biomass was weighed (to the nearest 0.001 g); then the weight of isopods + millipedes was subtracted, to give the mass of potential prey items (isopods and millipedes are not collected by Y. pensylvanica foragers, and are not considered in the following analysis). After weighing, arthropods were transferred to vials containing 70% EtOH.

To measure arthropod size, each specimen was suspended in a 6-cm petri dish of 70% EtOH and examined under a dissecting microscope with a scale attached to the stage. Size was estimated by measuring the length from the front of the head to the tip of the abdomen, excluding appendages such as antennae, mouthparts, legs, wings, and cerci. For case-bearing caterpillars the length of the case was measured. Arthropods shorter than 4.5 mm were classified as small, others as large. Although this was a somewhat arbitrary demarcation, it effectively grouped many taxa into single categories; for example, all Psyllidae, Psocoptera, and Aloha were small, and all adult Siphanta acuta and Nabis were large. Other taxa, such as spiders, crickets, and cockroaches, were well represented in both size classes.

RESULTS & DISCUSSION

Qualitative Studies

At HALE a total of 19 collection lots yielded 233 identified specimens. Two specimens, an earthworm and a centipede, are exceptional, and are omitted
from the following analysis. At HAVO, 59 collection lots (including 5 prey items taken from wasps not associated with any known nest) yielded 291 identified specimens. Table 8 summarizes the yellowjacket diet according to geographic location and major taxa. The diversity of prey at the population (geographic) and colony levels indicates the V. pensylvanica does not specialize in particular prey taxa, although individual foragers may do so. The recovered prey items suggest that V. pensylvanica foragers harvest arthropods at or near surfaces, and neither dig in soil nor probe the interiors of plant parts to seek food.

The yellowjacket diet is influenced by several characteristics of potential prey items: their presence within foraging range, their acceptability, and the ease with which they can be located and captured. Two arthropod taxa, pillbugs (Isopoda) and millipedes (Diplopoda) were common and fairly conspicuous at all sites, yet they were absent from the V. pensylvanica diet. Immunity from predation may be due to a combination of biochemical defenses, which make them unacceptable, and physical/behavioral mechanisms that render them difficult to subdue. In contrast, Araneae and Lepidoptera were apparently ubiquitous, acceptable, and not difficult to find and subdue; these made up a relatively constant part of the yellowjacket diet regardless of location. Of the Lepidoptera, most were taken as larvae; the 100 specimens included 1 egg mass, 1 pupa, and 11 adults. For other taxa, variations between sites in the proportions of items taken may reflect circumstances peculiar to those sites and taxa. The lack of Blattodea and Orthoptera in HALE samples reflects their near-absence from native habitats there. Coleoptera were poorly represented in V. pensylvanica prey samples, except at HALE, where 24 of 34 (70.6%) were of a single species, the introduced weevil Pantomorus cervinus (Boheman). Perhaps this represented an abundance of this species unique to the HALE site; alternatively, it may be a less preferred species whose appeal increased after populations of more desirable species had been depleted by a prolonged spell of intense area-wide V. pensylvanica predation.

Native and introduced bees and wasps were common at all sites, yet only two Nesoprosopis sp. and four Apis mellifera L. specimens were recovered, suggesting that healthy aculeates are able to actively defend against predation better than other taxa. MacDonald et al. (1974) also found live aculeates to be relatively immune from V. pensylvanica predation. However, Hymenoptera constituted 10.4% of prey items at HALE. In this sample, taken during the late summer of 1986 when foragers were very abundant (Gambino et al. 1990; Gambino 1991), 13 (54%) of the Hymenoptera prey items were other V. pensylvanica. This most likely represents scavenging on V. pensylvanica cadavers, which were not uncommon at the site, rather than predation.

It must be noted that the sampling/identification process may give an incomplete picture of yellowjacket predation, because not all prey items could be identified. For instance, at the Puhimau site, a total of 322 items were collected, but only 57 (17.7%) could be identified, a rate typical for the entire study. Thus, there may be bias in favor of taxa easily recognized due to distinctive diagnostic characters that withstand processing by yellowjacket foragers; taxa that are soft bodied or lacking in good diagnostic characters may be underrepresented in Table 8.

Another bias in the sampling procedure is related to prey size, as the smallest items (1 mm diameter) carried by foragers were the most difficult to identify. Nonetheless, there is a size threshold below which a V. pensylvanica forager will not collect potential prey arthropods (Duncan 1939). Small arthropods may be neglected due to difficulties in perceiving or capturing them, but more likely, the cost/benefit ratio is much more favorable for V. pensylvanica to hunt large prey. Smaller arthropods may thus be spared because they cannot be efficiently harvested. However, if large prey items cannot be found in foraging range, V. pensylvanica may adjust its threshold to accept smaller prey. In the present study, it seemed that few of the boluses carried to colonies could have derived from arthropods less than 3 mm in length.

A total of 170 prey items could be determined to genus or species level (Appendix 1). Of these, 112 (65.9%) were of endemic (to Hawaii) taxa, and 58 (34.1%) were of alien or non-endemic native taxa.
Table 8. Summary of prey taken by *V. pensylvanica* in Hawaii. Values shown represent percentages of N items.

<table>
<thead>
<tr>
<th>Site</th>
<th>N</th>
<th>ARA</th>
<th>ORT</th>
<th>BLA</th>
<th>HEM</th>
<th>NEU</th>
<th>COL</th>
<th>DIP</th>
<th>LEP</th>
<th>HYM</th>
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<tbody>
<tr>
<td>KP</td>
<td>120</td>
<td>25.0</td>
<td>18.3</td>
<td>6.7</td>
<td>4.2</td>
<td>1.7</td>
<td>3.3</td>
<td>26.7</td>
<td>12.5</td>
<td>1.7</td>
</tr>
<tr>
<td>PU</td>
<td>57</td>
<td>33.3</td>
<td>22.8</td>
<td>3.8</td>
<td>17.5</td>
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<td>3.5</td>
<td>0.0</td>
<td>19.3</td>
<td>0.0</td>
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<td>OT</td>
<td>30</td>
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<td>10.0</td>
<td>6.7</td>
<td>6.7</td>
<td>3.3</td>
<td>6.7</td>
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<tr>
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<td>6.7</td>
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<td>3.3</td>
<td>6.7</td>
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<td></td>
<td>522</td>
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<td>10.2</td>
<td>2.5</td>
<td>16.3</td>
<td>1.1</td>
<td>7.9</td>
<td>11.1</td>
<td>19.2</td>
<td>5.0</td>
</tr>
</tbody>
</table>

**a**KEY TO TAXA
- ARA - Araneae
- ORT - Orthoptera
- BLA - Blattodea
- HEM - Hemiptera + Homoptera
- NEU - Neuroptera
- COL - Coleoptera
- DIP - Diptera
- LEP - Lepidoptera
- HYM - Hymenoptera

**b**KEY TO SITES
- KP - Kipuka Puaulu (HAVO)
- OL - Olaa Tract + Olaa Forest Reserve (HAVO)
- PU - Puhimau (HAVO)
- OT - Other (HAVO)
- HK - Haleakala (HALE)

The roughly 2:1 ratio of endemic/non-endemic taxa may underestimate the true proportion of native prey, considering that: 1) some prey items were identified only to endemic subfamily level; 2) many native taxa lack formal taxonomic designations due to insufficient study; and, 3) many alien species are distinctive and easily identified.

**Quantitative Studies**

Table 9 summarizes forager and prey intake parameters for the three monitored colonies. The colonies differed substantially in total numbers of trips and prey per wasp; the most active colony (HV08905) also collected the most prey per wasp, harvesting in one day about 16 times as many prey items (22,055) as the least active nest (HVO8904). These results, and subsequent observations of colony activity, size, and longevity, suggest that colonies HVO8904 and HVO8906 were well into their decline phase when sampled, while HVO8905 was more vigorous. During the course of the day there were within-colony fluctuations within each colony in foraging rate (Figure 5) and prey per wasp (Figure 6), but no clear patterns emerged.

Calculating prey consumption for single colonies or populations requires extrapolation from the limited data available. One way to estimate a colony's total input is to calculate the number of wasps reared and to multiply it by the number of prey needed to rear one wasp. Assuming that 1) most prey are small in relation to a final instar larva; 2) only a portion of each prey is used as food; and 3) biomass would also include the saliva fed back to adults during the duration of the larval stage and the voided meconium, one final instar might conservatively be expected to account for 20 prey items. A colony rearing a total of 20,000 individuals (also conservative for the sizes and population structures of annual *V. pensylvanica* colonies in Hawaii) would consume about 400,000 prey items. For colony HVO8905 this would represent less than three weeks of foraging at its rate of 24 November (which was probably lower than an earlier maximum rate). For this colony, an estimate of 60,000 wasps reared and 1,200,000 prey consumed would still be conservative. The consumption of a single overwintered colony such as HVO8903 (600,000 cells) would probably be in the tens of millions, spread out over two years! The impact of *V. pensylvanica* predation is hardly trivial.
<table>
<thead>
<tr>
<th>Time</th>
<th>Traps Off</th>
<th>Prey/Wasp</th>
<th>Foraging Rate (Sorties/Minute)</th>
<th>Interval (Minute)</th>
<th>Total Trips</th>
<th>Total Prey</th>
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</thead>
<tbody>
<tr>
<td>VO8904</td>
<td>06:46</td>
<td>0.0000</td>
<td>90</td>
<td>46</td>
<td>4140</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>08:04</td>
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<td>78</td>
<td>5928</td>
<td>97</td>
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<td>72</td>
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<td>900</td>
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<td></td>
<td></td>
<td></td>
<td><strong>TOTAL</strong></td>
<td><strong>5211</strong></td>
</tr>
</tbody>
</table>

Ohia foliage sampling was scheduled to compare the effects of different levels of *V. pensylvanica* predation pressure. The initial late fall sample was taken following several months of high forager populations. Furthermore, there was a gradient in predation pressure, with highest numbers of foragers in the Kokoolau area, and lowest numbers at Lua Manu. In contrast, the spring sample was taken after several months of negligible *V. pensylvanica* population levels; colonies had died out during early 1990, and no foragers were captured on the first monitoring date. Newly founded colonies were in their early developmental stages, and predation pressure would have
Table 10. Effects of Yellowjacket Predation on the Standing Crop of Ohia Foliage Arthropods (Potential Prey).

<table>
<thead>
<tr>
<th>Wasp Forager Density</th>
<th>Weight</th>
<th>Number of Small Items</th>
<th>Number of Large Items</th>
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<tbody>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lua Manu</td>
<td>4.2</td>
<td>31.75</td>
<td>6.30</td>
</tr>
<tr>
<td>Puhimau</td>
<td>23.2</td>
<td>21.95</td>
<td>5.50</td>
</tr>
<tr>
<td>Kokoolau</td>
<td>60.9</td>
<td>12.55</td>
<td>3.60</td>
</tr>
<tr>
<td>Hilina Pali</td>
<td>13.5</td>
<td>25.45</td>
<td>5.60</td>
</tr>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lua Manu</td>
<td>0.1</td>
<td>25.50</td>
<td>2.20</td>
</tr>
<tr>
<td>Puhimau</td>
<td>1.6</td>
<td>25.85</td>
<td>6.15</td>
</tr>
<tr>
<td>Kokoolau</td>
<td>0.2</td>
<td>23.35</td>
<td>4.55</td>
</tr>
<tr>
<td>Hilina Pali</td>
<td>0.3</td>
<td>18.60</td>
<td>3.00</td>
</tr>
</tbody>
</table>

been insignificant, and relatively uniform for the four sites.

Table 10 summarizes the seasonal indices of *V. pensylvanica* abundance, and the three measures of arthropod abundance, at the four sites. These figures must be interpreted with caution, because baseline data on arthropod abundances are lacking. Here, it is possible only to identify apparent trends and to suggest links to *V. pensylvanica* predation. For 1989 the correlations between *V. pensylvanica* forager density and all three measures of prey abundance are striking; the lowest values were at Kokoolau, where *V. pensylvanica* was most abundant. However, there is also substantial variability in values from the following spring, in the absence of *V. pensylvanica* predation at all four sites. Factors besides predation effects, especially seasonal fluctuations of arthropod populations, may play an important role here, but because of the lack of information, they cannot be systematically accounted for.

Only one measure of arthropod abundance gave consistent evidence of predation effects over both years: numbers of large (4.5 mm) arthropods. At all four sites values were lower in 1989 than in 1990. This accords well with the concept of a size threshold for *V. pensylvanica* prey; if larger arthropods are more preferentially harvested, then small arthropods would be expected to be less affected. Furthermore, when large arthropods are predators, their removal from the habitat may actually release populations of smaller arthropods. Thus, *V. pensylvanica* predation may have a subtle effect of altering the composition of local arthropod communities rather than causing wholesale depletion of arthropod biomass. By removing massive numbers of larger arthropods from ohia foliage, *V. pensylvanica* may also affect native birds, for which insects and spiders are important components of the diet. Birds also likely have a size threshold for prey, and to the extent that *V. pensylvanica* harvests the same items as the birds, there is direct competition for these resources, and a possibility of additional stress on native bird populations.

The threat to native Hawaiian ecosystems posed by *V. pensylvanica*'s invasion is exacerbated by a number of factors. Many endemic taxa are highly precinctive within native Hawaiian habitats, and local populations may be unable to recover from perturbations arising from intense predation pressure. The *V. pensylvanica* monitoring programs show that areas of high yellowjacket abundance may also be extremely localized, and predation pressure may vary substantially over relatively short distances (1-2 km). Hawaiian arthropods have evolved in the absence of predation pressure from social Hymenoptera, and may thus lack antipredator mechanisms selected for elsewhere (Gagne & Christensen 1985). *Vespula pensylvanica* has penetrated into a variety of native Hawaiian habitats (Howarth 1985; Gambino et al. 1990; Gambino 1991) where, under favorable circumstances, it can form very large annual and overwintered colonies. The latter, which occur unpredictably, reduce the effectiveness of seasonality.
as a temporal refuge from *V. pensylvanica* predation. Although *V. pensylvanica* is a generalist predator (characteristic of the genus), there is evidence that *Vespula* species adjust their foraging habits to focus on abundant prey species (Broekhuizen & Hordijk 1968; Gambino 1986). Thus, species which have pronounced peaks of abundance, even of short duration, may stimulate a functional response in *V. pensylvanica* that would reduce the effectiveness of predator satiation (May 1981) as an antipredator mechanism.

SECTION III
YELLOWJACKET ABATEMENT

INTRODUCTION
A prime objective of this project is the development of a practical pest management program for Hawaii's National Parks. Because *V. pensylvanica* is only one of a large number of pest organisms that the Parks' Resources Management Divisions must deal with, every effort was made to consider their staff and time limitations in the design of the control program. The details of *V. pensylvanica* biology in Hawaii, outlined in Section I, need to be incorporated into the program. The persistence, widespread distributions, and dispersal potential of *V. pensylvanica* populations on Hawaii and Maui suggest that eradication is either impractical or impossible, and that management efforts ought to focus on abatement. Additional studies reported here address relevant practical and logistical details of an effective abatement program.

The most feasible abatement methods involve applications of pesticides to kill wasps, and hopefully, entire colonies. These are applied according to strategies designed to limit the impact on non-target organisms. Pesticides can be effectively used against *V. pensylvanica* in two ways. First, when an active nest is located, pesticide is applied directly to it. This fairly obvious technique no doubt has a long history; spot treatment of colonies probably started as soon as early man could associate wasps with the nests from which they came. From the point of view of the National Park Service, other factors beside effectiveness against wasps must be weighed, such as the overall environmental effects of the pesticide toxicant, risks to applicators, and ease of use.

Sometimes an outbreak is caused by a population of colonies, making it impractical to find them all. In this situation, the scavenging habit of *V. pensylvanica* can be exploited by deploying a toxic bait distribution system. The effectiveness of toxic baits was first demonstrated by Grant et al. (1968), who used a mixture of a horsemeat bait base and the toxicant chlordane to reduce forager populations of *V. pensylvanica* and *V. vulgaris* (L.) in California. Since then, the strategy has been modified for use against scavenging *Vespula* species in a number of situations (Keh et al. 1968; Ruddock & Rohe 1968; Wagner & Reierson 1969, 1971; Rogers 1972; Ennik 1973; Perrott 1975; Chang 1988). In Hawaii, Chang (1988) conducted an abatement program against *V. pensylvanica* in sugar cane fields on O'ahu, investigating the effects of different baits and toxicants, dispenser designs, and bait distribution schedules. Forager behavior, including food preference, varies among *Vespula* species (MacDonald et al. 1976; Akre & MacDonald 1986), and possibly among geographic strains within species (Akre et al. 1980). Thus, the design of an optimal pest management program incorporates characteristics of the specific pest in the area of concern.

This section is subdivided into three subsections: 1) results of nest treatments with two pesticides, Ficam D and PT 515 Waspfreeze; 2) investigation of factors affecting the toxic baiting program; and, 3) results of control efforts at HALE and HAVO combining nest treatment and toxic baiting strategies.

NEST TREATMENTS

Materials & Methods
The effectiveness of Ficam D (dust formulation, active ingredient = bendiocarb) and Whitmire PT515 Waspfreeze (aerosol spray can, active ingredients = pyrethrins) were evaluated by monitoring activity at active nests before and after their application. For Ficam, dust was dumped directly into the entrance tunnel leading to the yellowjacket nest. For Waspfreeze, varying amounts, up to one 12-ounce can, were sprayed into the entrance tunnel.
Results & Discussion

The results of pesticide treatments of individual V. pensylvanica colonies are summarized in Tables 11 (Ficam) and 12 (PT515). Neither treatment was always effective in destroying active colonies with a single application. Reasons for failure probably included large colony size (and the ability to recover as new adults emerged within the nest) and difficulty in applying the pesticide to ensure exposure of wasps (allowing them to avoid exposure when exiting or entering the nest). The advantage of Ficam is that as a dust, it is perhaps more easily picked up on the legs of workers and spread among colony members, whereas the aerosol PT515 would tend to soak into the soil. Although toxicity data were not available, Ficam seemed to be more lethal to V. pensylvanica. This is an advantage in terms of efficacy, but its broad spectrum toxicity is a disadvantage in terms of exposure of nontarget organisms. Three of the Ficam-treated nests were subsequently attacked by vertebrates (probably rats or mongooses) and combs were dug up and scattered. These attacking animals were thus also likely exposed to the pesticide, and there is potential for the poisons to move up the food chain (to endangered predator/scavenger birds, for example). As a dust, Ficam is also cumbersome to store and apply safely, and exposure of applicators or other people is a potential hazard. The National Park Service is justified in seeking a substitute for Ficam D for treatment of nests, but the results of trials with Whitmire PT515 Waspfreeze indicate considerable room for improvement.

FACTORs AFFECTING TOxIC BAITING

Material & Methods

Several factors affecting the baiting program were evaluated. First, baits were screened to find a suitable bait base by testing nine different foods to determine relative attraction. The three most attractive were then tested to determine which one yellowjackets preferred to collect. The use of heptyl butyrate to enhance bait collection, and the effects of aging on bait acceptance were also tested in the field. Finally, the attraction of heptyl butyrate to V. pensylvanica foragers in a specialized habitat, the Ola'a Tract ohia-Cibotium rainforest, was studied.

Bait Attraction: Nine baits were evaluated for attraction of V. pensylvanica foragers: Swanson’s Premium White and Dark Chicken (CHK), Hormel Chunk Turkey (TKY), Hormel Chunk Ham (HAM), Sea Alaska Fancy Sockeye Red Salmon (SAL), Spam (SPM), Coral Tuna in Water (TNA), Swanson’s Chunky Chicken Spread (SRD), Figaro Tuna Cat Food (CAT) and Nebraska Brands Feline Food (NBF). With the exception of NBF, all were canned meat- or fish-based products available at local retail stores. Preliminary screening showed that CHK was highly attractive, so a mixture of CHK and the toxicant Knoxout 2FM formulated according to label instructions (3 ml per 100 g bait) was also included as a tenth bait (KOC). For each test ca. 25 grams of bait was put into a Yellowjacket Inn trap. Ten traps were suspended at intervals of 0.75 m in random order from a line 1.5 m above ground, oriented across the prevailing wind. Numbers of wasps were counted after 24 hours. Tests were run at four locations within HAVO: Kipuka Nene (15 Sep, 6 Oct, 11 Oct 1989), Kipuka Puaulu (15 Sep), Ka‘u Desert (15 Sep), and Puhimau (13 Oct). Data were log transformed to correct for unequal variances, and analyzed as six independent trials in a randomized block analysis of variance (ANOVA) with means separated by Duncan’s test, using the GLM procedure of SAS Institute (1985, 183-260).

Bait Acceptance: The four most attractive baits (CHK, KOC, TKY, HAM) were selected for tests of bait acceptance. For each test, 25 g of bait was placed in an 88-ml paper cup; a fifth cup, containing bait covered by a screen to keep out yellowjackets, was included as a control for each replicate. Since baits were similar in density and water content, CHK was selected as the representative control bait. Cups were suspended at intervals of 0.5 m from a horizontal pole 1.5 m above ground; the middle cup was the control, and other baits were placed randomly. The dependent variable was amount of bait taken; to correct for weight loss through evaporation, the amount was calculated as (total weight loss - weight loss from screened cup). Tests were replicated at three sites in the Ka‘u Desert (where foragers were
Table 11. Tests of Ficam D treatments on nests of *V. pensylvanica*.

<table>
<thead>
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<th>Nest</th>
<th>Amount (oz.)</th>
<th>Results</th>
</tr>
</thead>
<tbody>
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<td>HVO8802</td>
<td>1</td>
<td>Activity terminated; vertebrate feces found</td>
</tr>
<tr>
<td>HVO8803</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8804</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8805</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8806</td>
<td>1</td>
<td>Activity terminated; combs dug up and scattered</td>
</tr>
<tr>
<td>HVO8807</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8808</td>
<td>1</td>
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</tr>
<tr>
<td>HVO8809</td>
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<td>HVO8811</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8812</td>
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<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8813</td>
<td>1</td>
<td>Required additional application</td>
</tr>
<tr>
<td>HVO8818</td>
<td>1</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HVO8821</td>
<td>1</td>
<td>Activity terminated; combs dug up and scattered</td>
</tr>
<tr>
<td>HVO8832</td>
<td>2</td>
<td>Required additional application</td>
</tr>
<tr>
<td>HVO8833</td>
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</tr>
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<td>HVO8816</td>
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<tr>
<td>HVO8830</td>
<td>1</td>
<td>Required additional application</td>
</tr>
</tbody>
</table>

Table 12. Tests of Whitmire PT515 Waspfreeze treatments on nests of *V. pensylvanica*.

<table>
<thead>
<tr>
<th>Nest</th>
<th>Amount</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>HVO9002</td>
<td>1 can</td>
<td>Additional treatment necessary</td>
</tr>
<tr>
<td>HVO9006</td>
<td>1 can</td>
<td>Activity terminated</td>
</tr>
<tr>
<td>HAL9001</td>
<td>1/2 can</td>
<td>Additional treatment necessary</td>
</tr>
<tr>
<td>HAL9002</td>
<td>1/2 can</td>
<td>Activity terminated</td>
</tr>
</tbody>
</table>

most abundant) on 3 July, 24 July, and 31 July 1990. Data were analyzed in a two-way ANOVA with baits and dates as treatment factors.

**Enhancement of Bait Acceptance:** The chemical heptyl butyrate is one of a series of synthetic esters attractive to *V. pensylvanica* foragers (Davis et al. 1969). Its effect on the amount of KOC collected by wasps was tested in the context of an ongoing abatement program at HAVO. The test area was approximately 26 acres at Namakani Paio. Dispensers similar to that designed by Chang (1988) were suspended from trees ca. 1.5 m above ground at intervals of ca. 70 m around the perimeter. Each dispenser held 60 g bait; alternating dispensers had an added open 1.8 ml microfuge tubule, containing 0.4 ml heptyl butyrate with a paper towel wick, affixed. Dispensers were put out on 2 Aug 1990 at approximately 0800. Bait remaining was weighed after eight hours; amounts of bait taken (uncorrected for evaporation) were analyzed by t-test (two-tailed).

**Repellency of Formulated Bait:** In preliminary toxic baiting experiments using KOC, it was noticed that when baits were put out early in the day, *V. pensylvanica* foragers at dispensers were more abundant in the morning than in the afternoon. It was not clear if this was due to decreasing attraction of the bait as it aged, or to incapacitation of foragers resulting from their contact with the insecticide. To decide between these competing hypotheses, the acceptability of aged bait was tested. Fresh KOC was put
out on 20 Aug 1990, using the same sites and dispensers as the heptyl butyrate bait enhancement test. Bait was collected after eight hours and stored overnight at 5°C. The next day the aged KOC and fresh CHK were offered to naive yellowjackets using the techniques and sites of the previous bait acceptance trials. Because the aged KOC had already lost some of its moisture through evaporation the previous day, separate screened cups were put out for both it and fresh chicken at each site. Amount of bait taken was corrected by subtracting the loss through evaporation at the control from the total weight loss of the test bait. Data were analyzed using a t-test (one-tailed).

Attraction of heptyl butyrate in Ola’a Tract: HAVO contains a diversity of habitats that vary in suitability for supporting a baiting program. The Ola’a Tract is a rainforest with large areas of dense ground-level vegetation where yellowjacket foragers were rarely seen. The discovery of a series of four active colonies within a span of 170 meters along a fence line provided an opportunity to investigate foraging behavior. On 1 Dec 1988, foragers at the four colonies were marked by dumping 25 grams of colored fluorescent powder into the nest entrance tunnel. A series of 14 heptyl butyrate-baited Yellowjacket Inn traps were suspended from a 430 m section of fence line (height = 1 m) that overlapped with the locations of all four nests. Ten of the traps were within 50 m of at least one nest; the farthest trap was 250 m from the nearest nest. Traps were put out at 1030 and checked five hours later.

Results & Discussion

Bait Attraction: Baits differed significantly in their attractiveness to V. pensylvanica foragers (F = 5.75; df = 9.40; P < 0.01), with two chicken formulations (KOC, CHK) most preferred (Table 13). The texture of chicken had a substantial effect; CHK consisted of fairly large chunks of flesh, whereas the paste SRD, presumably differing only in the processing, drew in significantly fewer yellowjackets. This contrasts with the results of Reid & MacDonald (1986), who found the number of V. germanica (F) visits to be relatively uninfluenced by grinding treatments of NBF. The addition of Knoxout 2FM to CHK (to make KOC) did not reduce its attractiveness (consistent with the findings of Reid & MacDonald, [1986]); if anything, attraction was slightly enhanced.

Bait Acceptance: Regardless of inherent attractiveness, a toxic bait will be ineffective unless yellowjackets carry it away from the dispensers. Reid & MacDonald (1986) demonstrated that acceptance of different preparations of the same bait base may vary according to texture. The four baits chosen for the acceptance test (CHK, KOC, TKY, HAM) showed some difference in the amounts removed by V. pensylvanica foragers (F = 5.89; df = 3.24; P 0.01). In pairwise comparisons (Table 14), CHK and KOC did not differ significantly, but less ham was taken than chicken with or without pesticide. The close proximity of baits to each other was intended to reduce the effect of differential attractiveness by having baits generate a single pooled odor plume effective over long distances, but some fine discrimination by wasps nearing the baits was inevitable. However, increasing reliance on visual cues at close range would minimize this effect. There was a significant influence of date (F = 18.84; df = 2.24; P < 0.01), likely due to a combination of seasonal variation in the wasp populations and different weather conditions on the test dates. The interaction of bait with date did not produce a significant effect.

Enhancement of Bait Acceptance: Of the scavenging Vespula species, V. pensylvanica is exceptional in that effective synthetic attractants are available. So far, heptyl butyrate has proven useful for monitoring V. pensylvanica populations (MacDonald et al. 1973; Chang, 1988; Gambino et al. 1990) and for population depletion trapping (Davis et al. 1973). At HAVO, wasps took significantly more KOC bait from dispensers with heptyl butyrate wicks (means of 16.9 g versus 7.4 g; t = 3.14; df = 16; P < 0.01). Thus, the potential for chemical manipulation of V. pensylvanica forager behavior in the context of a toxic baiting program, shown for heptyl crotonate (Wagner & Reierson, 1969), is also demonstrated for heptyl butyrate.

Repellency of Formulated Bait: The microencapsulation process for Knoxout 2FM reduces the repellency of its active ingredient, diazinon, to yellowjackets (Ennik, 1973). The stability of the formu-
Table 13. Numbers of *V. pensylvanica* workers attracted to ten baits.

<table>
<thead>
<tr>
<th>Bait</th>
<th>Type of food a</th>
<th>No. of wasps caught</th>
<th><em>x</em></th>
<th>log(x+1) ± SD b</th>
</tr>
</thead>
<tbody>
<tr>
<td>KOC</td>
<td>Chunk chicken + Knoxout 2FM</td>
<td>60.8</td>
<td>60.8</td>
<td>1.65 ± 0.28 a</td>
</tr>
<tr>
<td>CHK</td>
<td>Chunk chicken</td>
<td>51.3</td>
<td>51.3</td>
<td>1.55 ± 0.42 a</td>
</tr>
<tr>
<td>TKY</td>
<td>Chunk turkey</td>
<td>35.3</td>
<td>35.3</td>
<td>1.23 ± 0.66 abc</td>
</tr>
<tr>
<td>HAM</td>
<td>Ham</td>
<td>28.0</td>
<td>28.0</td>
<td>1.18 ± 0.52 abc</td>
</tr>
<tr>
<td>SPM</td>
<td>Spam</td>
<td>19.2</td>
<td>19.2</td>
<td>1.05 ± 0.17 abc</td>
</tr>
<tr>
<td>SAL</td>
<td>Salmon</td>
<td>22.5</td>
<td>22.5</td>
<td>0.97 ± 0.16 bc</td>
</tr>
<tr>
<td>TNA</td>
<td>Chunk tuna</td>
<td>7.5</td>
<td>7.5</td>
<td>0.78 ± 0.13 cd</td>
</tr>
<tr>
<td>SRD</td>
<td>Chicken spread</td>
<td>13.0</td>
<td>13.0</td>
<td>0.77 ± 0.13 cd</td>
</tr>
<tr>
<td>NBF</td>
<td>Horsemeat</td>
<td>1.0</td>
<td>1.0</td>
<td>0.23 ± 0.04 d</td>
</tr>
<tr>
<td>CAT</td>
<td>Tuna cat food</td>
<td>1.2</td>
<td>1.2</td>
<td>0.19 ± 0.03 d</td>
</tr>
</tbody>
</table>

a  See text for full descriptions of baits.
b  Means within a column followed by the same letter are not significantly different (*P* = 0.05, Duncan's multiple range test).

Table 14. Amounts of baits collected by *V. pensylvanica* workers.

<table>
<thead>
<tr>
<th>Bait</th>
<th>Grams taken x ± SD a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chicken</td>
<td>9.9 ± 4.7 a</td>
</tr>
<tr>
<td>Chicken + Knoxout 2FM</td>
<td>8.4 ± 3.2 ab</td>
</tr>
<tr>
<td>Turkey</td>
<td>7.0 ± 5.0 bc</td>
</tr>
<tr>
<td>Ham a</td>
<td>4.3 ± 2.7 c</td>
</tr>
</tbody>
</table>

a  Means within a column followed by the same letter are not significantly different (*P* = 0.05, Duncan's multiple range test).

Attraction of heptyl butyrate in Ola'a Tract:

Only one (unmarked) yellowjacket was caught in one of the fourteen traps, which was 200 meters from the nearest nest. This result corroborated the informal observation that wasps exiting nests in vegetationally dense areas of rainforest flew straight up to forage in well-lit regions of the canopy, and rarely flew at ground level. It suggests that the effectiveness of heptyl butyrate as an attractant is very reduced under rainforest conditions, probably because a coherent odor plume that wasps can follow to its source does not form. A combination of high humidity, low wind, and restricted straight lines of vision and flight might contribute to this effect. These results would also call for further study.
into question the attractiveness of food bait bases under rainforest conditions at Ola’a.

This study underscores the importance of screening a variety of bait bases before selecting the one to use in a toxic baiting program. Past studies of yellowjacket feeding preferences have concentrated on canned pet foods and fish (Ruddock & Rohe 1968; Wagner & Reterson 1969, 1971; Ennik 1973; Ferrott 1975; Ross et al. 1984; Chang 1988); in the present study, such baits ranked low in attractiveness. Nebraska Brands Feline Food, which showed potential for incorporation into a V. germanica management program (Ross et al. 1984) would be totally unsuitable for V. pensylvanica control in Hawaii, considering its inability to attract workers and its specialized storage requirements. Of the three most attractive bait bases, only ham has been comparatively evaluated in past studies (Reid & MacDonald 1986).

From a land manager’s point of view, acceptance of a bait by yellowjackets is only one of several considerations in implementing a baiting program; ease of bait base acquisition and storage are also important. Thus, for the sake of the intended users of the present research results, the focus was on widely available canned meat and fish products, from which several suitable candidates were selected. Overall, canned chunk chicken was unsurpassed as a bait base in both attraction and acceptability. Formulation with Knoxout 2FM did not diminish these qualities. The problem of reduced acceptability of aging bait remains, but a more limiting factor may be the knockdown of bait-collecting foragers. Performance of the baiting system is also affected by physical factors at the baiting site; success is more likely in relatively open areas where yellowjackets can easily find the baits. If competing attractions draw workers away from the baits, and especially if baits cannot be easily placed where yellowjackets prefer to forage, it may be difficult to justify the expenditure of resources on a baiting program. Regarding the conservation of native arthropods, the reluctance of V. pensylvanica to hunt in well-shaded sections of the rainforest suggests that this may offer a refuge for arthropods that occur there, while those favoring well lit areas of the canopy may be more at risk.

YELLOWJACKET ABATEMENT TRIALS

Area-wide baiting research in 1988 and 1989 was conducted concurrently with research described in previous sections. Consequently, the selection of sites and schedules for baiting did not always coincide with the most favorable opportunities to demonstrate the baiting technique. By 1990, a better understanding of factors affecting baiting permitted greater confidence in the effectiveness of the technique. The 1990 trials were conducted as demonstrations for Resources Management Division staff, to provide hands-on experience. This, combined with the Resource Manager’s Guide (Appendix I), represented the final technology transfer aspect of the project.

Materials & Methods

For each yellowjacket abatement trial there was a treatment area and an untreated area of similar size. Although we tried to control for such factors as altitude, vegetation type, and other environmental conditions, matches were only approximate. A separation of at least 800 m was necessary to minimize spillover effects of baiting on populations outside the bait distribution area (especially in the untreated areas). However, non-uniformity of environmental conditions and of yellowjacket populations in matched areas increased with distance. This was not a trivial consideration, because in both parks fairly steep gradients of a number of environmental factors occur.

For each trial, populations in each area were monitored with a battery of five heptyl butyrate baited Yellowjacket Inn traps. Data from at least two sampling intervals were gathered prior to bait distribution. An arbitrary action threshold of five wasps per trap per day (5 W/T/D) was assigned. There was no firm objective justification for this value; rather, it was chosen because at this level, yellowjackets were observed to be fairly conspicuous and somewhat bothersome to people. Furthermore, above this level, the effects of V. pensylvanica predation on
some populations of arthropods may be detectable. Thus, the objective was to maintain forager populations below 5 W/T/D in treated areas, in contrast to untreated areas.

Table 15 summarizes area-wide abatement research from 1988-1990. A total of seven trials were conducted. Generally, 28 grams (one ounce) of toxic bait per dispenser was sufficient; only in a few instances was this amount depleted. The amount of bait can easily be adjusted upwards in proportion to higher density populations; two ounces might be more appropriate where the W/T/D exceeds 10. During 1988 and 1989 dispensers similar to that of Chang (1988) (See Appendix 1) were distributed in a regular grid pattern (slightly irregular for Kipuka Puaulu, 1988) throughout treatment areas; numbers of baiting applications ranged from one to five. Baits were put in dispensers around sunrise, left out for at least one day, and collected as soon as practical.

In 1990 several modifications were made. A new dispenser, consisting of a suspended open paper cup, was used (Appendix 1). At HALE, based on successful demonstrations the previous two years, a large-scale baiting (1100 hectares = 2700 acres), without a comparable untreated area, was conducted. Bait dispensers were deployed along the paved road from 2275 m to 2850 m elevation, with an additional 23 dispensers along transects away from the road. For evaluation, the population in the treated area (monitored with single Yellowjacket Inn traps at 2438, 2591, and 2693 m elevations) was compared with the population upslope from the treatment area (traps at 2835 and 2957 m elevation), where populations are usually less dense than those around 2591 m (the center of the treatment area).

Placement of dispensers along the road rather than in a grid created an opportunity to investigate the effects of distance from the nearest dispenser. Two upslope-downslope transects were established and monitored with 10 traps per transect. For each transect we designated the four central traps as “distant” (minimum distance to the nearest dispenser: Leleiwi-Halemau transect, 350 m; Motley Gulch transect, 300 m) and compared W/T/D counts with the six peripheral traps (three at each end of the transect) designated “near”.

Baiting programs were conducted in conjunction with destruction of individual nests in the treatment areas, and it was impossible to separate the effects of the two techniques. The extent to which results may be confounded will be discussed for each specific trial. In 1988 and 1989 nests were treated with Ficam D; in 1990 they were treated with PT515.

Results & Discussion

Each baiting trial represents a unique situation (Table 15); results from each trial will be discussed separately. Then conclusions from the series of trials will be summarized.

1988: HAVO: Kipuka Puaulu/Kipuka Ki: These sites are mature native mesic forests intermixed with open grasslands. They have substantial well shaded areas, difficult to penetrate due to dense ground level vegetation. Baiting at Kipuka Puaulu was fairly labor-intensive, and despite a moderately high yellowjacket population, very little bait was taken from dispensers in well-shaded areas. The forager population was definitely depressed due to control measures (Figure 9), but the destruction of 18 colonies may have been more influential than the baiting program. One nest that was missed apparently overwintered and developed into the massive HVO8903, the only colony discovered in Kipuka Puaulu in 1989.

1988: HAVO: Kipuka Kulalio/Kipuka Maunau: These sites are mostly open areas dominated by a mixture of scrub and grasslands, with some sections of dense old growth koa (Acacia koa). Due to the large size (140 acres), it was very labor-intensive to distribute baits throughout the treatment area. The passage of a hurricane one day after the initial bait application confounded the results, as populations dropped in both treated and untreated areas. However, subsequent developments indicated good success of baiting (Figure 10). No colonies were discovered within the treatment area. However, HVO8816, presumably overwintered from the previous year, was found slightly upslope of the treatment area, and could easily have contributed many foragers to the monitored population. The colony was destroyed on 1 September, which probably depressed the forager population within the treatment area; this was after the positive effects of baiting had
Table 15. Yellowjacket abatement trials, 1988-1990.

<table>
<thead>
<tr>
<th>Treated/Untreated</th>
<th>Year</th>
<th>Site</th>
<th>Area (Acres)</th>
<th>No. of Dispensers</th>
<th>No. Nests Destroyed</th>
<th>Bait Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>U</td>
<td>1988</td>
<td>Kipuka Ki</td>
<td>60</td>
<td>80</td>
<td>58</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>Kipuka Puaulu</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2 Aug</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>20 Oct</td>
</tr>
<tr>
<td>U</td>
<td>1988</td>
<td>Kipuka Maunaiu</td>
<td>140</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>Kipuka Kulalio</td>
<td>140</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>26 Aug</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>29 Aug</td>
</tr>
<tr>
<td>U</td>
<td>1988</td>
<td>HALE2</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>HALE1</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7 Sep</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9 Sep</td>
</tr>
<tr>
<td>U</td>
<td>1989</td>
<td>Rt 11/Ka’u Desert Footprints</td>
<td>60</td>
<td></td>
<td></td>
<td>19 Aug</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>1989</td>
<td>HALE2</td>
<td>80</td>
<td></td>
<td></td>
<td>19 Sep</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>HALE1</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>1990</td>
<td>Kipuka Puaulu</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>1990</td>
<td>Namakan Paio</td>
<td>26</td>
<td></td>
<td></td>
<td>2 Aug</td>
</tr>
</tbody>
</table>

been demonstrated. Forager populations were extremely low during 1989 (consistent with a carryover effect of abatement in 1988 into the following year), while they reached moderate levels in untreated Kipuka Maunaiu.

1988: HALE: HALE1/HALE2: These are both open subalpine scrub habitats, although HALE1 also includes a small (acres) grove of introduced trees (mostly eucalyptus and conifers). Baiting results were good (Figure 11); probably, not all five baits were necessary. The two colonies destroyed were both quite small, and did not substantially confound the effect of the baiting program.

1989: HAVO: Footprints/Route 11 (Ka’u Desert): These sites are basically rocky desert with stunted scrub vegetation; the Footprints site contains a few small sand dune kipukas of several acres with somewhat larger trees. These sites were chosen after V. pensylvanica populations failed to develop in preferred sites during 1989. The forager peak probably occurred early in the summer; by the time monitoring was initiated the population was very high, but about to crash. Although forager populations in the treatment area declined after each baiting, they also dropped (though not so dramatically) in the untreated area (Figure 12). This trial was not a clear demon-
stration of the success of the baiting program, probably due to the confounding independent population declines.

1989: HALE: HALE1/HALE2: The baiting program was repeated at the same sites used in 1988. Only one bait application was used, and it produced the desired population reduction (Figure 13). However, the effects of baiting might have been more clearly demonstrated had it been started earlier. The destruction of two small colonies in the treatment area probably had little influence on the effect of baiting.

1990: HAVO: Namakani Paio/Kipuka Puaulu: The Namakani Paio site is a small, eucalyptus-dominated grove (26 acres) with a fairly open understory, surrounded by mixed desert/scrub vegetation. A portion of Kipuka Puaulu, similar to Namakani Paio in density of vegetation (and different from the section used for treatment in 1988) was monitored as the untreated area. This trial was a successful demonstration of the revised baiting technique (Figure 14).

1990: HALE: This was the largest scale baiting trial attempted (2700 acres). The treatment area encompassed both HALE1 and HALE2 from the previous years. The logistics of baiting were simplified considerably by putting dispensers along the road. Results were very good; the success shown in Figure 15 is likely a conservative estimate, because the treatment area included areas where yellowjacket forager populations are usually most dense (Table 3). The baiting seemed to kill off two active colonies within the treatment area (the first time this had been observed), while the destruction of 3 other colonies probably had little influence on the overall effect of baiting.

The effect of distance from baiting stations is summarized in Figure 16. Differences between near and distant populations were not great, with all sites remaining below threshold of 5 W/T/D. We interpret this as evidence that baits are effective over distances reaching to the most isolated monitoring trap (360 m).

ACKNOWLEDGEMENTS

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### Appendix 1.

**Arthropods identified to genus among Y. pensylvanica prey items.**

*Asterisks indicate endemic taxa.*

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Genus/Species</th>
<th>N</th>
<th>Sitesa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneae</td>
<td>Lycosidae</td>
<td><em>Lycosa hawaiensis</em> Simon</td>
<td>4</td>
<td>HK, OT</td>
</tr>
<tr>
<td></td>
<td>Salticidae</td>
<td><em>Sandalodes</em> spp.* Simon</td>
<td>2</td>
<td>PU, OT</td>
</tr>
<tr>
<td></td>
<td>Tetragnathida</td>
<td><em>Tetragnatha</em> spp.* Simon</td>
<td>18</td>
<td>KP, PU, OT</td>
</tr>
<tr>
<td></td>
<td>Theridiidae</td>
<td><em>Theridion</em> sp.</td>
<td>1</td>
<td>OL</td>
</tr>
<tr>
<td></td>
<td>Thomisidae</td>
<td><em>Misumenops vitellinus</em> (Simon)</td>
<td>4</td>
<td>HK</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Misumenops</em> spp.*</td>
<td>3</td>
<td>HK</td>
</tr>
<tr>
<td>Blattodea</td>
<td>Blattidae</td>
<td><em>Allacta similis</em> (Saussure)</td>
<td>7</td>
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</tr>
<tr>
<td>Orthoptera</td>
<td>Gryllidae</td>
<td><em>Anaxipha</em> sp.*</td>
<td>22</td>
<td>KP, OL</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Leptogryllus</em> sp.*</td>
<td>6</td>
<td>KP</td>
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<tr>
<td>Hemiptera</td>
<td>Alydidae</td>
<td><em>Ithamar hawaiensis</em> (Kirkaldy)</td>
<td>4</td>
<td>HK</td>
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<tr>
<td></td>
<td>Flatidae</td>
<td><em>Siphanta acuta</em> (Walker)</td>
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<td>OT</td>
</tr>
<tr>
<td></td>
<td>Nabidae</td>
<td><em>Nabis</em> spp.*</td>
<td>26</td>
<td>PU, HK</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>Sphingidae</td>
<td><em>Hyles wilsoni</em> (Rothschild)</td>
<td>1</td>
<td>KP</td>
</tr>
<tr>
<td></td>
<td>Geometridae</td>
<td><em>Eupithecia</em> spp.*</td>
<td>16</td>
<td>PU, HK</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Cerambycidae</td>
<td><em>Plagithmysis funebris</em> Sharp</td>
<td>1</td>
<td>HK</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Plagithmysis</em> sp.*</td>
<td>3</td>
<td>HK</td>
</tr>
<tr>
<td></td>
<td>Coccinellida</td>
<td><em>Olla abdominalis</em> (Say)</td>
<td>1</td>
<td>HK</td>
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<tr>
<td></td>
<td></td>
<td><em>Hippodamia convergens</em> (Guerin-Meneville)</td>
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<td></td>
<td>Curculionidae</td>
<td><em>Pantomorus cervinus</em> (Boheman)</td>
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<td>HK, KP</td>
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<td>Colletidae</td>
<td><em>Nesoprosopis</em> sp.*</td>
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<td>Apidae</td>
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<tr>
<td></td>
<td>Vespidae</td>
<td><em>Vespula pensylvanica</em> (Saussure)</td>
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<td>Diptera</td>
<td>Tachinidae</td>
<td><em>Gonia longipulvilli</em> Tothill</td>
<td>2</td>
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</tr>
<tr>
<td></td>
<td></td>
<td><em>Trichopoda</em> sp.</td>
<td>1</td>
<td>KP</td>
</tr>
</tbody>
</table>

**a**KEY TO SITES

- KP - Kipuka Puaulu (HAVO)
- OL - Olaa Tract + Olaa Forest Reserve (HAVO)
- PU - Puhimau (HAVO)
- OT - Other (HAVO)
- HK - Haleakala (HALE)
Appendix 2.
RESOURCE MANAGER'S GUIDE TO YELLOW JACKET ABATEMENT IN HAWAII'S NATIONAL PARKS
by
Parker Gambino

Introduction
As of 1990, the western yellowjacket *Vespula pensylvanica* (Saussure) was the only vespine wasp established in the Hawaiian islands. Detailed descriptions of its biology in its native range (western North America) and in the Hawaiian Islands are available elsewhere. Information presented here is limited to what is pertinent for local abatement programs.

Yellowjacket abatement in Hawaii is desirable for two basic reasons. Their stinging behavior can cause pain and discomfort; for allergic individuals, a sting may result in medical complications such as anaphylactic shock and even death. High concentrations of foragers may intimidate people without stinging. Thus, when populations are high, they can interfere with recreational, research, and management activities in the park. Fortunately, legal complications arising from stinging incidents have not been a problem thus far, although this possibility cannot be dismissed indefinitely.

The second rationale for yellowjacket abatement derives from their feeding behavior; they are generalist predators of other arthropods. In native Hawaiian ecosystems, predation pressure on native arthropods may cause problems for the conservation of biotic resources. The survival of local populations of some arthropod species may be seriously challenged. The total number of arthropods consumed by a vigorous overwintered colony is surely in the millions, possibly in the tens of millions.

Biology of *V. pensylvanica*
Since its invasion of the Hawaiian Islands, *V. pensylvanica*'s adaptations to local conditions have resulted in variations of the life cycle that complicate management efforts. Some understanding of both the typical pattern of *V. pensylvanica* colony development and the atypical (but not uncommon) Hawaiian variants is necessary to design an effective abatement program. It is convenient to classify colonies as annual (typical) or overwintering (atypical), although some colonies do not fit clearly into either pattern. Queens, males, and workers all play their role in the colony cycle, but the negative impacts on human activities and native arthropod faunas are almost exclusively due the activities of workers.

Annual Colonies: A typical colony is started in the spring by a solitary queen. It takes several months for her to generate the first clutch of workers; once they start foraging, the queen does not venture outside the nest. For the next few months, colony resources go into increasing the worker population, and the colony grows, slowly at first, and then exponentially. Later in the summer, colony production shifts to rearing reproductives (new queens and males). The worker population of the colony stabilizes and then declines. The function of the reproductives is to mate and disperse, and they contribute little to the welfare of their natal colony, which eventually declines and is abandoned. Fertilized queens hibernate individually and emerge the following spring to initiate new colonies. The total number of wasps produced by a successful annual colony is usually less than 40,000 (mainland colonies are seldom even half that productive). Only a very small proportion of queens from any year produce successful colonies the following year.

Overwintered Colonies: Overwintered colonies start out as annual colonies, but instead of dying out in their first year, they continue into a second year. Although there is no documented case of a colony lasting three or more years, there are no obvious constraints against it, and this possibility cannot be excluded. Whereas annual colonies phase out worker production when reproductives are reared,
overwintering colonies produce workers continuously through the reproductive phase. Instead of dying out, the colony remains active, acquiring new queens to replace the original foundress. The colony then has several or many egg-laying queens and an abundant worker force as it enters its second year. Colony production reverts to workers, at a rate orders of magnitude greater than annual colonies just getting started. Additional reproductives may be generated during the second season. The largest analyzed colony from Hawaii (Kipuka Puaulu) had about 560,000 small cells and 40,000 large (queen) cells, and produced at least one million wasps.

The general pattern of yellowjacket forager populations in Hawaii resembles that in its native range; worker activity is low (or more likely, completely absent) during the winter and early spring, rises during the summer, peaks during the late summer and fall, and then crashes. The presence of foraging workers (and also large numbers of males) during the early spring is a good indication of overwintering colonies.

Weather exerts a dominant influence on yellowjacket phenology and abundance. Highly localized variations in yellowjacket populations can be traced to the extremely variable and sometimes unpredictable Hawaiian weather patterns. Thus, at Hawaii Volcanoes National Park (HAVO), forager populations may peak during July in the western Kau Desert, while further east, the peak does not occur until September or October. During the same year, yellowjackets may be abundant in dry localities and nearly absent from wetter areas, especially if the period of nest initiation during the spring was particularly wet. The dominant influence at HAVO seems to be the rain.

At Haleakala National Park (HALE) there is a fairly steep elevational gradient on the northwestern slope of Haleakala volcano, and a moderate east-west moisture gradient. The mid-Pacific summer temperature inversion commonly produces a dense layer of fog that is thickest below the park boundary, but also extends up to the lower elevations within the park. The fog apparently inhibits development of yellowjacket colonies. Population trends on the northwest slope of Haleakala volcano are more predictable than at HAVO. Prime yellowjacket habitat is consistently centered near the 8500 ft (2591 m) bend in the road. While there is annual variation in the magnitude of yellowjacket populations, they are well synchronized, peaking regularly from late August to mid-October.

**Population Monitoring**

Monitoring of pest populations is a basic tenet of integrated pest management. The attraction of *V. pensylvanica* foragers to the synthetic chemical heptyl butyrate (which is a non-toxic substance sometimes used as a food additive) provides a convenient mechanism for measuring populations.

The trap chosen for monitoring is the Seabright Yellowjacket Inn, baited with a heptyl butyrate wick. To load the trap, pipette 0.4 ml heptyl butyrate into a 1.5 ml polyethylene microfuge tube. Add a wick, which can be made from a rolled up piece of paper towel. The wick should not extend so far as to interfere with closing the tube. For each area to be monitored, it is recommended that 5 traps be set out, separated by at least 25 meters, but preferably distributed evenly throughout the area. Traps should be suspended between 1-2 meters above ground, and not placed in dense shade. Metal shower curtain rings work very well to suspend traps. Heptyl butyrate tubules can be carried closed into the field, and opened just prior to replacing the old tubule + wick. Numbers of yellowjackets captured are counted when the attractant is replaced. An interval of one week is recommended; at intervals longer than two weeks, counts are less valid because the heptyl butyrate evaporates and attraction decreases. Population levels are expressed as wasps per trap per day, calculated by adding the number of wasps for all 5 traps and then dividing by 5 times the monitoring interval. Forager density can then be plotted against time, demonstrating the seasonal nature of population fluctuations. Populations can also be compared between different monitoring areas.

Two factors have been found to interfere with accurate counts of trapped yellowjackets. Ants sometimes enter the trap and remove dead wasps. This problem is solved by suspending the trap + curtain ring from a second curtain ring (or a bent
paper clip will also do) that has been coated with Tacktrap or some other sticky substance. Tacktrap may need to be reapplied after several months. It is also necessary to ensure that the suspending ring or wire is the only ant access to the trap. If leaves or twigs touch the sides of the trap, ants will use these as bridges, thus avoiding the sticky barrier.

The second problem is due to yellowjackets themselves. Some will enter the trap seeking to harvest the dead wasps as food. They cut up the dead wasps into smaller fragments, and some can even successfully exit the trap to carry wasp fragments back to their nest. This both lowers the accuracy of the trap catch and makes counting more difficult. When there are wasp fragments instead of intact wasps in the trap, it is best to count abdomens (or more properly, gasters), as these are the least desirable pieces for foragers to remove.

Additional notes of caution:

1. Sometimes there are live yellowjackets in the trap when you wish to count them. There are two options for dealing with this. The trap can be removed, tape placed over the openings, and held until the wasps die (a few hours in a freezer will do it). Alternatively, the trap can be quickly opened and placed on the ground, allowing the wasps to escape (they should be counted as they fly out). The latter method is more convenient; it is slight more hazardous, but can be done safely with a sensible degree of caution. Live wasps in the trap are much more eager to escape than to aggressively attack.

2. Heptyl butyrate can quickly attract hordes of yellowjackets, so all effort should be made to minimize contamination of any extraneous surfaces. Prepare all tubules in advance, and carry them in a closed container. Styrofoam or polystyrene containers are inappropriate; heptyl butyrate dissolves these plastics. It is best to test the container to make sure it doesn’t dissolve before carrying it into the field and being surprised. Try to minimize exposure of heptyl butyrate where it is not needed in the field (i.e. don’t have open vials in the back of your truck, or inside a vehicle with the windows open). Despite your best efforts, heptyl butyrate will end up on your fingers. Carry paper towels and wipe your fingers constantly to avoid spreading the attractant around on your clothes, body, or the interior of your vehicle.

Spot Treatment of Colonies

When an active nest is located it can be treated directly. Two pesticide treatments have been approved for NPS use: Ficam D dust and Whitmire PT515 WaspFreeze II. Successful treatment of a nest requires that the insecticide be applied into the nest entrance and that good coverage is achieved. Most of the time a single application (1 oz of Ficam D poured into the nest entrance; one can of WaspFreeze sprayed into the entrance) will work. When the entrance is irregular, or upward-sloping, it is very difficult to get the pesticide in to where it will do the most good; in such cases, the cumbersome Ficam duster (a gadget that uses a piston to force dust into the nest entrance) may give better results. It is preferable to treat a colony at night and to cover the entrance with soil after the pesticide has been applied. This is not logistically feasible for most resource managers; daytime treatments are usually satisfactory.

Toxic Baiting

The toxic baiting strategy takes advantage of yellowjacket feeding behavior to deliver pesticide to colonies within the baiting area without locating the nests. Foraging workers collect the toxic bait from bait dispensers and carry it back to the colony, where it is distributed among colony members. During times of colony growth, the greatest nutrient demand is for protein; thus protein-based baits are most useful in attacking populations that are increasing. Most of the protein is fed to immatures, so a successful toxic bait program has an immediate effect by killing foragers that collect it, and a delayed effect by killing larvae that might become foragers several weeks after the baiting episode.

A number of protein-based baits have been evaluated by other researchers, including some that are recommended elsewhere in the literature. The criteria used in Hawaii included local availability, easy storage, attractiveness to *V. pensylvanica* (they come to it), acceptability to *V. pensylvanica* (they carry it away), and acceptability of the bait/toxicant
The best bait is canned Swanson's Premium Chunk White and Dark Chicken in Water, available in 5 ounce cans (larger sizes are only sometimes available). Somewhat less effective substitutes are (canned) Hormel Turkey and Hormel Ham.

The toxicant used in the baiting program is Knoxout 2FM, a microencapsulated flowable formulation of diazinon. This is the only toxicant registered for this use in Hawaii; although there is room for improvement, there are currently no legal alternatives. This situation may change in the future, as at least two mainland research teams are making progress on developing alternative bait/toxicant systems. The main problem with Knoxout is that as it ages, the microcapsules break down, releasing the toxicant. Free diazinon is foul-smelling to humans and makes baits less acceptable to yellowjacket foragers. Experience on Hawaii shows that local supplies of Knoxout may vary in age and quality; it is hard to know how long the container has been sitting in a hot Kona warehouse. In two and a half years we have had one unsatisfactory batch and one good batch.

Yellowjacket foragers searching for food use their senses of smell and sight. To locate dead meat (such as canned chicken), foragers follow an odor plume to the general area, and then rely increasingly on vision to find the specific source. To hunt live arthropods, vision probably plays the primary role throughout the entire process. Yellowjackets can remember the location of a site where they have successfully collected food, and returned to the same site to continue foraging. Thus, foragers from a colony do not become uniformly distributed locally; basically, they either follow an odor plume to a dead meat source, or hunt in sunny well-lit areas. Conditions at ground level in densely forested areas interfere with both senses used in seeking food; dense vegetation may prevent the formation of an odor plume that can be followed to its source, and yellowjacket vision is poor at low light densities. Foragers concentrate their attentions in open areas or the tops of tree canopies; consequently, baiting programs do not work equally well in all these areas. The best results are obtained in fairly open areas, such as the northwest slope of Haleakala or Kipuka Kulalio along upper Mauna Loa Strip Road. Less satisfactory results can be anticipated in shaded and densely forested areas, such as Olaa Tract and much of Kipuka Puaulu. While this is somewhat discouraging from the standpoint of using a baiting program to protect native arthropods in some of the most biologically diverse forested areas, it also suggests that the sub-canopy layers may offer some degree of refuge from yellowjacket predation.

The density and arrangement of bait dispensers in a treatment area depends on several factors, such as the distribution of open sunny spots, numbers of foragers present at the time of baiting, and manpower and logistical considerations. A density of one dispenser per acre (which corresponds to a grid arrangement with dispensers at 64 m [=209 ft] intervals) provides good results. If optimum baiting conditions are met, one dispenser per two acres is probably satisfactory.

Before baits can be put out, the treatment area needs to be surveyed and bait dispensers put out. This is more labor intensive than the actual distribution of baits. In accordance with the previous discussion of yellowjacket foraging habits, the best location for a bait dispenser is in a conspicuous sunny spot. In the placement of dispenser, it is preferable to deviate slightly from a strict grid (or other) arrangement than to put one in a spot where it will not be well attended. Each bait dispenser should have a tubule of heptyl butyrate attractant (similar to that used in the monitoring program), which draws in yellowjackets and increases the amount of bait taken. Do not mix the attractant in together with the bait. Dispensers should be blatantly visible, marked with conspicuous flagging if necessary, so that they can be easily found on baiting day; it is frustrating and counterproductive to waste time playing hide-and-seek with bait dispensers.

We used two different types of dispensers; each had its shortcomings. Future yellowjacket management effort should include the design of a better bait dispenser. Initially we used a dispenser modified from the version designed by Chang (Journal of Economic Entomology 81:228-235, 1988). It consisted of a 4-inch diameter white PVC pipe segment 12 inches long (Figure 1). To hang the dispenser,
nylon cord was passed through 4 holes drilled at each end of the dispenser. A slip knot was tied in the middle of the cord and used to suspend it from a metal shower curtain ring hung from the vegetation. A bent metal paper clip attached to one of the drilled holes held the heptyl butyrate tube + wick; the free end of the paper clip was passed through the tube cap. Bait was apportioned into 8-cm plastic weigh boats. This dispenser proved to be cumbersome to lug around in the field, and it also may confuse the yellowjackets, making it difficult for them to locate the bait. Another problem with this style of dispenser is that the weigh boat containing the bait is unstable; a strong gust of wind can tip it over, causing bait to fall to the ground where non-target organisms may feed on it.

A simpler dispenser was designed and used at HALE during 1990. It consisted of a 3-ounce waxed paper cup, with wires (28-gauge or thicker galvanized steel wire works well) attached at three points along the rim (Figure 2). It was suspended from vegetation by wrapping the free end of the wire around a branch. Bait was apportioned into 1-ounce plastic cups; these fit neatly into the paper cup, did not become dislodged even in windy areas, and left enough room in the paper cup to also put in a heptyl butyrate tube + wick. At the end of the baiting session, the plastic cup could be easily removed and the dispenser left in place. This dispenser was less durable than the PVC model, but was cheaper and easier to build and transport.

Baits should be distributed early in the day on sunny days (good luck predicting weather!). We have delayed baiting until after populations reach a threshold of 5 per trap per day, and recommend this as the action level until better evidence suggests it be raised or lowered. Thus the monitoring program provides information for scheduling the baiting. Baiting is most successful when applied while populations are still rising. This is the time when foragers are most hungry for protein, and also when the population peak can be most effectively truncated. As with any pre-emptive preventative program, it is hard to document effectiveness without a matched untreated area for comparison.

When mixing and distributing baits, precautions against pesticide exposure need to be taken. In the spectrum of pesticide hazards, Knoxout is relatively safe for humans. Recommended gear for mixing is a respirator with cartridges and filters appropriate for pesticides, goggles, and rubber gloves; for distributing the mixed baits, just rubber gloves.

To mix bait, first determine how much bait is to be made. Empty enough cans of chicken into a bowl, and break up the chunks by mixing it thoroughly before adding toxicant. Knoxout is added at the rate of 4.2 ml per five ounce can of chicken (or 5 ml per 6-oz can of other baits). Stir it thoroughly to ensure even distribution of Knoxout in the chicken. Capped plastic 1-oz cups are the easiest way to carry baits into the field. After cups are filled and capped, they can be carried in a large covered plastic tub (Rubbermaid or similar style).

Results have suggested that foragers removing toxic bait die after making several trips, and the numbers of foragers at baits drop off after several hours. Our experience in Hawaii has shown that one ounce of bait per dispenser is usually sufficient. For heavy populations (10 per trap per day), 2 ounces per dispenser may be recommended. The State of Hawaii Knoxout registration information suggests 3 ounces per dispenser, but I think that at a rate of 1 dispenser per acre, this could only be justified by a total inundation of yellowjackets.

Baits left in the field longer than 2 days probably don't affect yellowjackets very much, and increase the risk of exposure of non-target organisms, so after each baiting a followup session should be planned to remove baits.

For any toxicant-based pest control program there is legitimate concern about exposure of non-target organisms. The Knoxout/protein bait in dispensers is a potential site for non-target organism exposure. We made the following observations, adaptations, and compromises in the baiting program with regard to the following groups of organisms.

Invertebrates: Several types of muscoid flies were attracted to both fresh and aged baits; staphylinid beetles were attracted to baits older than several days. Both groups suffered some mortality, which we considered unfortunate but acceptable.
Birds: We saw no evidence that birds were attracted to or feeding on baits at either HAVO or HALE.

Mammals: We did not see mammals at any of the bait stations, but suspected that they would be interested. To reduce the risk of exposure we tried to suspend stations above ground level on vegetation where it would be difficult for rats, mongooses, cats, or dogs to reach it. At one point baits were put out in the vicinity of Volcano House, where the manager was concerned about the safety of the house cats. PVC dispensers were used; slots were sawed at each end of the dispenser, and a 3” x 4-1/2” rectangle of 1/2” hardware cloth was inserted, making it quite tamper-proof.

Humans: Warnings were written onto the outside of bait dispensers. The PVC units had “WARNING - Pesticide - Do Not Disturb” stenciled in red. The small paper cups did not have room for such an elaborate message, so we just marked them “POISON”. For applicators mixing bait, standard personal protection measures were taken (respirator, goggles, gloves). People distributing baits into dispensers wore rubber gloves. Haleakala National Park is in need of a proper facility to mix pesticides and clean soiled equipment; construction of such a facility is recommended.
SOURCES FOR MATERIAL USED IN *Vespula pensylvanica* MANAGEMENT PROGRAM

**MONITORING PROGRAM**

1. Yellowjacket Inn Traps
   - Seabright Enterprises
   - 4026 Harlan St.
   - Emeryville, CA 94608
   - 415-655-3126

2. Heptyl butyrate
   - Aldrich Chemical Co. Inc.
   - 1101 West St. Paul Ave.
   - Milwaukee, WI 53233
   - 1-800-227-2463

3. Dropper/Pipettor
   - Nothing special needed; calibrate ordinary eyedropper to 0.4 ml.

4. 1.5 ml Microfuge tubules
   - Brinkmann Instruments, Inc.
   - Cantiague Road
   - Westbury, NY 11590
   - 1-800-645-3050

5. Metal shower curtain rings
   - Available locally (Woolworth's, etc.)

6. Knoxout 2FM
   - Van Waters & Rogers
   - 3160 Ualena St.
   - Honolulu, HI 96819
   - 836-1361

7. Baits
   - Swanson's Premium White & Dark Chunk Chicken in Water (canned)
   - (Suboptimal substitutions are [canned] Hormel Ham or Hormel Turkey)
   - Available locally (KTA in Hilo)

8. PVC pipe for dispensers
   - 4" gravity drain pipe (thinner walls, cheaper than regular PVC pipe)
   - Island Supply
   - 30 Halekauila
   - Hilo, HI
   - 935-2881

9. Paper Cups
   - S303 = 3-oz., w/o lids ("Reflections" variety best)
   - Hawaii Paper Products, Inc.
   - 167 Makaala St.
   - Hilo, HI
   - 935-9796

10. Plastic Cups
    - US1 = 1-oz size
    - LUS1 = lids for US1
    - Hawaii Paper Products, Inc.

**OTHER**

11. Whitmire PT515 WaspFreeze
    - Schedule of availability in Hawaii not certain.
    - Company representative Jonathan Berger 314-225-5371
    - Bremer Chemical Co. 808-244-3761
    - Van Water & Rogers 808-836-1361
Figure 1. *Vespula pensylvanica* seasonality at Haleakala National Park, 1981-1988
Figure 2. Vespula pensylvanica seasonality at Hawaii Volcanoes National Park, 1984-1989.
Figure 3. Vespula pensylvanica queen capture data.
Figure 4. Yellowjacket prey sampling trap.
Base (A) with attached T-unit (C) is affixed to ground with opening (B) over nest entrance tunnel and top plug (E) inserted into T-unit. Wasp traffic flows through elbow (D). To sample, top plug is removed, and elbow is replaced with trap chamber (F), which has removable proximal plug (G) and removable distal inward facing screen cone (H).
Figure 5. Foraging rates at three Vespula pensylvanica colonies at Puhimau, 24 November 1989.
Figure 6. Foraging success (prey per wasp) at three *Vespula pensylvanica* colonies at Puhimau 24 November 1989.
Figure 7. Effect of Vespula pensylvanica predation on ohia arthropod abundance - weights.

Mean weight of arthropod sample (mg)

Log ((Mean Wasps/Trap/Day) + 1)

1989 1990

Kokoolau △ Hilina Pali ○
Puhimau ⋄ Lua Manu □

SITES
Figure 8. Effect of *Vespula pensylvanica* predation on ohia arthropod abundance - numbers.
Figure 9. Yellowjacket abatement: HAVO, 1988

Untreated: Kipuka Ki

Treated: Kipuka Puaulu

Baiting

Colony Treatments
Figure 10. Yellowjacket abatement: HAVO, 1988

Untreated: Kipuka Maunaiu

Treated: Kipuka Kulalio

Baiting

Colony Treatments
Figure 11. Yellowjacket abatement: HALE, 1988

Untreated: HALE2

Treated: HALE1

Baiting
Figure 12. Yellowjacket abatement: HAVO, 1989

Untreated: Rt 11/Ka' u

Treated: Footprints

Baiting
Figure 13. Yellowjacket abatement: HALE, 1989

Untreated: HALE2

Treated: HALE1

Baiting

FORAGERS PER TRAP PER DAY
Figure 14. Yellowjacket abatement: HAVO, 1990

Untreated: Kipuka Puaulu

Treated: Namakani Paio

Baiting
Figure 15. Yellowjacket abatement: HALE, 1990

Untreated: HALE Upslope

Treated: HALE1 + HALE2

Baiting
Figure 16. Effect of distance from toxic baits: HALE, 1990.

Near traps

Distant traps

Baiting
Figure 1. Toxic Bait Dispenser: PVC pipe, after Chang, 1988
Figure 2. Toxic Bait Dispenser - 3-oz. paper cup