

Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp

E. E. WILSON¹ AND D. A. HOLWAY

University of California, San Diego, Division of Biological Sciences, 9500 Gilman Drive,
Mail Code 0116, La Jolla, California 92093 USA

Abstract. Variation in invasion success may result from the divergent evolutionary histories of introduced species compared to those of native taxa. The vulnerability of native biotas to ecological disruption may be especially great on oceanic islands invaded by continental species with unique ecological traits. In part because Hawaii lacks native eusocial insects, social invaders may threaten endemic taxa that are ecologically similar but solitary. Using a combination of field manipulations, molecular analyses, physiological data, and behavioral assays, we identify the mechanisms underlying the displacement of two genera of native solitary Hymenoptera in Hawaii by a social continental invader, the western yellowjacket (*Vespa pensylvanica*). Experimental removal of *V. pensylvanica* colonies resulted in increased densities of native Hymenoptera. Endemic *Hylaeus* bees directly suffer through predation by yellowjackets, and perhaps as a consequence, avoid floral resources occupied by *V. pensylvanica*. Native *Nesodynerus* wasps also avoid *V. pensylvanica* but are negatively affected by yellowjackets not through predation, but through exploitative competition for caterpillar prey. Displacement of native solitary Hymenoptera may be heightened by the ability of *V. pensylvanica* to prey upon and scavenge honey bees and to rob their honey stores, resources unavailable to endemic bees and wasps because of their specialized niches. Our study provides a unique example of an ecologically generalized social invader that restructures native assemblages of solitary Hymenoptera by interacting with endemic taxa on multiple trophic levels.

Key words: *exploitative competition; Hawaii; Hylaeus; invasions; Nesodynerus; predation; Vespa pensylvanica; yellowjacket.*

INTRODUCTION

Evolutionary histories influence the ecological effects of biological invasions (Courchamp et al. 2003, Strauss et al. 2006). The phylogenetic relatedness of an invader to native taxa may be used to predict the magnitude of ecological effects resulting from a successful introduction. Evolutionary mismatches between donor and recipient biotas explain in part why some introduced species become such problematic invaders (Strauss et al. 2006).

The evolutionary histories of invaders and those of recipient biotas are often most divergent on oceanic archipelagoes (Howarth and Ramsay 1991). Oceanic islands differ from continental regions in that they exhibit low diversity at the order, family, and genus levels, but relatively high diversity at the species level (Paulay 1994), a pattern that results from adaptive radiations of select taxa (Zimmerman 1970). Furthermore, non-native continental species may be better adapted to a greater range of habitats, parasites, and pathogens because they evolved in a more diverse species

pool (Vermeij 1991) compared to island taxa. Differences between island endemics and invaders may increase the vulnerability of recipient communities to herbivory, predation, and disease (Diamond and Case 1986, Fritts and Rodda 1998).

The Hawaiian Islands provide striking examples of disparities between donor and recipient taxa. This remote oceanic archipelago has a largely endemic biota lacking in many phylogenetic groups common to continental regions. The native flora and fauna in Hawaii, for example, evolved in the absence of any social insects (Wilson 1996), which behaviorally and numerically dominate many continental ecosystems (Wilson 1990). Because of conspicuous differences in life history traits between social and solitary species (Goulson 2003, Cane et al. 2006), native solitary bees and wasps that colonized and radiated in Hawaii may be highly susceptible to social invaders. Despite the fact that social insects devastate island ecosystems (Beggs 2001, O'Dowd et al. 2003, Krushelnycky and Gillespie 2008), little is known about interactions involving native solitary Hymenoptera and their introduced social counterparts. Because social bees and wasps tend to be ecological generalists, unlike many solitary species (Heithaus 1979, Itino 1992, Biesmeijer et al. 2005, Cane et al. 2006), a single introduction of a social invader in

Manuscript received 1 July 2009; revised 5 March 2010;
accepted 7 April 2010. Corresponding Editor: D. H. Feener, Jr.

¹ E-mail: eewils@gmail.com

Hawaii may affect a wide range of native solitary Hymenoptera.

In this study, we investigate the effects of a social wasp invasion on native solitary bees in the genus *Hylaeus* and solitary wasps in the genus *Nesodynerus*. These two genera have undergone evolutionary radiations in Hawaii and may play important ecological roles as pollinators and predators, respectively. Combining behavioral, ecological and genetic approaches, we (1) examine how *Vespula pensylvanica* (hereafter simply “yellowjacket”) influences the local distribution and abundance of endemic solitary Hymenoptera, and (2) provide a detailed experimental assessment of the mechanisms underlying the displacement of *Hylaeus* and *Nesodynerus*. Our study reveals how an ecologically generalized social invader affects more specialized native solitary counterparts through a surprisingly diverse array of mechanisms.

MATERIALS AND METHODS

Study sites and system

We examined the ecological effects of western yellowjacket invasions on native Hymenoptera in Hawaii Volcanoes (HAVO) and Haleakala (HALE) National Parks. Both parks support large populations of *Vespula pensylvanica* and diverse arthropod assemblages. Study sites were located in open *Metrosideros polymorpha* (ohia) woodlands between 1000 and 1200 m elevation (HAVO) and subalpine shrublands between 2500 and 3000 m elevation (HALE).

Two of the largest Hawaiian insect radiations occur in *Hylaeus* (Colletidae: Hylaeinae) and *Nesodynerus* (Vespididae: Eumeninae) (Magnacca and Danforth 2007), which together comprise >40% of endemic Hymenoptera. The native bees of Hawaii form a single clade of 60 species, all within *Hylaeus* (yellow-faced bees) (Daly and Magnacca 2003). These short-tongued solitary bees serve as important pollinators of native plants, such as Hawaiian silversword (Forsyth 2003). While *Hylaeus* vary in size across species (Daly and Magnacca 2003), the most common bees at our study sites included *H. difficilis*, *H. laetus*, and *H. nivicola*, with wing lengths of 4–5 mm. The genus *Nesodynerus* is endemic to Hawaii and contains 94 described species; however, little is known about their ecology other than their role as predators of Microlepidoptera (Carpenter 2008). At our sites, the most common species were *N. nubicola* and *N. sociabilis*, which exhibited wing lengths of 8–10 mm. *Nesodynerus*, like many vespids, including *V. pensylvanica*, are nectivorous as adults but forage for arthropods to provision their offspring. Similar to other potter wasps, *Nesodynerus* mass provisions individual eggs with live caterpillars, but provides no maternal care. In this way, developing wasp larvae are provided with fresh prey throughout development (Hunt 1993). In contrast, the niche of the generalist scavenging predator *V. pensylvanica* envelops those of both *Hylaeus* and *Neso-*

dynerus, which by comparison exhibit strong niche conservatism at the genus level.

Patterns of floral visitation by Hymenoptera

To examine associations among yellowjackets and other Hymenoptera at floral resources, we adapted the methodology of Minckley et al. (2003) at four sites in HAVO and four sites in HALE. Within each park, sites were separated by at least 1.5 km. During August and September 2005, we walked four 200-m transects (separated by at least 200 m) at each site for a total of 32 transects. We focused sampling on native perennial plants in bloom during the sampling period that were visited by all common Hymenoptera, which included *Hylaeus*, *Nesodynerus*, *V. pensylvanica*, and *Apis mellifera* (honey bees). All transects were >100 m from any known honey bee or yellowjacket colony. Common plant taxa included *Metrosideros polymorpha*, *Santalum paniculatum*, and *Styphelia tameiameiae* in HAVO and *Coprosma* spp., *Santalum haleakalae*, *Sophora chrysophylla*, and *Styphelia tameiameiae* in HALE. Flowering vegetation with volumes >0.01 m³ and trees >0.02 m in diameter were sampled up to 2 m above the ground, the maximum height at which we could collect foragers with a sweep net. The number and identity of all bee and wasp visitors to native vegetation were noted; any unidentified bees or wasps were collected for identification. For *Apis*, *Hylaeus*, *Nesodynerus*, and *Vespula*, we calculated the mean number of plants occupied per site (averaged across transects within a site) and the mean number of individuals per occupied plant (averaged within transects). For *Apis*, *Hylaeus*, and *Nesodynerus*, we conducted separate one-way ANOVAs to test for differences in mean numbers of plants occupied and also the mean abundance of these species per occupied plant. The experimental groups in these analyses were defined as the number of yellowjackets present (0, 1, ≥2) on plants visited by *Apis*, *Hylaeus*, and *Nesodynerus*. We used post hoc Tukey HSD tests to evaluate effects of yellowjacket abundance on patterns of floral visitation. These statistical analyses (and all others in this study) were performed with JMP v. 8.0.1 (SAS Institute 2009).

Effect of Vespula colony removal on endemic Hymenoptera

To assess whether yellowjackets displace *Hylaeus* and *Nesodynerus*, we conducted colony removal experiments. Focal yellowjacket colonies were distributed within HAVO (2006, *n* = 14; 2007, *n* = 17) and HALE (2006, *n* = 6; 2007, *n* = 13); each colony was randomly assigned to a treatment: yellowjacket removal (*n* = 27) or control (*n* = 23). Removals were coordinated with the U.S. Geological Survey (HAVO) and National Park Service (HAVO and HALE), where qualified personnel excavated nests or applied approved pesticides directly to removal colonies. Colonies in the control treatment were left undisturbed for the duration of the experiment. Before colony removal and twice following removal

(monthly), we sampled native Hymenoptera visiting floral resources at all sites. Around each *Vespa* nest, we established a 40 × 40 m experimental plot, which was divided into 10 × 10 m subplots. Within each sampling period at each plot, we identified all bees and wasps visiting floral resources in five randomly selected subplots. Using separate repeated-measures MANOVAs for *Hylaeus* and *Nesodynerus*, variation in hymenopteran densities was analyzed with year, park, and treatment as main factors, time as the within-subjects factor, and interactions between year, park, and treatment included. Post hoc *t* tests were applied for comparison of treatments where treatment was significant in MANOVA, and Bonferroni corrections for multiple comparisons were used to correct for Type I error.

Molecular analysis of diet items

To determine whether yellowjackets consume native solitary Hymenoptera, we collected diet items obtained from returning yellowjacket foragers. Previous studies conducted at these same sites found that Hymenoptera represent ~15% of the yellowjacket diet (Wilson et al. 2009). In the present study, we determined the identity of 64 hymenopteran diet items from multiple colonies in both parks. Over half of these items could be identified to species based on morphological characters. For the remaining diet items ($n = 23$), we sequenced the cytochrome oxidase I (COI) gene using the primers in Magnacca and Danforth (2006) (C1-J-2183 and TL2-N-3014, C1-J2777 and modified C2-N-3389). DNA was extracted using the QIAamp DNA Micro Kit (Qiagen, Germantown, Maryland, USA). PCR reactions were performed in a 15- μ L volume on Eppendorf Mastercycler Gradient thermal cyclers (Eppendorf, Hamburg, Germany). We used 2 μ L of template DNA, 10X Taq Buffer (Eppendorf), 1.5 μ L of 1.5mmol/L MgCl₂, 1.5 μ L of 10X BSA, 0.3 μ L of 10 μ mol/L dNTPs, 0.6 μ L of each 10 μ mol/L primer, and 0.2 μ L of Taq DNA Polymerase (Eppendorf). Reaction conditions were performed as follows: an initial denaturation step of 94°C for 3 min, followed by 40 cycles of denaturation at 94°C for 45 s, annealing at gradient of 48–53.2°C for 45 s, and extension at 72°C for 60 s. A final extension step was performed at 72°C for 10 min. Voucher specimens of six common hymenopteran taxa from our study sites were also sequenced. Diet items were first compared to voucher sequences and if necessary identified using BLAST (Basic Local Alignment Search Tool) searches, where BLAST scores >400 and percent match >95% were considered putative matches.

Mechanisms underlying displacement: predation vs. scavenging

Yellowjackets obtain arthropod resources through a combination of scavenging and predation (Greene 1991). To determine the relative importance of these mechanisms, we employed three complementary approaches: (1) pH analysis of thoracic muscle of diet

items; (2) retrieval of hymenopteran corpses from scavenging plots; and (3) choice tests between dead and live honey bees. We used post mortem thoracic muscle pH to distinguish fresh-killed prey from decaying corpses (Wilson et al. 2010). After death, animal muscle remains metabolically active (Lindahl et al. 2006), which can cause a decline in pH as oxidative phosphorylation ceases while glycolysis continues (Crabtree and News-holm 1972, Vishnudas and Vigoreaux 2006). Because muscle pH declines predictably after death, this metric can reveal information concerning stress level at the time of death. When animals experience stress, muscle pH declines at a faster rate compared to no-stress situations (Rees et al. 2003, Wilson et al. 2010). Therefore, scavenged carrion (low to no stress) has lower muscle pH compared to that of killed prey (high stress) when measured at similar times since death (Wilson et al. 2010).

To determine whether yellowjackets preferentially prey on or scavenge different hymenopteran species, we compared pH measurements of diet items to standards with known stress levels and times since death. We first measured thoracic muscle pH of diet items (*Apis* and *Hylaeus*) retrieved by yellowjacket foragers. For *Apis* standards, we used those reported in Wilson et al. (2010). For *Hylaeus* standards, we collected 24 females and randomly assigned them to one of two experimental groups: high stress ($n = 13$) and control ($n = 11$). Bees in the high-stress treatment were physically restrained and agitated for one minute, and then decapitated. Decapitation was used because it is a common killing behavior of predatory wasps. In the control treatment, bees were freeze-killed prior to decapitation. Thoracic pH was measured immediately after death following the methods of Wilson et al. (2010).

As an additional measure of the relative importance of predation vs. scavenging, we determined the extent to which yellowjackets discover and retrieve freshly killed Hymenoptera. At five different sites in both parks, we distributed individual hymenopteran corpses on the ground at 10-m intervals in $\approx 40 \times 40$ m plots, which lacked ants and other common diurnal scavengers. In three plots, we interspersed 10 honey bees and 10 yellowjackets, and in two plots, we distributed 15 honey bees and 10 yellow-faced bees. At each plot, we observed which corpses were scavenged by *V. pensylvanica*. Data were pooled across homogenous trials (*Apis* vs. *Vespa*, $\chi^2_2 = 2.92$, $P = 0.23$; *Apis* vs. *Hylaeus*, $\chi^2_1 = 2.03$, $P = 0.15$). Chi-square tests were used to evaluate interspecific differences in scavenging preferences.

Because the odor of decaying insect carcasses may facilitate location by scavengers (Gullan et al. 2005), we also examined the relative attractiveness of honey bees at different stages of decomposition. At each of 10 *V. pensylvanica* colonies (HAVO, $n = 5$; HALE, $n = 5$), we conducted six choice tests, pairing a bee that was killed 3–5 days previously with a bee that was killed earlier

that day. All bees were killed in ethanol because preliminary studies of five *Vespa* colonies (six trials each) indicated wasps do not distinguish bees killed in ethanol from those killed in water ($\chi^2_4 = 4.67$, $P = 0.32$). Choice tests were conducted 10 m upwind of the focal wasp colony and bees were placed 10 cm apart. Each colony was tested once a day. Paired *t* tests were used to evaluate preferences between decaying and newly dead honey bees.

At six colonies, we subsequently conducted an additional five trials in which we offered yellowjackets a choice between a newly killed bee and a live bee. Both bees were pinned through the thorax to a Styrofoam platform and separated by 10 cm; such restraint prevented live bees from flying away, but allowed the bees to sting and fight with attacking yellowjackets. Paired *t* tests were used to evaluate preferences for freshly dead or live honey bees.

*Mechanisms underlying displacement:
exploitative competition for prey*

To determine how the distribution and abundance of solitary *Nesodynerus* wasps change with yellowjacket nest removal, we dispersed 635 trapnests in subalpine shrubland (2250–2500 m elevation) in HALE. Because Eumenine wasps and other solitary Hymenoptera often maintain the same nest sites from year to year (Sears et al. 2001), trap nesting of these insects using the methods of Krombein (1967) serves as an effective way to examine interspecific patterns of distribution and abundance. In addition, trap nests provide detailed information about diet and provisioning behaviors of *Nesodynerus* wasps.

Each trap nest consisted of a $3.8 \times 3.8 \times 10$ cm piece of white pine wood dipped in paraffin wax. On one face, nine holes (diameters 3.2 mm [$n = 5$] and 4.8 mm [$n = 4$]) were bored to the depth of 7.5 cm. Traps were attached to vegetation 0.5–1.0 m above the ground. Each October from 2006 to 2008, traps were laid in the following areas: (1) sites where yellowjackets were absent or had been removed >8 months previously ($n = 400$ traps), (2) sites where yellowjackets had been removed within 2 months ($n = 108$ traps), and (3) sites where yellowjacket nests were present ($n = 127$ traps). All trap nests were collected the April following their deployment and dissected to detect and identify any current occupants. Microscopic analysis of trap nests also revealed evidence of past occupation by insects other than our species of interest. To examine solitary Hymenoptera levels prior to peak yellowjacket activity in late summer/early fall, we put out an additional 29 traps in April 2008; these traps were collected and dissected in August 2008. Trap occupancy was analyzed by plot treatment using a *G* test.

To determine whether *Vespa* may engage in exploitative competition with *Nesodynerus* wasps for caterpillar prey, we identified caterpillars used to provision developing *Nesodynerus* larvae by sequencing the COI gene using primers LCO1490 and HCO2198

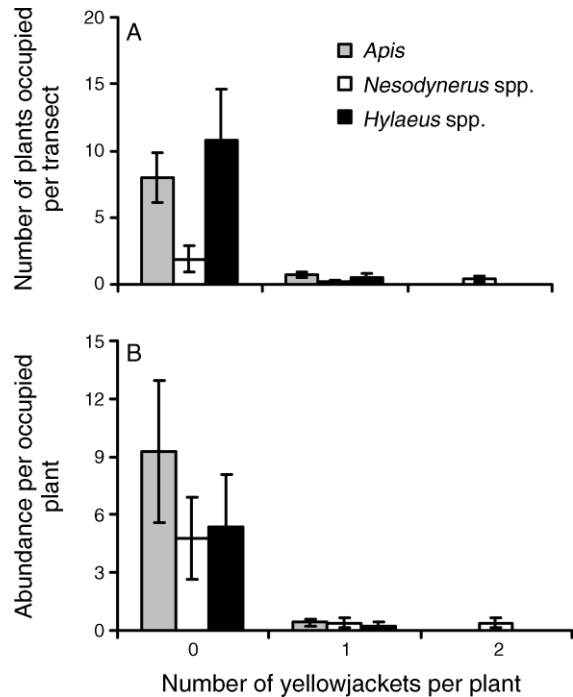


FIG. 1. This study examines the interactions among native and introduced Hymenoptera in open ohia woodlands (Hawaii Volcanoes National Park) and subalpine shrubland (Haleakala National Park). *Apis*, *Nesodynerus*, and *Hylaesus* abundances on floral resources vs. yellowjacket (*Vespa pensylvanica*) density per plant. Data are means \pm SE. (A) Number of plants occupied per transect, and (B) abundance per occupied plant, as functions of yellowjacket density per plant.

(Folmer et al. 1994), and Lepidoptera-specific primers LepF and LepR, reported in Hajibabaei et al. (2006). PCRs were performed using the same reaction volumes and conditions as described in *Molecular analysis of diet items*. Because each developing larva was provisioned with multiple caterpillars (range: 2–30), we randomly selected five caterpillars (when possible) to sequence for each developing wasp. We compared the caterpillars in the diet of *Nesodynerus* to those consumed by *Vespa* from nearby sites (Wilson et al. 2009) using Sørensen's index of similarity (Wolda 1981).

RESULTS

Patterns of floral visitation by Hymenoptera

The distributions of yellowjackets and other Hymenoptera on floral resources were largely mutually exclusive regardless of plant identity. *Apis*, *Nesodynerus*, and *Hylaesus* foraged on plants that lacked yellowjackets (Fig. 1A, *Apis*, $F_{2,18} = 4.25$, $P = 0.031$; *Nesodynerus*, $F_{2,18} = 3.73$, $P = 0.040$; and *Hylaesus*, $F_{2,18} = 6.35$, $P = 0.022$). Similarly, mean hymenopteran abundances were highest on plants without yellowjackets and sharply decreased as *V. pensylvanica* visitation increased (Fig. 1B, *Apis*, $F_{1,21} = 6.77$, $P = 0.017$; *Nesodynerus*, $F_{1,21} = 4.92$, $P = 0.038$; and *Hylaesus*, $F_{1,21} = 4.46$, $P = 0.040$).

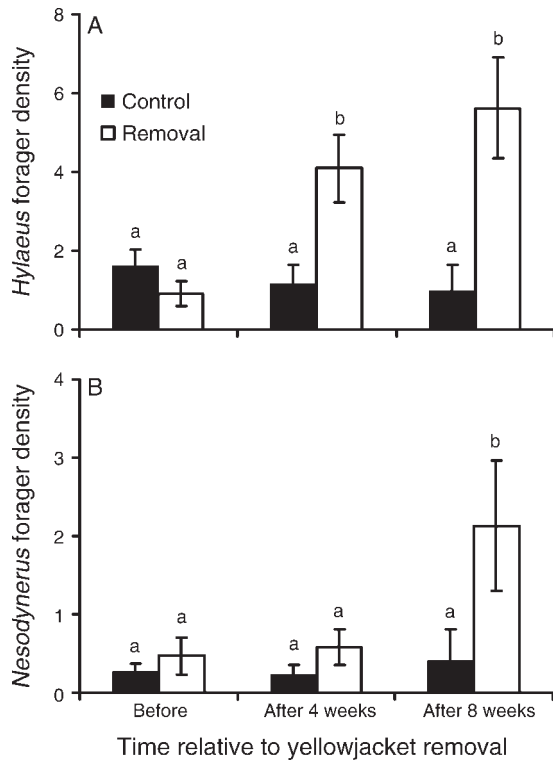


FIG. 2. (A) *Hylaesus* densities (mean \pm SE) before and after *Vespula* colony removal ($n = 27$ removal plots and 23 control plots). Forager density is expressed as mean abundance within 100-m² subplots. Different lowercase letters above bars indicate significant differences ($P < 0.05$) based on post hoc *t* tests. (B) *Nesodynerus* densities (mean \pm SE) over time before and after *Vespula* colony removal ($n = 27$ removal plots and 23 control plots). Different lowercase letters indicate patterns of significance as in panel (A).

Effect of *Vespula* removal on endemic Hymenoptera

Removal experiments demonstrated that yellowjackets exclude both *Hylaesus* and *Nesodynerus* (Fig. 2). *Hylaesus* densities increased following nest removal in removal plots compared to control plots (overall MANOVA model, Wilks' lambda = 3.92, $P = 0.0074$; treatment, $F_{1,27} = 13.53$, $P = 0.001$), and continued to increase as time after removal increased ($F_{2,26} = 4.03$, $P = 0.029$) with densities consistent across parks ($F_{1,27} = 2.60$, $P = 0.12$). *Nesodynerus* also increased following nest removal, although this response took two months to develop (Fig. 2B) (overall MANOVA, Wilks' lambda = 3.59, $P = 0.0029$; treatment, $F_{1,22} = 6.63$, $P = 0.017$; time since removal, $F_{2,21} = 10.8$, $P = 0.0006$). *Nesodynerus* densities in HALE were always higher than those in HAVO ($F_{1,22} = 10.63$, $P = 0.0036$).

Molecular analysis of diet items

Yellowjackets commonly consume solitary and social Hymenoptera (64 of 412 diet items sampled) (Wilson et al. 2009). Of all Hymenoptera in the yellowjacket diet,

Hylaesus and introduced *Apis mellifera* comprised 27% ($n = 18$) and 23% ($n = 14$), respectively. Three species of *Hylaesus* were found in the yellowjacket diet: *H. difficilis* ($n = 1$), *H. laetus* ($n = 15$), and *H. nivicola* ($n = 2$). In contrast, *Nesodynerus* was completely absent. Sequencing analyses indicated that the remaining Hymenoptera in the yellowjacket diet included braconid wasps (Braconidae) ($n = 1$), *Paratrechina bourbonica* (Formicidae) ($n = 1$), *Spilichneumon superbus* (Ichneumonidae) ($n = 2$), and *V. pensylvanica* ($n = 27$).

Time of day and ambient temperature influenced the prevalence of Hymenoptera in the yellowjacket diet. *Hylaesus* individuals were collected from returning yellowjacket foragers only in cool ambient temperatures (10–16°C) or during the first hours of daylight. In contrast, *A. mellifera* and *V. pensylvanica* were collected throughout the day across a range of ambient temperatures.

Mechanisms underlying displacement: predation vs. scavenging

Thoracic pH measurements indicate that *V. pensylvanica* preys upon *Hylaesus*, but it both preys upon and scavenges *Apis*. We compared thoracic muscle pH from the diet items (*Apis*, $n = 10$; *Hylaesus*, $n = 3$) to standards of stressed and nonstressed bees; data for *Apis* standards originate from Wilson et al. (2010). In Fig. 3, the low pH measurements of all three *Hylaesus* and those of six honey bees suggest that these items were prey, whereas the higher thoracic pH of the four other *Apis* suggests that these individuals were carrion.

Scavenging plots provide additional evidence that yellowjackets prey upon *Hylaesus* but obtain *Apis* in part

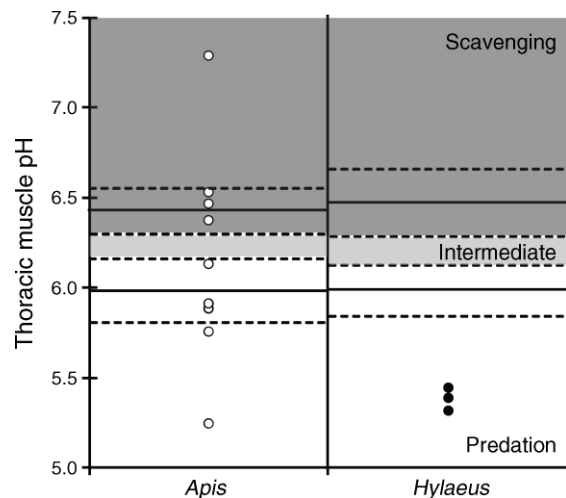


FIG. 3. Diet items classified as carrion or prey based on pH measurements. Mean pH (solid lines) \pm SD (dashed lines) by species and putative ecological mechanism. The dark-shaded area encompasses scavenging and control pH measurements. The white area encompasses predation and stress pH measurements. The light-shaded area represents pH range between predation and scavenging. Circles represent individual bees.

TABLE 1. Scavenging of *Apis mellifera*, *Hylaeus* spp., and *Vespula pensylvanica* by the western yellowjacket *V. pensylvanica* in two choice experiments.

| Hymenopteran taxon | Number presented | Number scavenged | Proportion scavenged | χ^2 | Standardized residuals |
|-----------------------------|------------------|------------------|----------------------|----------|------------------------|
| <i>Apis mellifera</i> | 30 | 26 | 0.87 | 0.074 | -0.19 |
| <i>Vespula pensylvanica</i> | 30 | 28 | 0.93 | | 0.19 |
| <i>A. mellifera</i> | 30 | 25 | 0.83 | 25† | 3.54 |
| <i>Hylaeus</i> spp. | 20 | 0 | 0.00 | | -3.54 |

Note: *Apis mellifera* and *V. pensylvanica* are scavenged equally, whereas all *Hylaeus* remain uncollected.

† $P < 0.0001$.

through scavenging (Table 1). While not a single *Hylaeus* bee (0/20) was scavenged, 50% of *Apis* corpses disappeared in the first two hours, and all scavenged *Apis* corpses were collected within six hours (51/51). Choice tests further support the hypothesis that yellowjackets prey upon and scavenge honey bees. Scavenging yellowjackets preferred fresh-killed bees over long-dead bees (Fig. 4A: $t_9 = 2.99$, $P = 0.015$), but live bees were preferred over fresh-killed bees in nearly all of the individual trials (30/31) (Fig. 4B: $t_5 = 29$, $P = 9.14 \times 10^{-7}$).

In addition to preying upon and scavenging honey bees in the field, yellowjackets rob honey bee colonies. During the course of this study, we observed two types of robbing behavior by *V. pensylvanica*. The first type of raid was characterized by slow but steady traffic of *V. pensylvanica* foragers entering and leaving apparently healthy *Apis* hives. In these attacks, which can continue on and off for weeks, honey bees aggressively defend their nests and produce large amounts of alarm pheromone; these behaviors appear to deter a fraction of the robbers. The second and more common type of robbing occurs when individual yellowjackets enter mature colonies of *A. mellifera* and experience no apparent opposition. Because of the low number of robbers and the large time lapses between isolated robbing events, this second type of attack appears opportunistic in nature. In both raid types, exiting wasps were observed to carry away bee larvae in their mandibles; wasps with empty mandibles presumably collected honey.

*Mechanisms of displacement:
exploitative competition for prey*

Trap nest data and yellowjacket colony removal revealed that *Nesodynerus* avoid nesting in areas with *Vespula* ($n = 43$ traps). Solitary wasps occupied more traps in removal plots compared to control plots ($G^2 = 10.38$, $df = 2$, $P = 0.0054$). While more traps were occupied in areas where yellowjackets had been absent for longer periods of time ($n = 33$), the two removal treatments did not differ in total occupation rate (8.25% and 8.33%). Control plots (with yellowjackets) had the fewest traps occupied ($n = 1$) and the lowest occupation rate (0.78%).

Molecular analysis of provisioned caterpillars ($n = 119$) in occupied traps indicated *Nesodynerus* collected noctuid (60%), crambid (32.8%), and geometrid larvae (1.7%). Comparisons of trap nest contents to molecular analysis of Lepidoptera in the yellowjacket diet revealed overlap in the types of caterpillars consumed (Sørensen's index of similarity = 0.50), with both *Nesodynerus* and *Vespula* consuming geometrids and noctuids.

DISCUSSION

Our study illustrates how native solitary Hymenoptera experience displacement (sensu Reitz and Trumble 2002) by introduced *Vespula pensylvanica*, as a result of both direct and indirect interactions. While *Hylaeus* and *Nesodynerus* readily forage for nectar on the same plant species (e.g., *Metrosideros polymorpha*, *Styphelia tameiameia*) as does *V. pensylvanica*, native bees and wasps avoid visiting plants occupied by yellowjackets. Yellowjacket colony removal experiments demonstrate that this distributional pattern does not result from different habitat preferences. Both *Hylaeus* and *Nesodynerus* were absent from areas near yellowjacket colonies, but increased in abundance after yellowjacket colonies were removed. While solitary Hymenoptera responded positively to experimental removals, the timing of these increases differed for *Hylaeus* and *Nesodynerus*. The relatively fast response of *Hylaeus* compared to the

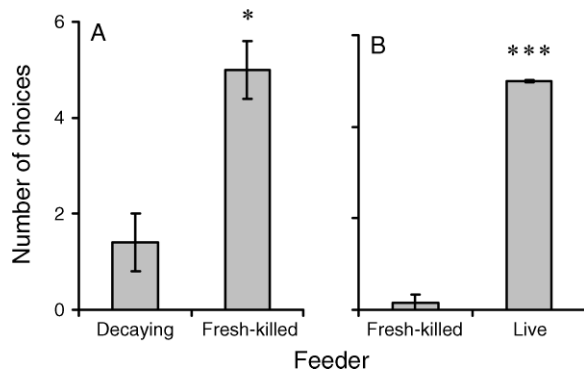


FIG. 4. Choice tests of yellowjackets between (A) decaying and fresh-killed honey bees, and (B) fresh-killed and live honey bees. Error bars represent \pm SE.

* $P < 0.05$; *** $P < 0.001$.

response of *Nesodynerus* suggests that unique mechanisms underlie each displacement.

Analyses of diet items and the results of scavenging plots provide compelling evidence that yellowjackets prey upon *Hylaeus*. The frequency of *Hylaeus* in the *V. pensylvanica* diet is surprisingly high (Wilson et al. 2009) considering that these solitary bees do not aggregate or forage in groups (Daly and Magnacca 2003) and that wasps typically do not kill flying bees (Koeniger et al. 1996). Interspecific differences in thermoregulation may in part explain the unexpected frequency of *Hylaeus* in the yellowjacket diet. Because of their sociality (Ishay 1973) and their ability to thermoregulate (Eckles et al. 2008), yellowjackets may kill *Hylaeus* under cool conditions before these solitary bees heat up sufficiently to avoid attack. Consistent with this hypothesis, we collected *Hylaeus* from *V. pensylvanica* foragers predominantly in cool ambient temperatures. Under such environmental conditions, *Hylaeus* often appear sluggish and will bask in the sun (E. Wilson, *personal observation*); this may be in part to utilize solar radiation to warm their flight muscles (Stone and Willmer 1989, Larsson 1991, Stone et al. 1995). Given the contrasting thermoregulatory abilities, it seems likely that yellowjackets encounter torpid *Hylaeus* on cool mornings when they are vulnerable to predation.

While yellowjackets consume substantial numbers of *Hylaeus*, predation by itself cannot sufficiently explain patterns of floral visitation along transects and in removal experiments. Because the development time of *Hylaeus* larvae (Daly and Coville 1982) exceeds the four-week period of time during which *Hylaeus* numbers increased in the removal experiments, the observed effects (Fig. 2A) must in part stem from behavioral avoidance, a defensive strategy against yellowjackets. Solitary wasps were also displaced, but not as a result of predation by yellowjackets. Moreover, exploitative competition between these solitary Hymenoptera and yellowjackets for nectar probably contributes to the observed displacements, but also cannot solely explain why these species fail to co-occur. *Hylaeus* and *Nesodynerus* do not appear to avoid honey bees despite the fact that a single *Apis* colony can harvest 10–60 kg/yr of pollen (Goulson 2003) and 17–414 kg/yr of nectar (Southwick and Pimentel 1981). Likewise, interference competition at nectar resources between honey bees and *Hylaeus* and *Nesodynerus* was never observed. Taken together, these results indicate that yellow-faced bees and solitary wasps behaviorally avoid *V. pensylvanica*, although likely for different reasons. As a consequence of this avoidance, the presence of *V. pensylvanica* may limit pollen and nectar collection by native bees and nectar consumption by native wasps.

Unlike *Hylaeus*, *Nesodynerus* provision their young with lepidopteran larvae and thus compete directly with yellowjackets for caterpillar prey. Thus, interspecific competition seems likely given that invasive *Vesputula*

devastate caterpillar populations (Beggs and Rees 1999, Wilson et al. 2009). Based on the results of the removal experiments, *Nesodynerus* appears to move into removal plots only after caterpillar populations have begun to recover from yellowjacket predation. Densities of *Nesodynerus* at floral resources increased following yellowjacket colony removal, but only after two months, which previous studies at these sites have shown to be the time interval required for caterpillar densities to rebound (Wilson et al. 2009). Trapnest data further support the hypothesis of exploitative competition. Diet overlap analysis shows that *Nesodynerus* and *V. pensylvanica* overlap in the lepidopteran families consumed. The exception to this general pattern was the microlepidopteran family, Crambidae, which were common prey of *Nesodynerus*. Crambids are concealed feeders that live in leaf shelters, bore into stems, and mine leaves (Solis 2007); these traits may protect them from yellowjackets, which have a broad generalist diet and may lack the appropriate search image for concealed prey such as crambids.

Honey bees as a resource subsidy for Vesputula

Trophic subsidies in the form of carrion may facilitate the population growth of predators (Stapp and Polis 2003), thus increasing their ability to suppress prey and competitor species (Polis and Strong 1996). Several lines of evidence suggest that honey bees play an important but underappreciated role in mediating interactions between native arthropods and invasive yellowjackets. *Vesputula pensylvanica* often nests in proximity to perennial *Apis* colonies. At our study sites, >65% of *V. pensylvanica* colonies were within 600 m of at least one well-established honey bee colony, and no *Vesputula* colony was >1 km from an active honey bee hive. Western yellowjackets mostly forage within 600 m of their nest (Akre et al. 1975), and molecular diet analyses reveal that yellowjackets commonly forage on honey bees (Wilson et al. 2009). Muscle pH analysis, scavenging plots, and choice tests all indicate that yellowjackets collect honey bees through a combination of predation and scavenging. Thus, honey bee colonies with their large, perennial workforce provide reliable and abundant supplies of prey, carrion (Visscher 1983, Coelho and Hoagland 1995), and honey (De Jong 1990).

Honey bee-derived resources provide yellowjackets with additional food sources that are unavailable to native solitary wasps. *Nesodynerus* do not scavenge (Carpenter 2008) and thus cannot exploit nor be subsidized by the protein resources of honey bee carrion. Moreover, *Nesodynerus* were never observed visiting or robbing honey bee colonies. For these reasons, the aggregated and constant production of protein and carbohydrate resources in honey bee colonies solely benefits yellowjackets, and may thus magnify the top-down effect of yellowjacket predation on native solitary bees and accentuate competition with solitary wasps.

Conclusions

This study demonstrates how a continental invader displaces functionally similar native endemics through an unexpected diversity of mechanisms. Because oceanic islands are naturally colonized by a small subset of continental species pools, successful invaders of these systems can differ markedly from endemic taxa in their phylogenetic histories (Proches et al. 2008). Consequently, the most disruptive island invaders often exhibit traits or adaptations not represented among native taxa (Fritts and Rodda 1998). In the case of Hawaii, the complete absence of native eusocial insects has left this region open to invasion by aggressive and abundant social species (Zimmerman 1970). Despite having undergone extensive radiations, both *Hylaesus* and *Nesodynerus* appear to exhibit substantial intrageneric niche conservatism, and the relatively narrow ecological roles of each genus are encompassed within the broad ecological niche of invasive yellowjackets. As a consequence, the ecological effects of yellowjacket invasions in Hawaiian natural areas span multiple trophic levels: *Hylaesus* is displaced through a combination of behavioral avoidance and predation, whereas *Nesodynerus* competes with yellowjackets for caterpillar prey. The displacement of native solitary bees and wasps may be further enhanced by the introduction of yet another social invader, the honey bee, which can subsidize yellowjacket populations but does not provide similar benefits for native Hymenoptera, and may in fact compete with endemic species for nectar. This study highlights the importance of considering shared evolutionary histories between the donor and recipient biota and reveals that phylogenetic disparities (e.g., with respect to sociality and generalist ecological traits) can influence the types of mechanisms by which invaders displace ecologically similar endemics.

ACKNOWLEDGMENTS

We thank D. Foote, R. Kaholoa'a, C. Hanna, A. Smith, E. Martinez, and P. Fitzpatrick for logistical help and yellowjacket removal; M. Eckles, E. Goldberg, A. Lin, C. Sidhu, and J. Wilson for field assistance; and C. Sidhu and K. LeVan for lab assistance. We gratefully acknowledge P. Krushelnycky and R. Kaholoa'a for help with species identifications and P. Hastings, J. Kohn, J. Nieh, K. Visscher, E. M. Wolkovich, and two anonymous reviewers for comments on the manuscript. Financial support was provided in part by an NSF Doctoral Dissertation Improvement Grant (E. E. Wilson), an EPA STAR Fellowship (E. E. Wilson), the San Diego Chapter of the ARCS Foundation (E. E. Wilson), and a UCSD Academic Senate grant. Work was conducted under permits HAVO-2005-SCI-0044 and HALE-2004-SCI-0009.

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