Yellowjacket (*Vespula pensylvanica*) Predation at Hawaii Volcanoes and Haleakala National Parks: Identity of Prey Items.

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ABSTRACT. Predation by *Vespula pensylvanica* (Saussure) was studied at Haleakala and Hawaii Volcanoes National Parks in Hawaii. Prey items were sampled by removing them from foragers returning to nests. *V. pensylvanica* preyed on a diverse taxonomic assortment of arthropods; 522 prey items belonging to 9 orders were identified. Of 170 prey items determined to genus level, approximately two thirds were of endemic taxa, indicating a substantial threat of *V. pensylvanica* to Hawaiian biodiversity. The design of a prey sampling trap is given.

Although social insects are lacking in the native fauna of the Hawaiian Islands (Perkins & Forel 1899), there have been numerous invasions in historical times, with many social species currently well established (Williams 1927; Howarth 1985; Medeiros et al. 1986; Chang 1988; Reimer et al. 1990). The western yellowjacket, *Vespula pensylvanica* (Saussure), was first recorded from Kauai in 1919, but did not reach the islands of Maui and Hawaii until 1978 (Nakahara 1980). The subsequent population explosion of this predaceous wasp on the easternmost islands (Nakahara & Lai 1981; Gambino et al. 1990) raised concern over its impact on Hawaiian arthropods, particularly in relatively undisturbed habitats where native species are well represented (Howarth 1985; Carson 1986; Gambino et al. 1987).

A first step in evaluating the impact of *V. pensylvanica* predation is to identify the arthropods upon which it 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 (Kleinhout 1958; Broekhuizen & Hordijk 1968; Archer 1977; Gambino 1986), 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 to provide a qualitative assessment of the effects of wasp predation in Hawaiian natural areas.

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MATERIALS AND METHODS

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 obstructing the nest entrance, returning workers could be induced to hesitate before entering, increasing the opportunity for inspection and capture. At very active 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.

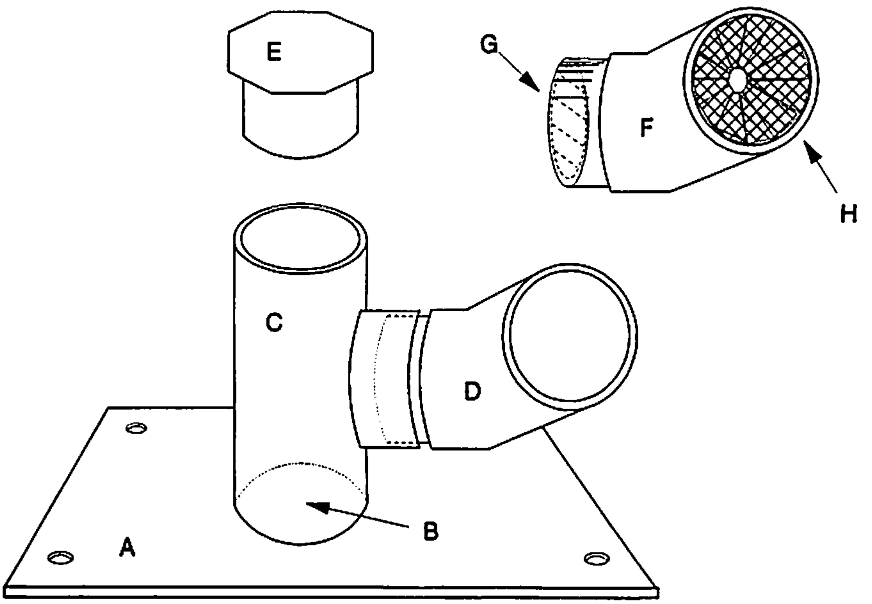

FIGURE 1. Yellowjacket prey sampling trap. Base (A) with attached T-unit (C) is affixed to ground with opening (B) over nest entrance tunnel and top plug (E) inserted into T-unit. Wasp traffic flows through elbow (D). To sample, top plug is removed, and elbow is replaced with trap chamber (F), which has removable proximal plug (G) and removable distal inward facing screen cone (H).

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 elbow (Figure 1). 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 unobstructed pipes to exit and return. Wasps sometimes constructed new tunnels around the trap base to bypass the modified entrance; this behavior was discouraged by covering the holes with soil. Once a regular traffic pattern through the trap was established, 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, allowing wasps exiting the nest to leave. Sampling sessions 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 CO_2 gas and dumped into a sorting tray. Prey items were collected with forceps into a vial; wasps recovering from anaesthesia were placed 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 included 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. Individual 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 of taxa 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. *V. 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 analysis of yellowjacket diets, HAVO nests were grouped into the following geographic units: Kipuka Puaulu, Ola'a Tract + Ola'a Forest Reserve, and Puhimau.

RESULTS AND DISCUSSION

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 1 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.

TABLE 1. Summary of prey taken by *V. pensylvanica* in Hawaii.

(Values shown represent percentages of N items)

		Taxa[a]								
Site[b]	N	ARA	ORT	BLA	HEM	NEU	COL	DIP	LEP	HYM
KP	120	25.0	18.3	6.7	4.2	1.7	3.3	26.7	12.5	1.7
OL	84	31.0	21.4	0.0	22.6	2.4	0.0	6.0	16.7	0.0
PU	57	33.3	22.8	3.8	17.5	0.0	3.5	0.0	19.3	0.0
OT	30	36.7	0.0	10.0	6.7	6.7	3.3	6.7	30.0	0.0
HK	231	23.4	0.0	0.0	21.2	0.0	14.7	8.2	22.1	10.4
	522	26.8	10.2	2.5	16.3	1.1	7.9	11.1	19.2	5.0

[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 = Ola'a Tract + Ola'a Forest Reserve (HAVO); PU = Puhimau (HAVO); OT = Other (HAVO); HK = Haleakala (HALE).

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 (50.0%) 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.

TABLE 2. Arthropods identified to genus among *V. pensylvanica* prey items.

(Asterisks indicate endemic taxa.)

Order	Family	Genus/Species	N	Sites[a]
Araneae	Lycosidae	*Lycosa hawaiiensis** Simon	4	HK, OT
	Salticidae	*Sandalodes* spp.*	2	PU, OT
	Tetragnathidae	*Tetragnatha* spp.*	18	KP, PU, OT
	Theridiidae	*Theridion* sp.	1	OL
	Thomisidae	*Misumenops vitellinus** (Simon)	4	HK
		Misumenops sp.*	3	HK
Blattodea	Blattidae	*Allacta similis* (Saussure)	7	KP, OT
Orthoptera	Gryllidae	*Anaxipha* sp.*	22	KP, OL
		Leptogryllus sp.*	6	KP
Hemiptera	Alydidae	*Ithamar hawaiiensis** (Kirkaldy)	4	HK
	Flatidae	*Siphanta acuta* (Walker)	2	OT
	Nabidae	*Nabis* spp.*	26	PU, HK
Lepidoptera	Sphingidae	*Hyles wilsoni** (Rothschild)	1	KP
	Geometridae	*Eupithecia* spp.*	16	PU, HK
Coleoptera	Cerambycidae	*Plagithmysis funebris** Sharp	1	HK
		Plagithmysis sp.*	3	HK
	Coccinellidae	*Olla abdominalis* (Say)	1	HK
		Hippodamia convergens (Guerin-Meneville)	1	HK
	Curculionidae	*Pantomorus cervinus* (Boheman)	26	HK, KP
Hymenoptera	Colletidae	*Nesoprosopis* sp.*	2	HK
	Apidae	*Apis mellifera* L.	4	KP, HK
	Vespidae	*Vespula pensylvanica* (Saussure)	13	HK
Diptera	Tachinidae	*Gonia longipulvilli* Tothill	2	HK
		Trichopoda sp.	1	KP

[a]Key to Sites: KP = Kipuka Puaulu (HAVO); OL = Ola'a Tract + Ola'a Forest Reserve (HAVO); PU = Puhimau (HAVO); OT = Other (HAVO); HK = Haleakala (HALE).

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 1.

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. There is a size threshold below which a *V. pensylvanica* forager will not collect potential prey arthropods (Duncan 1939). Considering how *V. pensylvanica* workers process captured prey, it would seem that few of the boluses carried to colonies could have been derived from arthropods less than 3 mm in length. However, the possibility that small prey are harvested differently (i.e. by ingesting liquids from chewed up bodies that are then discarded, or by combining several prey items into a single bolus [Duncan 1939]) cannot be ruled out; predation in this fashion would be undetected by the present methods, making it impossible to determine with accuracy the nature of the prey size threshold, or the impact of *V. pensylvanica* predation on smaller arthropods.

A total of 170 prey items could be determined to genus or species level (Table 2). Of these, 112 (65.9%) were of endemic (to Hawaii) taxa, and 58 (34.1%) were of alien or non-endemic native taxa. 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.

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. Hawaiian arthropods have evolved in the absence of predation pressure from social Hymenoptera, and may thus lack antipredator mechanisms selected for elsewhere (Gagné & Christensen 1985). *V. 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.

V. pensylvanica is one of a number of non-native invertebrate species whose invasion has been to the overall detriment of native Hawaiian ecosystems (Howarth 1985). Although quantitative effects of *V. pensylvanica* predation have not been demonstrated for populations of any Hawaiian arthropods, including those identified in the present study, it is unlikely that the impact is trivial. A single overwintered colony at Kipuka Puaulu contained approximately 600,000 cells (Gambino 1991), and no doubt harvested millions of arthropods during its two year existence. The direct impact of yellowjackets on humans and their economic activities is usually the prime consideration in clarifying their pest status and designing control strategies (MacDonald et al. 1976). However, recognition of the value of conservation of biotic resources suggests that attention also be paid to the status of *Vespula* species as threats to biodiversity in Hawaii and elsewhere (Moller & Tilley 1989).

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