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Reproductive plasticity of *Vespula pensylvanica* (Hymenoptera: Vespidae) on Maui and Hawaii Islands, U.S.A.

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Abstract Reproductive activities of *Vespula pensylvanica* (Saussure) were studied on the recently invaded (1978) islands of Maui and Hawaii. Aspects of reproductive behaviour were inferred from the use of attractant traps to monitor foraging worker and queen populations, observations of architecture and traffic rates of nests, and dissections of queens occupying active nests or captured while foraging. Most wasp colonies adhered to the basic annual cycle dominant throughout *V. pensylvanica*'s native temperate range. Atypical overwintering colonies, indicated by at least one episode of large cell construction and a subsequent reversion to small cell construction, occurred on both islands, but were detected in only some years. Overwintered colonies had peak traffic rates in excess of 300 worker sorties per minute, but some large annual colonies also had traffic rates greater than 300 per minute. Flying queens were most abundant during the spring (March–June), but were captured in every month except January. Among autumn queens taken from nests on Hawaii, oviposition-ready queens were more common than hibernation-ready queens, suggesting that winter hibernation is not obligatory. Polygyny, achieved by adding queens to an established colony, is a likely prerequisite for successful colony overwintering. Two gyne-addition mechanisms are proposed for this: retention of daughter queens, and joining by outside queens. Expression of *V. pensylvanica* reproductive plasticity is correlated with relaxation of climate-related constraints. Relaxation of genetic constraints is also hypothesised to contribute to the emergence of polygyny in Hawaiian Island populations.

Keywords *Vespula pensylvanica*; wasp; reproductive plasticity; overwintering colonies; polygyny

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INTRODUCTION

Wasps of the genus *Vespula* Thomson are essentially north temperate zone organisms. This may be deduced from the distribution of native ranges of the various species (Miller 1961; Akre & Davis 1978; Akre et al. 1980). Climate is a major constraining factor influencing *Vespula* reproductive behaviour; cold weather, especially prolonged periods of sub-freezing temperature, affects colonies directly by interfering with the development and survival of insects, and indirectly by limiting the availability of food. For the *V. vulgaris* species group, climate-driven colony level selection has favored an annual cycle in which reproductive output coincides with the end of favorable summer conditions, and fertilised queens disperse to enter dormancy during winter. Selection favors individual queens adapted to endure winter, i.e., with storage of food reserves in fat body tissues, suspension of ovarian development until spring, and appropriate dispersal and hibernation behaviour.

The typical *Vespula* colony is monogynous, founded by a lone queen (Spradbery 1973; Akre et al. 1980; Edwards 1980). She and her daughter workers resist accepting outside queens into the colony; intraspecific nest usurpation attempts (records summarised in Archer 1985) lead to monogyny regardless of which queen prevails (unless both die). Sometimes, however, the prohibition against polygyny is occasionally relaxed in annual colonies (Akre & Reed 1981). Although weather may impose limits on colony phenology, climate alone would not seem to influence the number of queens in a colony, and an explanation for the prevalence of monogyny in *Vespula* must be sought elsewhere. Kin selection theory (Hamilton 1964; Hölldobler & Wilson 1977; Noonan 1981; Nonacs 1988) posits genetic constraints: generally, monogyny should prevail unless the benefits associated with polygyny can compensate for the costs of sharing reproduction. Among unrelated females, the costs (diminished fitness) are often too high for polygyny to be favored.

Some *Vespula* species have shown considerable reproductive plasticity, including colony overwintering, along the mild-wintered margins of their native ranges, e.g., Florida (Tissot & Robinson 1954; Akre et al. 1980; Ross & Matthews 1982; Ross & Visscher 1983), the Mediterranean (Vuillaume et al. 1969), and coastal California (Duncan 1939; Gambino 1986). Atypical reproductive behaviour also occurs in regions where *Vespula* is a recent invader, such as New Zealand (Thomas 1960; Plunkett et al. 1989), Australia (Spradbery 1973), Hawaii (Nakahara 1980; Nakahara & Lai 1981; Gambino et al. 1990), and Chile (Jeanne 1980).

This paper describes some of the variability in reproductive behaviour of *V. pensylvanica* (Saussure), found on two recently invaded Hawaiian Islands, Maui and Hawaii. Before the late 1970's, *V. pensylvanica* was restricted to the westernmost Hawaiian Islands of Kauai (first record, 1919) and Oahu (first record, 1935). Invasion of the four easternmost islands was nearly simultaneous, with clustered initial records from Hawaii (1978), Maui (1978), Molokai (1979), and Lanai (1979). Persistent populations on Maui and Hawaii suggest that *V. pensylvanica* can be considered established permanently on those two islands.

Previous studies of the biology of *V. pensylvanica* in its native range (Duncan 1939; MacDonald et al. 1974; Akre et al. 1976; Roush & Akre 1978; Long et al. 1979; Akre et al. 1980; Akre & MacDonald 1986; unpublished data) form the basis for comparison between Hawaiian populations and the more typical North American pattern. Although male production and behaviour are components of *V. pensylvanica* reproductive biology, this study focuses on the adaptations and activities of queens.

MATERIALS AND METHODS

Population monitoring

V. pensylvanica forager populations were monitored at Haleakala National Park (HALE) on Maui and Hawaii Volcanoes National Park (HAVO) on Hawaii, using traps baited with the synthetic attractant, heptyl butyrate (Davis et al. 1969). Queens and workers are both attracted to heptyl butyrate; separate capture records were kept for each caste. Generally, new queens seeking hibernation sites are not attracted to heptyl butyrate (MacDonald et al. 1973), and queens caught in traps were assumed to be either seeking nest sites, or foraging during the initiation or pre-emergence phases of the colony cycle.

The main study site at HALE consisted of approximately 1000 hectares on the north-west slope of Haleakala volcano, ranging from 2050–3050 m elevation (Gambino et al. 1990). At HAVO, a much larger and more diverse area was sampled, ranging from 900–2165 m elevation. Several monitoring programmes were conducted from 1981–1989, with varying duration and sponsoring agency (Table 1). Two types of traps were used: a wet trap containing vegetable oil, water, and wick of attractant (Gambino et al. 1990); and a dry trap (Yellowjacket Inn) containing just the attractant wick. Within each monitoring regime the procedure was consistent, and quantitative comparisons of population levels can be made. However, comparisons of population levels between the two systems are not valid.

To supplement data on trap captures of queens, flying queens not associated with any known nest were captured by net. Whereas the trap monitoring programme consisted of a regular standardised sampling regime, aerial queens were captured opportunistically throughout 1989 during 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. They were designated "typical spring queens" (regardless of when they were caught) 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. This is because in queens coming out of hibernation, ovaries and eggs normally develop gradually over several months during the colony initiation and pre-emergence phases.

Colony analysis. Observations of nests were made from 1986–1989. A total of 107 colonies were visited; all colonies on Maui ($n = 33$) were in the HALE study area, on Hawaii ($n = 74$) sites visited included HAVO, Olaa State Forest Reserve, and the villages of Volcano, Glenwood, and Mountain View. Traffic rates of colonies (sorties per minute) were calculated based on counts of workers leaving in 5 minutes during fair weather. Multiple counts made on the same day were pooled to give a mean daily traffic rate; counts greater than 300 per minute were expressed as >300. For some nests, counts were taken on several days; in the present study only the highest recorded daily traffic rate is included as data. Because of the varying dates on which traffic rates were recorded (30 June–12 January at HAVO, 20 August–7 October at HALE), these figures indicate the range of values achieved by *V. pensylvanica* colonies in Hawaii, but cannot be used to make precise comparisons of colony activity. Traffic rates were also measured at 12 annual colonies in California (15 July and 24 August 1986).

A subset of 37 nests was excavated for laboratory analysis. The information available in nests varied according to their condition. We collected as much of the following data as possible: number of combs, cell sizes, and numbers and genders of immatures. In some instances 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, gastral 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; and "mothers" if they were the only oviposition-ready female in the colony or were clearly the most worn (wing wear and gastral 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.

Nests types were classified according to the following criteria: typical immature (TI) colonies were colonies collected before 1 October, before initiation of large cell construction; queen cell (QC) colonies were annual colonies that underwent a single episode of queen rearing, deduced from the presence of large cells containing meconia in the nest; 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.

Table 1 Yellowjacket population monitoring programmes on Maui and Hawaii.

Location	Elevation (m)	Dates	Agency	Type of Trap	No. of Traps
MAUI					
Haleakala Nat. Park	2050–3050	Jun 1980 Dec 1988	NPS Resources Management Division	Wet	10
HAWAII					
Kipuka Puaulu	1230	May 1984 – Dec 1986	Hawaii Dept of Health	Wet	1
Kipuka Puaulu	1230	Jun 1988 – Dec 1989	NPS Research Division	Dry	5
Kipuka Kulalio	2165	May 1984 – Dec 1986	Hawaii Dept of Health	Wet	1
Kipuka Kulalio	1890	May 1988 – Dec 1989	NPS Research Division	Dry	5
Kipuka Nene	900	May 1984 – Dec 1986	Hawaii Dept of Health	Wet	1
Kipuka Nene	900	Sep 1989– Dec 1989	NPS Research Division	Dry	5
Kipuka Ki	1320	May 1984 – Dec 1986	Hawaii Dept of Health	Wet	1
Kipuka Ki	1320	Jun 1988 – Nov 1989	NPS Research Division	Dry	5
Kau Desert	935	Oct 1988 – Dec 1989	NPS Research Division	Dry	5
Kilauea	1200	Jan1989 – Dec 1989	NPS Research Division	Dry	10

RESULTS

Maui

Population monitoring. The basic seasonal character of wasp colonies and population cycles was retained at HALE; numbers of foraging workers were highest from August to October, and low during late winter and spring (Fig. 1). 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.

Data for trap captures of 228 queens from 1982–88 (the years for which data are available for the full calendar year) are presented in Fig. 2A. The peak of queen activity was in June, but in some years queens were captured as early as February and as late as October.

Colony analysis. Traffic rates were measured at 23 HALE colonies (Fig. 3A). Rates at all five colonies that were measured in 1986 were >300; rates of 1987 and 1988 colonies were more modest, resembling those of typical annual colonies in California (Fig. 3C).

A total of 17 colonies were excavated (Table 2). Nests found in 1987 ($n = 3$) and 1988 ($n = 11$) resembled typical pre-reproductive annual nests generated by mainland *V. pensylvanica* populations, and are considered together here. They were basically spherical in shape, with numbers of small cells ($x =$

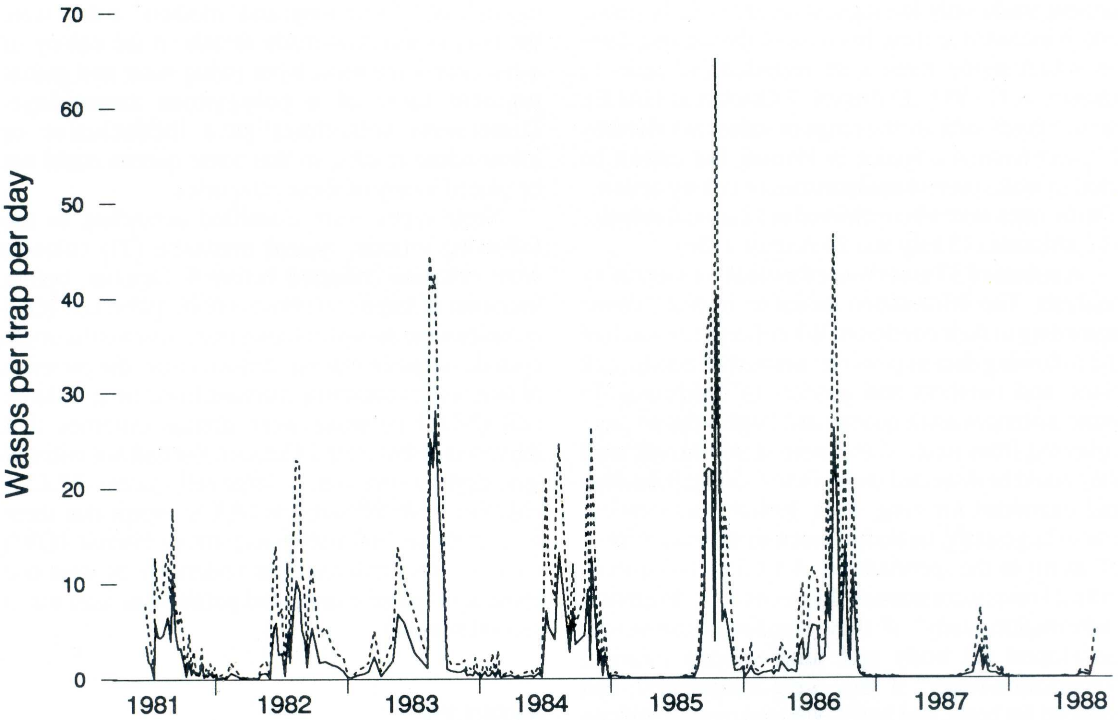

Fig. 1 *Vespula pensylvanica* population cycles at Haleakala National Park, Maui. Solid line indicates mean value for 10 traps (elevation 2050–3050 m); dotted line indicates upper 95% confidence limit.

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 (TI's, $n = 5$), but atypical for colonies that remained active into the autumn (NLC's, $n = 7$; NLCQ's, $n = 2$).

In four colonies no queen was recovered; three of these showed symptoms of queen loss (irregular pattern of brood in combs, high percentage of male brood). A single mother queen was recovered from eight colonies, including five 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).

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 ($n = 3$; $\bar{x} = 65737$; range = 58289–80508), and large (queen) cells were also constructed. In nest HAL8603 there were two distinct episodes of large cell construction, separated by three 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.

Nest HAL8601 was retrieved in excellent condition, and its architecture received more detailed study. Before 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

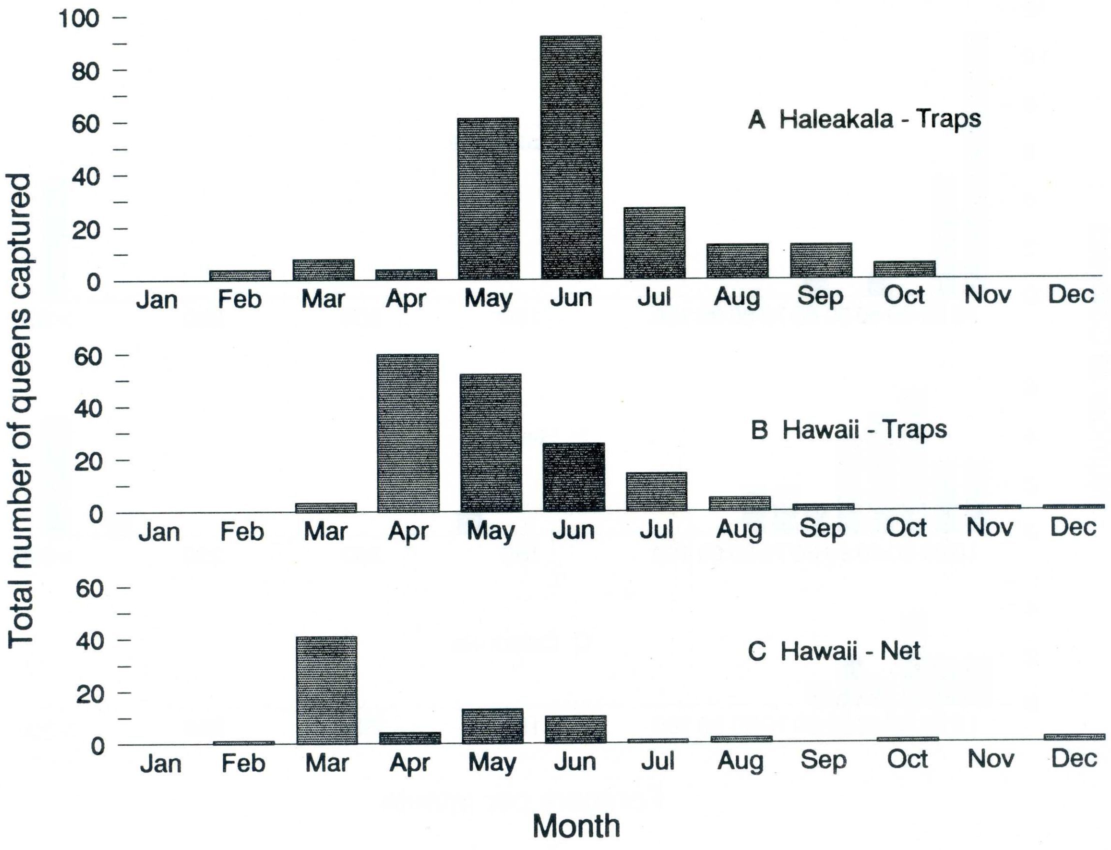

Fig. 2 Captures of *Vespula pensylvanica* queens on Maui and Hawaii. Bars indicate total numbers of queens captured (dates inclusive): A. January 1982–December 1988; B. January 1985–December 1986 and January–December 1989; C. January–December 1989.

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.

HAWAII

Population monitoring. As on Maui, worker populations were generally highest during the late summer and autumn, and colonies overwintered during some years, with evidence of this phenomenon in 1983–84 (Kipuka Kulalio, K. Ki, K. Puaulu), 1985–86 (K. Kulalio), and 1988–89 (K. Puaulu, Kau Desert) (Fig. 4). Colony HVO8816, discovered in Kipuka Kulalio in August 1988, was also classified as an overwinterer based on its architecture and the high populations of workers and males observed in its vicinity as early as mid April 1988.

Populations on Hawaii were not tightly synchronised, 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 programme: K. Kulalio 1986, K. Nene 1985, 1986, K. Ki 1984, 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, Kau Desert 1989).

Data for trap captures of 160 queens from years in which the entire calendar year was sampled (1985,

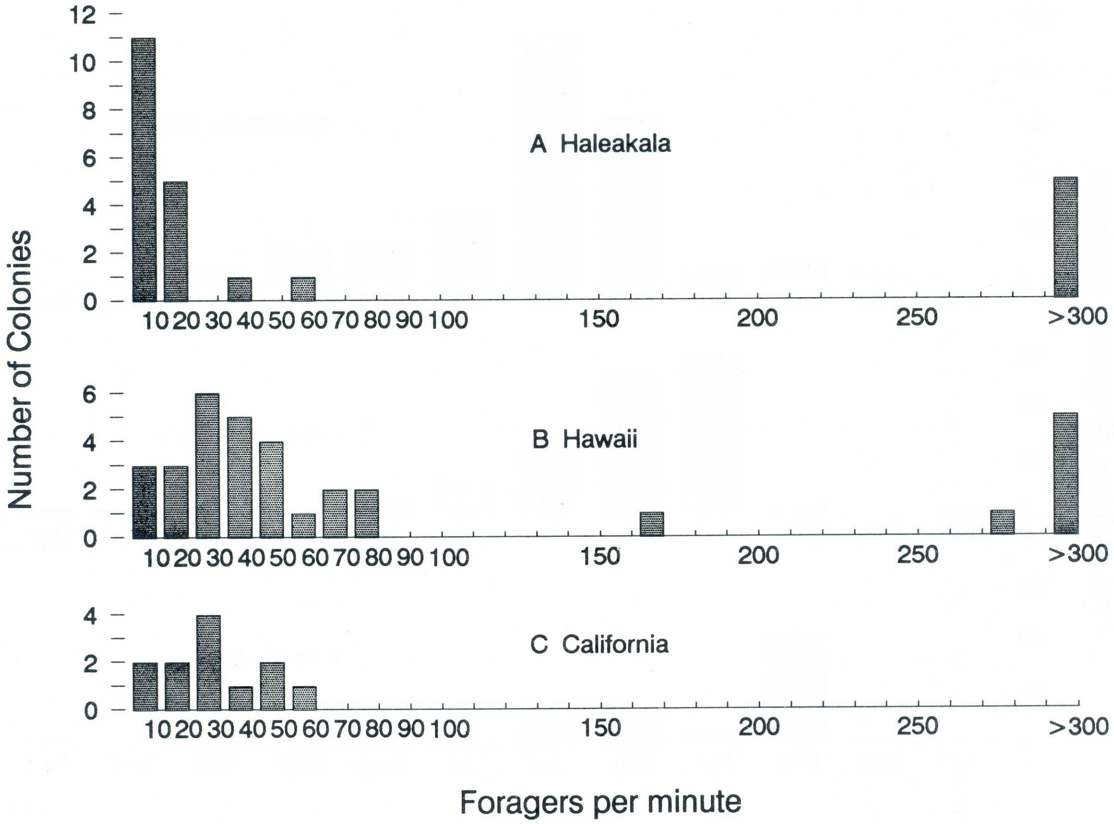

Fig. 3 Traffic rates at *Vespula pensylvanica* colonies.

1986, 1989) are presented in Fig. 2B. 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 (Fig. 2C), with a peak in March. Twenty-four net-captured queens were dissected, and all but two were typical spring queens; the exceptions were uninseminated, but still lacked the fat body deposits indicative of queens seeking hibernation sites.

Colony analysis. Traffic rates were extremely variable, ranging from 5.6 to >300 sorties per minute (Fig. 3B). Although both known overwintered colonies had rates consistently in excess of 300, at least three colonies known to be annuals also reached this level. Thus, extremely high traffic rate is not sufficient evidence to determine if a particular colony has overwintered.

Of 20 excavated nests, 11 had structures that might be considered typical (2 TI's, 9 QC's) (Table 3). 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.

Of the seven QC colonies in which queens were examined (at least 10 per colony), hibernation-ready queens were detected at only four, whereas oviposition-ready queens were present in all seven. This contrasts sharply with the typical situation, where autumn queen production yields hibernation-ready queens exclusively. It must be noted that the evidence that post-callow queens had been reared in the QC nest in which they were found is circumstantial; the possibility that queens had joined the nest from outside cannot be ruled out. However, the rarity of hibernation-ready queens (only 15 of 79 examined) in QC colonies suggests that at least some oviposition-ready queens had originated in the nest in which they were found.

Multiple oviposition-ready queens were found in all three NLCQ colonies. Polygyny in an NLCQ colony is evidence that queens have joined from outside. 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. Hopefully this subjective size evaluation can be more precisely characterised in the future using morphometric techniques.

Two overwintered nests were excavated. HVO 8816 was poisoned with insecticide on 1 September 1988 and dug up about 2 months later. Its irregular architecture was caused by 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.

Queens were first observed outside the nest on 26 January 1990. Their behaviour 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 min 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 behaviour (Ono et al. 1985), although no actual copulations were observed.

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. Many combs, from the second topmost to the bottom, 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.

There were fewer than 150 live workers present when the nest was excavated, 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.

Table 2 Characteristics of *Vespula pensylvanica* colonies from Maui.

Nest	Date of excavation	Type*	No. of cells small	large	Queens present** Mother	Ovip	Hiber
HAL8601	21 Sep 86	OW	58414	2107			
HAL8603	30 May 87	OW	58289	936			
HAL8606	01 Jun 87	OW	80508	1503			
HAL8701	30 Aug 87	TI	4150	0	-		
HAL8706	31 Aug 87	TI	1792	0	+		
HAL8708	31 Aug 87	TI	2442	0	-		
HAL8801	10 Sep 88	TI	558	0	+		
HAL8802	10 Sep 88	TI	832	0	+		
HAL8812	05 Oct 88	NLC	2423	0	+		
HAL8813	05 Oct 88	NLC	4479	0	+		
HAL8804	06 Oct 88	NLCQ	4452	0	+	+	-
HAL8810	06 Oct 88	NLC	4699	0	-		
HAL8811	06 Oct 88	NLC	7644	0	+		
HAL8807	14 Nov 88	NLC	2243	0	+		
HAL8808	14 Nov 88	NLC	2776	0	+		
HAL8814	14 Nov 88	NLC	2382	0	-		
HAL8816	14 Nov 88	NLCQ	8086	0	+	+	-

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

** Queen types (see text for full descriptions):
Ovip - Oviposition-ready **Hiber** - Hibernation-ready

DISCUSSION

Atypical *V. pensylvanica* behaviour on Maui and Hawaii correlates with the relaxation of constraints that normally operate throughout its native range. The Hawaiian climate differs substantially from most portions of western North America (Blumenstock & Price 1972); mean temperature differences between the warmest and coldest months are relatively slight. Except for the highest elevations, winter temperatures on Maui and Hawaii are sufficiently mild to preclude major direct negative effects on wasp adults and immatures, and prey arthropods are available year round. As a consequence of latitude, photoperiod varies relatively little compared to temperate areas.

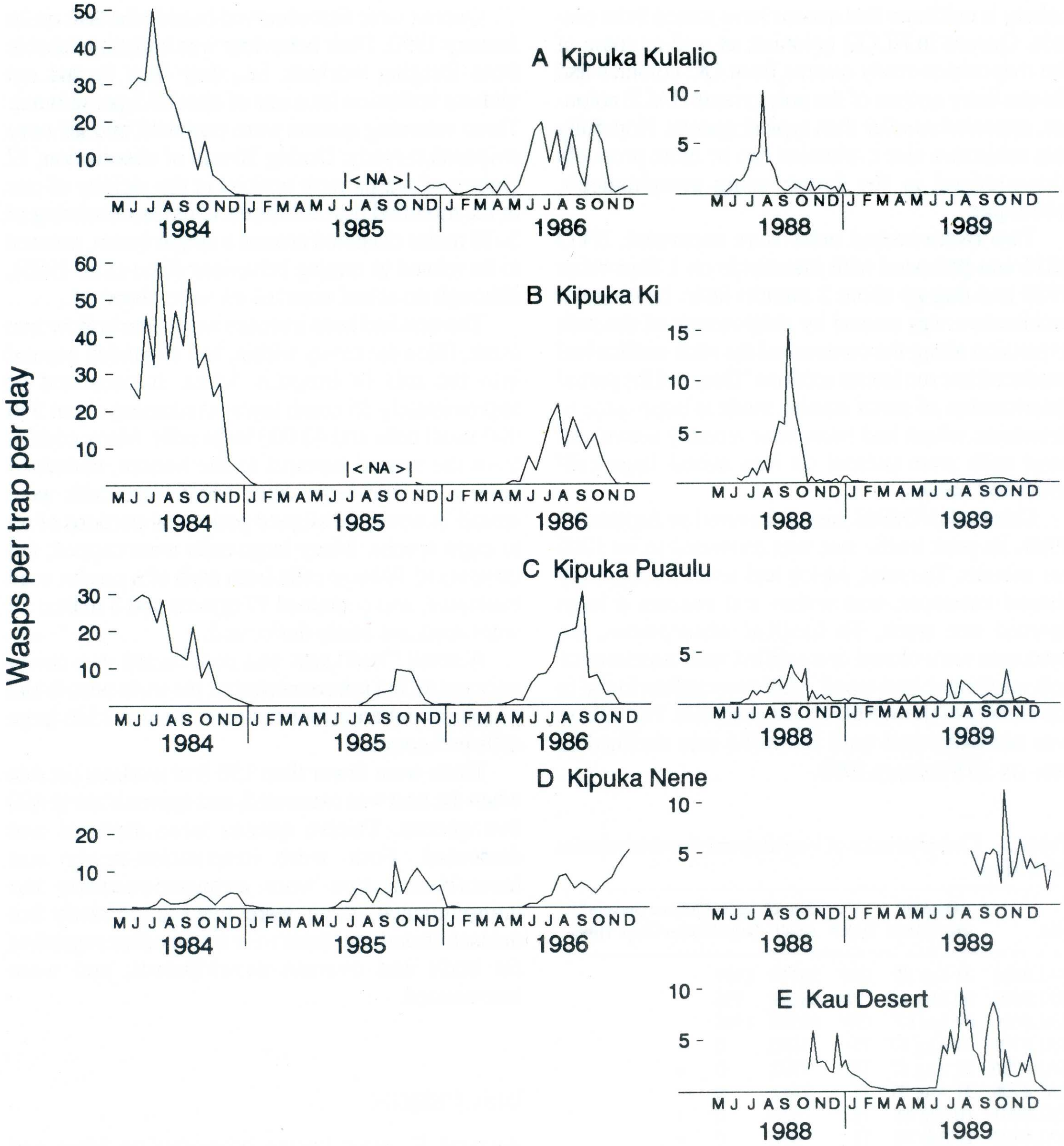

Fig. 4 *Vespula pensylvanica* population cycles at Hawaii Volcanoes National Park, Hawaii. From 1984–86 a single wet trap was used at each site. From 1988–89, five dry traps were used at each site, with the mean value indicated.

Adjustments of queen physiology and behaviour form the basis of *V. pensylvanica*'s reproductive plasticity. To the extent that hibernation is not required of *V. pensylvanica* queens, behavioural adaptations for it are de-emphasised. 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. Although hibernation-ready queens were not found in some QC colonies, they may have dispersed or transformed before the nests were excavated. Also unknown is the degree of retention of typical spring queen behaviours, such as nest construction, food foraging, and brood care. Spradbery (1973) reported that autumn queens of *V.*

germanica (F.) and *V. vulgaris* (L.) fed on food they had collected foraging, but these were assumed to be pre-hibernation queens. The presence of oviposition-ready queens in the foraging traffic of colony HVO8903 suggests that they participated in some extranidal activities.

Polygyny arising from the retention of daughter queens in the natal nest is widely accepted (Duncan 1939; Thomas 1960; Spradbery 1973; Edwards 1980; Ross & Visscher 1983; Akre & MacDonald 1986) despite the lack of unambiguous empirical evidence. Such kin associations, analogous to polygynous assemblages formed in the Polistinae (West-Eberhard 1969, 1981; Strassmann 1979; Noonan 1981), would provide a mechanism to circumvent genetic constraints against polygyny. This is because the classical Darwinian fitness of individual queens would be bolstered by the inclusive fitness contributions of other gynes (to whom they are closely related) sharing the nest.

In contrast, polygyny in NLCQ nests elucidates an alternate gyne-addition mechanism: nest-joining. 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 (Fig. 2). Although polygyny by the addition of outside queens would seem inconsistent with conventional fitness theory, the genetic structure of island populations of *V. pensylvanica* may effect a relaxation of normal constraints. The genetic bottleneck resulting from a small number of founders would create a population whose average degree of relatedness is higher than that among the presumed North American source population. Invasion-associated evolution of polygyny has also been suggested for North American populations of *Solenopsis invicta* Buren, which is typically monogynous in its native range (Glancey & Lofgren 1988; Pamilo 1989).

Table 3 Characteristics of *Vespula pensylvanica* colonies from Hawaii.

Nest	Date of excavation	Type*	No. of cells		Queens**		
			small	large	Mother	Ovip	Hiber
HVO8810	17 Aug 88	TI	15266	0			
HVO8819	18 Aug 88	TI	9959	0			
HVO8815	15 Oct 88	NCL	5418	0			
HVO8816	26 Oct 88	OW	43221	2341			
HVO8828	27 Oct 88	QC	15769	73	-		
HVO8823	10 Nov 88	QC	8227	356	-		
HVO8826	10 Nov 88	NCL	31246	0			
OLA8801	16 Dec 88	QC	22720	806	-	+	+
HVO8817	18 Jan 89	QC	6282	829	-	+	+
HVO8814	19 Jan 89	QC	22967	5060	-	+	+
HVO8822	19 Jan 89	QC	10155	1821	-	+	-
HVO8831	24 Jan 89	QC	4344	668	-	+	-
HVO8902	16 Oct 89	NCLQ	835	0	-	+	+
KAU8901	25 Oct 89	NCL	4309	0	+		
HVO8908	20 Nov 89	NCLQ	4896	0	-	+	-
HVO8907	25 Nov 89	QC	14857	645	-	+	+
HVO8906	11 Jan 90	NCLQ	27821	0	-	+	-
HVO8904	17 Jan 90	NCL	26263	0			
HVO9001	26 Jan 90	QC	14999	5271	-	+	-
HVO8903	10 Feb 90	OW	546260	47229	-	+	+

*Nest types: **TI** Typical immature; **QC** Queen cell; **NLC** No large cells; **NLCQ** No large cells queens; **OW** Overwintered.
** Queen Types (see text for full descriptions)
Ovip Oviposition-ready; **Hiber** Hibernation-ready.

Colony cycles in Hawaiian *V. pensylvanica* populations range from the predictable annual type to erratic but massively productive 2-year nests, with many intermediate variants. Overwintering colonies occur irregularly, with frequency varying among years and localities. Though making up 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. Polygyny through 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. By these criteria, late developing annual colonies that fail to construct large cells, or to revert to rearing workers, are excluded, regardless of whether their decline phase extends into the following spring. No 3-year colonies have been detected.

Pending a more complete understanding of vespine biology, several observations remain difficult to explain. For instance, some nests taken in winter are occupied by numerous oviposition-ready queens. Does such a colony represent incipient overwintering, an alternate form of pre-dispersal dormancy, or an aberration leading to a reproductive dead end? At the other extreme, some *Vespula* colonies construct abnormally high numbers of small cells, switching to large cell construction either very late in the cycle or not at all, suggesting a partial lack or ambiguity of environmental cues. Might this not provide additional temptation to foster the queen-parasitic tendencies of this species, or perhaps adaptive benefit as a source of males?

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REFERENCES

Akre, R. D.; Davis, H. G. 1978: Biology and pest status of venomous wasps. *Annual review of entomology 23*: 215–238.

Akre, R. D.; Garnett, W. B.; MacDonald, J. F.; Greene, A.; Landolt, P. 1976: Behavior and colony development of *Vespula pensylvanica* and *V. atropilosa* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society 49(1)*: 63–84.

Akre, R. D.; Greene, A.; MacDonald, J. F.; Landolt, P. J.; Davis, H. G. 1980: Yellowjackets of America North of Mexico. *USDA agriculture handbook No. 552*. 102 p.

Akre, R. D.; MacDonald, J. F. 1986: Biology, economic importance and control of yellowjackets. *In*: Vinson, S. B. *ed*., Economic impact and control of social insects. New York, Praeger. pp. 353–412.

Akre, R. D.; Reed, H. C. 1981: A polygynous colony of *Vespula pensylvanica* (Saussure) (Hymenoptera: Vespidae). *Entomological news 92(1)*: 27–31.

Archer, M. E. 1985: Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. *Journal of animal ecology 54:* 473–485.

Blumenstock, D. I.; Price, S. 1972: Climates of the states: Hawaii. *In*: Kay, E. A. *ed*., A natural history of the Hawaiian Islands. Honolulu, University of Hawaii Press. pp. 155–203.

Davis, H. G.; Eddy, G. W.; McGovern, T. P.; Beroza, M. 1969: Heptyl butyrate, a new synthetic attractant for yellow jackets. *Journal of economic entomology 62*: 1245.

Duncan, C. D. 1939: A contribution to the biology of North American vespine wasps. *Stanford University publications in biological sciences 8(1)*: 1–272.

Edwards, R. 1980: Social wasps, their biology and control. East Grinstead, Rentokil Limited. 398 p.

Gambino, P. 1986: Winter prey collection at a perennial colony of *Paravespula vulgaris* (L.) (Hymenoptera: Vespidae). *Psyche 93*: 331–340.

————1990: Mark recapture studies on *Vespula pensylvanica* queens (Hymenoptera: Vespidae). *Pan Pacific entomologist. 66*: 227–231.

Gambino, P.; Medeiros, A. M.; Loope, L. L. 1990: Invasion and colonization of upper elevations on East Maui (Hawaii) by *Vespula pensylvanica* (Hymenoptera: Vespidae). *Annals of the Entomological Society of America 83*: 1088–1095.

Glancey, B. M.; Lofgren, C. S. 1988: Adoption of newly-mated queens: a mechanism for proliferation and perpetuation of polygynous red imported fire ants, *Solenopsis invicta* Buren. *Florida entomologist 71(4)*: 581–587.

Hamilton, W. D. 1964: The genetical evolution of social behavior. II. *Journal of theoretical biology 7*: 17–52.

Hölldobler, B.; Wilson, E. O. 1977: The number of queens: an important trait in ant evolution. *Naturwissenschaften 64*: 8–15.

Jeanne, J. L. 1980: Evolution of social behavior in the Vespidae. *Annual review of entomology 25*: 371–396.

Long, G. E.; Roush, C. F.; Akre, R. D. 1979: A linear model of development for colonies of *Vespula pensylvanica* (Hymenoptera: Vespidae) collected from Pullman, Washington. *Melanderia 31*: 27–36.

MacDonald, J. F.; Akre, R. D.; Hill, W. B. 1973: Attraction of yellowjackets (*Vespula* spp.) to heptyl butyrate in Washington State (Hymenoptera: Vespidae). *Environmental entomology 2(3)*: 375–379.

MacDonald, J. F.; Akre, R. D.; Hill, W. B. 1974: Comparative biology and behavior of *Vespula atropilosa* and *V. pensylvanica* (Hymenoptera: Vespidae). *Melanderia 18*: 1–66.

Miller, C. D. F. 1961: Taxonomy and distribution of Nearctic *Vespula*. *Canadian entomologist, supplement 22*: 1–52.

Nakahara, L. 1980: Western yellowjacket (*Vespula pensylvanica*) - first record of aerial nest in state. *USDA cooperative plant pest report 14(5)*: 270.

Nakahara, L.; Lai, P. 1981: Hawaii pest report. *Hawaii Department of Agriculture, Plant Pest Control Branch 1(3)*. 4 p.

Nonacs, P. 1988: Queen number in colonies of social Hymenoptera as a kin-selected adaptation. *Evolution 42(3)*: 566–580.

Noonan, K. M. 1981: Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses. *In*: Alexander, R. D.; Tinkle, D. W., *ed*., Natural selection and social behavior: recent research and new theory. New York, Chiron Press. pp. 18–45.

Ono, M; Sasaki, M.; Okada, I. 1985: Mating behavior of the giant hornet, *Vespa mandarinia* Smith and its pheromonal regulation. *Proceedings of the 30th International Apicultural Congress*: 255–259.

Pamilo, P. 1989: Estimating relatedness in social groups. *Trends in ecology and evolution 4(11)*: 353–355.

Plunkett, G. M.; Moller, H.; Hamilton, C.; Clapperton, B. K.; Thomas, C. D. 1989: Overwintering colonies of German (*Vespula germanica*) and common wasps (*Vespula vulgaris*) (Hymenoptera: Vespidae) in New Zealand. *New Zealand journal of zoology 16*: 345–353.

Ross, K. G.; Matthews, R. W. 1982: Two polygynous overwintered *Vespula squamosa* colonies from the southeastern U. S. (Hymenoptera: Vespidae). *Florida entomologist 65(1)*: 176–184.

Ross, K. G.; Visscher, P. K. 1983: Reproductive plasticity in yellowjacket wasps: a polygynous, perennial colony of *Vespula maculifrons*. *Psyche 90*: 179–191.

Roush, C. F.; Akre, R. D. 1978: Nesting biologies and seasonal occurrence of yellowjackets in northeastern Oregon forests (Hymenoptera: Vespidae). *Melanderia 30*: 57–94.

Spradbery, J. P. 1973: Wasps. Seattle, Univ. Washington Press. 408 p.

Strassmann, J. E. 1979: Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. *Science 204*: 207–209.

Thomas, C. R. 1960: The European wasp (*Vespula germanica* Fab.) in New Zealand. *New Zealand Department of Scientific and Industrial Research information series no. 27*. 74 p.

Tissot, A. N.; Robinson, F. A. 1954: Some unusual insect nests. *Florida entomologist 37(2)*: 73–92.

Vuillaume, M.; Schwander, J; Roland, C; 1969: Note préliminaire sur l'existence de colonies pérennes et polygynes de *Paravespula germanica*. *Comptes rendu de l'Academie Scientifique de Paris 269*: 2371–2372.

West-Eberhard, M. J. 1969: The social biology of polistine wasps. *Miscellaneous publications of the Museum of Zoology, University of Michigan 140*: 1–101.

West-Eberhard, M. J. 1981: Intragroup selection and the evolution of insect societies. *In*: Alexander, R. D.; Tinkle, D. W. (eds). Natural selection and social behavior: recent research and new theory. New York, Chiron Press. pp. 3–17.