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Ecological Effects of an Invasive Social Wasp on Hawaiian Arthropod Communities

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by

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The Dissertation of Erin Elizabeth Wilson is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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ABSTRACT OF THE DISSERTATION

Ecological Effects of an Invasive Social Wasp on Hawaiian Arthropod Communities

by

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The introduction of non-native organisms is a leading cause of species imperilment. Detailed studies of damaging invasive species contribute importantly to the development of effective strategies for conserving biodiversity. Among the many problematic invasive social insects, the western yellowjacket (*Vespula pensylvanica)* represents an emerging and harmful introduction. Because Hawaii lacks any native eusocial insects, the invasion of *V. pensylvanica* poses a potentially devastating threat to the native and largely endemic biota of this region. This study examines the underlying mechanisms of a social wasp invasion in Hawaii. Using ecological approaches and molecular methods, I quantify the effects of an invasive yellowjacket on native prey and competitors. This study identifies factors affecting invasion success, and contributes to

the development of effective management strategies that minimize the ecological impacts of invasive social insects on native communities.

INTRODUCTION TO THE DISSERTATION

Species introductions disrupt ecosystems and can threaten biodiversity (Fritts and Rodda 1998; Sala et al. 2000). Invasions can be especially destructive when the evolutionary histories of introduced species differ greatly from those of native taxa. The evolutionary histories of invaders and those of recipient biotas are often most divergent on oceanic archipelagoes (Howarth and Ramsay 1991). Thus, the native taxa of oceanic islands may be especially vulnerable to ecological disruption when invaded by continental species with unique ecological traits (O'Dowd et al. 2003). Lacking native social insects, Hawaiian ecosystems may be especially sensitive to invasion by social Hymenoptera (Bowen and VanVuren 1997; Courchamp et al. 2003; Zimmerman 1970).

Vespula pensylvanica (the western yellowjacket) is a generalist and opportunistic predator (Foote and Carson 1995) that feeds on a wide variety of arthropod prey (Gambino 1992). This yellowjacket typically forms subterranean annual nests that decline in late fall (Akre and MacDonald 1985) consisting of 500-5,000 workers (Visscher and Vetter 2003). However, perennial nests occur in the southern parts of its native range and in its introduced range in Hawaii (Gambino 1991; Ratnieks et al. 1996). Such overwintering colonies requeen and can become >10 times more productive than annual nests (Plunkett et al. 1989; Visscher and Vetter 2003). This plasticity in colony structure has serious ecological implications for native prey and competitor species. *Vespula* (yellowjacket wasps) includes some of the world’s most ecologically damaging invasive insects (Beggs 2001; Lowe et al. 2000). The genus *Vespula* is divided into the *Vespula vulgaris* and *V. rufa* species groups (Smith et al. 2001). The *V. vulgaris* species group contains all *Vespula* that are successful invaders: *V. germanica, V. pensylvanica,* and *V. vulgaris*. Less well known than its congeners (*e.g. V. germanica* and *V. vulgaris*), *V. pensylvanica* became established about 30 years ago in Hawaii (Gambino et al. 1990), where it becomes locally abundant in natural areas (Gambino 1992). This invasion by western yellowjackets has reduced densities of certain endemic taxa (*e.g.* Hawaiian picture-wing flies (Foote and Carson 1995) and native honeycreepers (Banko et al. 2002)), but the full ecological effects of this invasion remain incompletely studied.

Foraging behavior of *Vespula pensylvanica*

Workers forage for fiber, carbohydrates, protein and water within 400 m of the nest (Akre et al. 1975; Akre and MacDonald 1985). Young foragers (< five days old) gather pulp and fluid but will hunt protein as they age (Spradbery 1973). The oldest foragers (20+ days) collect carbohydrate fluid almost exclusively (Potter 1964).

Vespula exhibit several foraging behaviors that may contribute to invasion success. Yellowjackets can vertically partition foraging space in the presence of other social wasps. Co-occurring *Vespula* species will forage at different strata of the vegetation, thus reducing competition for food resources (Akre and MacDonald 1985; Akre et al. 1982; Reed and Akre 1983). Aggression among foragers is rarely observed and only at low resource levels (MacDonald et al. 1974). Additionally, there is some evidence for social facilitation at the nest (Parrish and Fowler 1983; Spradbery 1973) and at the food source (D'Adamo et al. 2003; Free 1970; Richter and Tisch 1999). Modest levels of recruitment have been found in *V. germanica* and *V. vulgaris*, but have not been investigated in *V. pensylvanica.* By decreasing competition for prey through vertical partitioning and by increasing foraging efficiency through recruitment, *Vespula* wasps are highly adaptable to changes in resource availability.

Predators of *Vespula pensylvanica*

The western yellowjacket falls prey to many invertebrates and vertebrates in its native range of the western United States (Akre and MacDonald 1985), including ants (Dejean et al. 1998), dragonflies (Rowe 1987), flies, spiders (Nakamura and Nakamura 1977; Sugden and McAllen 1994) birds (Burger et al. 1999) and small mammals (Sugden and McAllen 1994). The local distribution of *V. pensylvanica* in Hawaii does not overlap with Argentine ants (*Linepithema humile*), and no native Hawaiian species are known to prey upon these yellowjackets.

Study sites

Vespula pensylvanica was first reported on the islands of Hawaii and Maui in 1978 (Gambino 1991). Hawaii Volcanoes National Park (HAVO) and Maui's Haleakala National Park (HALE) both support populations of *V. pensylvanica* as well as diverse assemblages of native and non-native arthropods. Study sites were located in open *Metrosideros polymorpha* (ohia) woodlands between 1000 and 1200 m (HAVO) and subalpine shrublands between 2500 and 3000 m (HALE).

Rationale and objectives

The western yellowjacket may be a recent arrival to Hawaii, but it has quickly become a major agricultural and recreational pest. Four studies have examined this invasion in Hawaii (Gambino 1990; Gambino 1991; Gambino 1992; Gambino et al. 1990) yet only one addressed the ecological effects (Gambino 1992). This study attempted to identify the species affected by *V. pensylvanica*, but identified fewer than 18% of the prey items due to the difficulty of visually identifying masticated prey. Although other invasive *Vespula* species have been extensively studied in their introduced ranges (Beggs 2001; Kasper et al. 2004; Wood et al. 2006), little is known about the foraging habits of the western yellowjacket or the factors influencing its establishment and spread.

My research addresses the ecological effects of this invasion and traits influencing its success using a combination of molecular, experimental and behavioral approaches. This study has three main objectives: to quantify the effects of *Vespula pensylvanica* on prey taxa, to quantify effects on native solitary bees and wasps, and to examine the role of recruitment in the success of this invasive species.

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Life history plasticity magnifies the ecological effects of a social wasp invasion

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An unresolved question in ecology concerns why the ecological effects of invasions vary in magnitude. Many introduced species fail to interact strongly with the recipient biota, whereas others profoundly disrupt the ecosystems they invade through predation, competition, and other mechanisms. In the context of ecological impacts, research on biological invasions seldom considers phenotypic or microevolutionary changes that occur following introduction. Here, we show how plasticity in key life history traits (colony size and longevity), together with omnivory, magnifies the predatory impacts of an invasive social wasp (*Vespula pensylvanica*) on a largely endemic arthropod fauna in Hawaii. Using a combination of molecular, experimental, and behavioral approaches, we demonstrate (*i*) that yellowjackets consume an astonishing diversity of arthropod resources and depress prey populations in invaded Hawaiian ecosystems and (*ii*) that their impact as predators in this region increases when they shift from small annual colonies to large perennial colonies. Such trait plasticity may influence invasion success and the degree of disruption that invaded ecosystems experience. Moreover, postintroduction phenotypic changes may help invaders to compensate for reductions in adaptive potential resulting from founder events and small population sizes. The dynamic nature of biological invasions necessitates a more quantitative understanding of how postintroduction changes in invader traits affect invasion processes.

biological invasions | predation

Species introductions disrupt ecosystems and can threaten biodiversity (1–3). Predicting the magnitude of these effects, however, has proved difficult (4), in part because invaders and members of the recipient biota may undergo microevolutionary changes or display phenotypic plasticity following introduction events (5–7). For invaders, postintroduction modifications in behavior, morphology, or life history traits may influence invasion success and alter the capacity of these species to disrupt the ecosystems they invade. In this way, trait plasticity may permit individuals to compensate for reduced genetic diversity (8) and the subsequent loss of adaptive potential that is assumed to result from translocation to new environments (9).

Trait plasticity may be especially important for invasive social insects, because small behavioral changes at the individual level can scale up to produce dramatic and unexpected changes at the colony level (e.g., the formation of supercolonies) (10). In this sense, the phenotypic envelope of the social superorganism can encompass a larger set of potential morphotypes compared with that of a typical solitary organism. Here, we quantify the ecological effects of trait plasticity in an omnivorous social insect invader (the western yellowjacket, *Vespula pensylvanica*) that is shaping Hawaiian arthropod assemblages through top-down effects on multiple trophic levels. In part because Hawaii lacks native eusocial insects (11), yellowjacket invasions pose a potentially devastating threat to endemic taxa. This study illustrates how postintroduction shifts in invader traits shape ecological interactions between native and invasive taxa (12) and helps to explain why some species become problematic invaders.

Vespula (yellowjacket wasps) includes some of the world's most ecologically damaging invasive insects (13, 14). Less well known than its congeners (e.g., *V. germanica* and *V. vulgaris*), *V. pensylvanica* became established about 30 years ago in Hawaii (15), where it is now a major pest (16). The invasion of natural areas by western yellowjackets has reduced densities of certain endemic taxa [e.g., Hawaiian picture-wing flies (17)], but the full ecological effects of this invasion remain incompletely studied. Furthermore, shifts in colony structure (18) may amplify ecological effects. Relative to native populations of *V. pensylvanica*, up to 20% of colonies in introduced populations become perennial (19). Plasticity in colony structure commonly occurs in introduced populations despite the likelihood of low effective population sizes associated with eusociality and decreased genetic diversity from founder effects. Perennial *V. pensylvanica* colonies in Hawaii can have orders of magnitude more wasps compared with colonies in the western United States, which are annual and contain a few thousand individuals (20, 21). The largest perennial colony of any *Vespula* species ever reported was a *V. pensylvanica* colony on Maui with nearly 600,000 individuals (21). Shifts in colony structure occur in other *Vespula* introductions, but little is known about the ecological significance of this transition.

We studied western yellowjackets in 2 national parks: Hawaii Volcanoes (HAVO) on Hawaii and Haleakala (HALE) on Maui; both parks support large populations of *V. pensylvanica* and diverse arthropod assemblages. Study sites were located in open *Metrosideros polymorpha* (ohia) woodland between 1,000 and 1,200 m (HAVO) and in subalpine shrubland between 2,500 and 3,000 m (HALE). We used molecular analyses to identify masticated diet items collected from ≈50 returning foragers at each of 10 colonies (5 in HAVO and 5 in HALE). We identified diet items by sequencing the 16S rDNA and COI genes following Kasper et al. (22) and Magnacca and Danforth (23). We extracted DNA from 93% of samples ($n = 465$), 90% of which were identified at least to the family level using a combination of BLAST searches, comparisons with voucher specimens collected on site, and phylogenetic analyses.

Molecular analyses revealed that *V. pensylvanica* exhibits an extraordinarily broad diet on both islands (Fig. 1*A* and Table 1). The yellowjacket diet spans 14 taxonomic orders of invertebrates and vertebrates. *Vespula pensylvanica* collected endemic and introduced taxa in relatively equal numbers (Fig. 1*B*), but orders differed in the proportion of endemic or introduced taxa consumed. Endemic Hawaiian arthropod genera commonly con-

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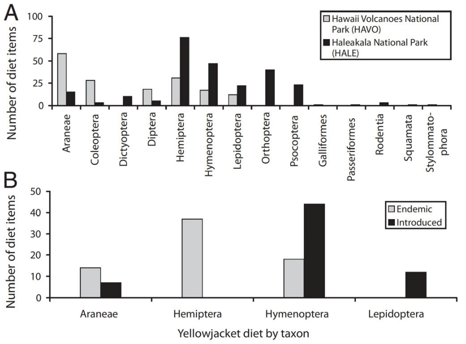

Fig. 1. (*A*) Molecular analysis of 412 diet items collected from foragers in 2 Hawaiian national parks. Invertebrates comprised the majority of the *Vespula* diet; vertebrate samples were scavenged carrion. (*B*) We classified diet items in the 4 most common orders of endemic arthropods at our field sites as endemic to Hawaii or introduced (n = 133 items shown).

sumed by yellowjackets included *Mecaphesa* spiders (Thomisidae), *Limonia* flies (Tipulidae), *Orthotylus* bugs (Miridae), *Laupala* crickets (Gryllidae), and the ecologically important *Hylaeus* bees (Colletidae). Yellowjackets also consumed a diversity of introduced taxa, especially *Asynonychus* weevils (Curculionidae), *Cheiracanthium* spiders (Miturgidae), *Agrotis* moths (Noctuidae), European honey bees, and western yellowjackets [see supporting information (SI)]. These and other abundant introduced arthropods may subsidize *V. pensylvanica* populations above levels that endemic taxa could support. This analysis provides a uniquely comprehensive overview of the yellowjacket diet and shows that *V. pensylvanica* often forages upon small inconspicuous taxa [e.g., barklice (Psocoptera: Psocidae) and planthoppers (Hemiptera: Fulgoroidea)].

The yellowjacket diet consists of items obtained both through predation and scavenging. Controlled and replicated colony removal experiments, however, demonstrate the importance of predation, especially on specific taxa. In pre- and postremoval sampling in natural areas of HAVO and HALE, we measured local spider and caterpillar densities in experimental plots surrounding yellowjacket colonies. Focal taxa were selected based on the results of Gambino (16) and confirmed by DNA sequencing of diet items (Fig. 1*A*). Following *Vespula* colony removal, spider and caterpillar densities rapidly increased in removal plots, whereas densities did not change in control plots (Fig. 2). Comparisons between control and removal plots demonstrate that yellowjackets depressed spider densities by 36% and caterpillar densities by 86%. Given the time scale of density responses and the presence of these same taxa in the yellowjacket diet (Fig. 1 and Table 1), our data unambiguously demonstrate that *V. pensylvanica* exerts considerable predatory pressure on Araneae and Lepidoptera. These experimental results are corroborated by our data set of 412 identified diet items: 68% were classified as fresh-killed prey (see SI for classification criteria).

Ecological effects of yellowjacket predation are greatly magnified when colonies become perennial. Perennial colonies maintained 230% higher activity rates compared with those of annual colonies (57.7 vs. 17.5 entrances/min: t_{45} = 2.76, P = 0.0083). These higher activity rates translated directly into 137% higher rates of prey collection (Fig. 3*A*) and 269% higher rates of nectar foraging (Fig. 3*B*). Elevated foraging rates of perennial colonies led to greater drawdown of prey (Fig. 3*C*) and carbohydrate resources (Fig. 3*D*). Perennial colonies depressed spider densities 30% more than did annual colonies; this disparity presumably reflected higher resource requirements of perennial colonies. We likely underestimated the ecological effects of perenniality because we sampled within 40 m of nests. Because the size of perennial colonies can vastly exceed that of typical annual colonies (18, 19, 21), one would expect the effects of perennial colonies per unit area to be much greater than the summed effects of multiple annual colonies. Foragers from perennial colonies may quickly deplete resources near their nests, forcing them to forage at greater distances; thus, the total predatory effect of a perennial colony will be greater in magnitude close to the nest, and the radius of the depleted zone will be larger compared with that of annual colonies.

Seasonal differences in colony activity further accentuate disparities in resource consumption between annual and perennial colonies (Fig. 3). Perennial colonies forage actively in early spring when the annual colonies are being founded and also remain active later in the season compared with annual colonies (21, 24). In November, when the annual colony cycle is nearing its end, perennial colonies exhibited a mean entrance rate of 94.7 wasps/min, whereas annual colonies exhibited a mean 16.1 incoming wasps/min (t_{16} = 2.53, P = 0.022).

The transition to colony perenniality occurs in multiple *Vespula* species, both in introduced populations (25) and, to a much lesser extent, in native populations (26, 27). In introduced populations, perennial colonies can exceed the sizes of annual colonies by 2 orders of magnitude in the introduced (28, 29) and native ranges (20). In introduced populations, perennial yellowjacket colonies attain sizes of 230,000 [*V. vulgaris* (27)] and 593,489 [*V. pensylvanica* (19)] individuals. Colony perenniality also occurs rarely in the southernmost portions of native ranges; such colonies can attain sizes approaching 55,000–65,000 [*V. pensylvanica* (18, 21)], 115,000 [*V. vulgaris (27*)], and 477,000 [*V. squamosa* (26)] individuals. Although the underlying causes of perenniality are unknown, contributing factors include the longer growing season typical of mild climates (21, 26) and changes in patterns of genetic relatedness within colonies (25).

The large and direct ecological effects caused by perennial colonies may give rise to unexpected indirect effects. For example, predation on prominent endemic pollinators [e.g., *Hylaeus* bees, *Agrotis* moths (Noctuidae)] may disrupt pollination of native plants (11), thus affecting plant fitness. Conceivably, yellowjackets may indirectly benefit some native arthropods through the consumption of nonnative parasitoids (e.g., ichneumonid wasps), predators (e.g., miturgid spiders), and pollinators (e.g., honey bees), all of which negatively interact with native pollinators. Indirect effects likely become stronger in the vicinity of perennial colonies.

Other eusocial Hymenoptera also exhibit postintroduction shifts in colony traits (10, 30, 31). In its introduced range, the multiple-queened form of the red imported fire ant (*Solenopsis invicta*), for example, maintains denser populations and is considered more ecologically disruptive compared with the single-queen form (30). Similarly, the greater size and longevity of perennial *V. pensylvanica* colonies contribute to their enhanced ability to deplete prey and other resources in Hawaii. The large effects detected in this study may have resulted in part because this continental species is invading an island ecosystem. Predators invading insular environments often restructure native assemblages (2, 32); however, most studies have been unable to identify the mechanism(s) underlying native displacement (33). This study demonstrates how an invasive predator affects multiple trophic levels within an arthropod food web directly through predation and indirectly through the exploitation of nectar and prey resources. Because phenotypic plasticity has a strong effect on the evolutionary and ecological success of invaders (8), postintroduction shifts in invader traits may com-

Table 1. Diet of *V. pensylvanica* by order, family, and most commonly occurring genera

Phylum	Order	Family (or suborder)	No. diet items (%)	Common genera in diet
Arthropoda	Araneae		73 (17.7%)	
		Miturgidae*	7 (1.7%)	*Cheiracanthium**
		Philodromidae	2 (0.1%)	
		Salticidae*	3 (0.1%)	*Habronattus*
		Theridiidae*	39 (9.5%)	*Theridion,* *Achaearanea*
		Thomisidae*	21 (5.1%)	*Mecaphesa**
	Coleoptera		31 (7.5%)	
		Coccinellidae	5 (1.2%)	
		Curculionidae	21 (5.1%)	*Asynonychus*
		Tenebrionidae	1 (0.2%)	
	Dictyoptera		10 (2.4%)	
		Blattaria (suborder)	4 (1.0%)	
		Blattidae	5 (1.2%)	
		Mantidae	1 (0.2%)	
	Diptera		23 (5.8%)	
		Calliphoridae	4 (1.0%)	*Calliphora*
		Pipunculidae	3 (0.7%)	
		Syrphidae	1 (0.2%)	
		Tephritidae	2 (0.5%)	
		Tipulidae	10 (2.4%)	*Limonia*
	Hemiptera		107 (26.0%)	
		Cicadellidae	3 (0.7%)	
		Cimicomorpha (infraorder)	17 (4.1%)	
		Clastopteridae	3 (0.7%)	
		Delphacidae	1 (0.2%)	
		Fulgoroidea (superfamily)	17 (4.1%)	
		Lygaeidae	10 (2.4%)	
		Miridae	47 (11.4%)	*Orthotylus*
		Pentatomorpha (infraorder)	6 (1.5%)	
		Psyllidae	3 (0.7%)	
	Hymenoptera		64 (15.5%)	
		Apidae	14 (3.4%)	*Apis*
		Apoidea (suborder)	1 (0.2%)	
		Braconidae	1 (0.2%)	
		Colletidae	18 (4.4%)	*Hylaeus*
		Formicidae	1 (0.2%)	*Paratrechina*
		Ichneumonidae	2 (0.5%)	
		Vespidae	27 (6.6%)	*Vespula*
	Lepidoptera		34 (8.3%)	
		Cosmopterigidae	1 (0.2%)	*Hyposmocoma*
		Geometridae	2 (0.5%)	
		Noctuidae	11 (2.7%)	*Agrotis*
		Papilionidae	1 (0.2%)	
		Tortricidae	8 (1.9%)	
	Orthoptera		40 (9.7%)	
		Acrididae	1 (0.2%)	
		Gryllidae	19 (4.6%)	*Laupala*
		Tettigoniidae	20 (4.9%)	
	Psocoptera		23 (5.6%)	
		Philotarsidae	1 (0.2%)	
		Psocidae	22 (4.9%)	*Ptycta*
Chordata	Galliformes		1 (0.2%)	
		Phasianidae	1 (0.2%)	*Alectoris*
	Passeriformes		1 (0.2%)	
	Rodentia		3 (0.7%)	
		Muridae	3 (0.7%)	*Rattus*
	Squamata		1 (0.2%)	
		Gekkonidae	1 (0.2%)	*Hemidactylus*
Mollusca	Stylommatophora		1 (0.2%)	
		Agriolimacidae	1 (0.2%)	*Deroceras*

Taxonomic groupings reflect highest resolution possible for each diet item.

*Taxon was present in vegetation sampling in removal experiments.

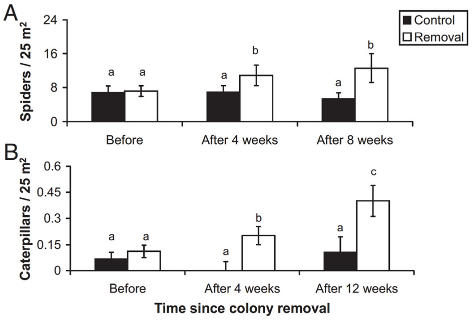

Fig. 2. (*A*) Mean spider densities increased after *Vespula* colony removal in treatment plots ($n = 18$) compared with densities in control plots ($n = 12$) in both parks. Repeated-measures MANOVA indicated significant effects of time since removal ($F_{2,22} = 3.49$, $P = 0.04$) and treatment ($F_{1,23} = 5.86$, $P = 0.024$). Different letters indicate significance ($P < 0.05$) from posthoc *t* tests. (*B*) In both parks, mean caterpillar densities increased in treatment plots ($n = 18$) after yellowjacket removal compared with control plots ($n = 12$). Repeated-measures MANOVA indicated significant effects of time since removal ($F_{2,25} = 3.63$, $P = 0.04$) and treatment ($F_{1,26} = 4.46$, $P = 0.04$). Letters indicate patterns of significance as in *A*.

pensate in part for the negative effects resulting from reduced genetic diversity. Given the inherently nonstatic nature of species introductions, disciplines from invasion ecology to evolutionary biology will benefit from a wider appreciation of how trait plasticity affects invasion processes.

Materials and Methods

Characterization of Yellowjacket Diet. In September 2006 and 2007, we collected diet items from returning foragers at each of 5 colonies in HAVO and 5 colonies in HALE. In addition, we collected voucher specimens of commonly occurring and putative prey taxa (Araneae, Hemiptera, and Hymenoptera) from study sites at each park.

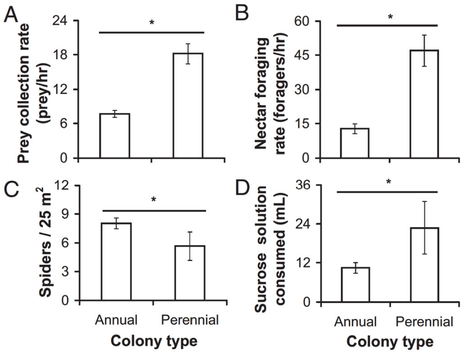

Fig. 3. Compared with annual yellowjacket colonies, perennial colonies exhibited higher rates of prey foraging ($t_{28} = 2.61$, $P = 0.014$) (*A*) and nectar foraging ($t_{21} = 4.79$, $P < 0.0001$) (*B*). Higher foraging rates translated into greater resource depletion: mean spider densities were lower in plots centered on perennial yellowjacket colonies compared with plots centered on annual yellowjacket colonies (effect of colony type: $F_{1,85} = 5.04$, $P = 0.022$) (*C*), and perennial colonies collected more sucrose solution from feeders compared with annual colonies ($t_{10} = 2.19$; $P = 0.027$, 1-tailed) (*D*). *, $P < 0.05$.

DNA was extracted using the QIAamp DNA Micro Kit (Qiagen). Diet samples were PCR-amplified using *LRN13398* and *LRJ12887* primers (22) to amplify 500–650 bp of the mitochondrial 16S rDNA gene. For reaction conditions, refer to SI. Purified PCR products were sequenced, and diet items were initially identified using BLAST searches. BLAST scores >400 and percent match >95% were considered putative matches. In 86% of these cases, we were able to resolve identification to the family level, and in 45%, we were able to resolve identification to the subfamily or genus level with the 16S sequence alone. For the remaining 3% of diet items, we also sequenced the COI gene using the primers (*C1-J-2183* and *TL2-N-3014*, *C1-J2777* and a modified *C2-N-3389*) and conditions outlined in the article by Magnacca and Danforth (23). For vouchers, we sequenced the 16S and COI genes as described for diet items. Phylogenetic analyses were used to confirm molecular identifications, adapting the methods of Kasper et al. (22).

Yellowjacket Colony Removal. We conducted experiments at 41 colonies at HAVO (10 experiments in 2005, 14 experiments in 2006, and 17 experiments in 2007) and 21 colonies at HALE (2 experiments in 2005, 6 experiments in 2006, and 13 experiments in 2007). During 2005–2007 in HAVO and HALE, we sampled arthropod densities before and after the removal of *V. pensylvanica* colonies at removal and control sites. Colonies were randomly assigned to treatment: yellowjacket removal ($n = 37$) or control (*V. pensylvanica* continuously present, $n = 25$). Sampling focused on the collection of moth larvae and spiders, which are common prey of *V. pensylvanica* (16). Centered on each *Vespula* nest, we established a 40-m × 40-m plot, which was divided into 64 subplots 5-m × 5-m in size. Within each sampling period, we randomly selected 10 subplots for sampling at each nest. We used beating techniques to sample Lepidoptera (34) and foliage-dwelling Araneae in every bush with a volume >0.002 m^3 (2 L), and every tree >0.02 m in diameter was sampled from 0.1 to 1.5 m above the ground (35).

Statistical Analyses. Overall yellowjacket removal effects on spiders and caterpillars were analyzed with repeated-measures multiple analysis of variance (MANOVA), with year, park, and treatment as the main factors; time as the within-subjects factor; and interactions between year, park, and treatment included. Posthoc *t* tests were applied for comparison of treatments when treatment was significant in MANOVA. For each MANOVA, we considered all factors fixed. Effects with $P < 0.05$ were regarded as statistically significant.

Resource Exploitation: Annual vs. Perennial Colonies. A nest was classified as perennial if (*i*) it had been observed in previous years or (*ii*) it exhibited nest structures (e.g., multiple entrances, extensive nest structure) early in the season when most annual colonies are being founded. At each nest, we determined activity and estimated colony size from entrance and exit rates following a protocol adapted from Malham et al. (36). To assess resource exploitation, we collected incoming foragers, removed any items carried by these foragers, and induced regurgitation by abdominal palpation. Thus, we determined whether foragers were carrying nectar, water, carton, diet items, or nothing. We classified wasps as nectar or water foragers only if more than 5 μL of liquid was regurgitated during palpation. Nectar was easily distinguished from water based on color (e.g., yellow or pink) and greater viscosity. Foraging rates were calculated based on the number of returning wasps collecting each resource per hour.

Next, we measured the volume of sucrose solution that wasp colonies collected from artificial feeders placed 10 m from the nest entrance at midday. After correcting for evaporation, we calculated the total sucrose volumes exploited over the time interval the feeder was available. No nontarget insects visited the sucrose feeders.

Statistical Analyses. We performed 2-sample *t* tests with data from 47 nests to examine the effect of colony type (annual or perennial) on entrance and exit rates. Using 2-sample *t* tests, we analyzed prey and nectar foraging rates between colony types. Differences in resource exploitation were examined using a multiway ANOVA on spider densities (mean abundance per 5-m × 5-m subplot) from vegetation beating around control colonies as described previously, with colony type, number of subplots sampled, season, park, and year treated as fixed effects. Using a 2-sample *t* test, we then analyzed the total volume of sucrose solution collected by wasps with colony type as the grouping factor.

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

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 (*Vespula 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. Displacemzent of native solitary Hymenoptera by yellowjackets may be heightened by the ability of *V. pensylvanica* to prey upon and scavenge honeybees and to rob their honey stores—resources unavailable to endemic bees and wasps because of strong niche conservatism. 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.

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 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 resulting 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 (Cane et al. 2006; Goulson 2003), native solitary bees and wasps that colonized and radiated in Hawaii may be highly susceptible to social invaders. Despite that social insects devastate island ecosystems (Beggs 2001; Krushelnycky and Gillespie 2008; O'Dowd et al. 2003), little is known about interactions involving native solitary Hymenoptera and their introduced social counterparts. Because social bees and wasps tend to be ecologically generalists, unlike many solitary species (Biesmeijer et al. 2005; Cane et al. 2006; Heithaus 1979; Itino 1992), a single introduction of a social invader in Hawaii may affect a wide range of native solitary Hymenoptera.

Here, 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 play important ecological roles as pollinators and predators respectively. Combining behavioral, ecological and genetic approaches, we (1) examine how *Vespula pensylvanica* 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 (HAVO) and subalpine shrublands between 2500 and 3000 m (HALE).

Two of the largest Hawaiian insect radiations occur in *Hylaeus* (Colletidae: Hylaeinae) and *Nesodyneryus* (Vespidae: Eumeninae) (Magnacca and Danforth 2007), which together comprise over 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). 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). Like other potter wasps, *Nesodynerus* mass provisions individual eggs in separate cells within a nest and provides no maternal care. As a generalist scavenging predator, the niche of *V. pensylvanica* extensively overlaps with those of *Hylaeus* and *Nesodynerus*, which by comparison exhibit strong niche conservatism. At our sites, the most common native species were *H. difficilis, H. laetus, H. nivicola, N. nubicola* and *N. sociabilis.*

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 eight sites in HAVO (n = 4) and in HALE (n = 4). 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* (honeybees). All transects were more than 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.*, Sa. haleakalae, Sophora chrysophylla* and *St. tameiameiae* in HALE. Flowering vegetation with volumes > 0.01 m^3 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 examine mean numbers of plants occupied and also their mean abundance 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).

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 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 *Vespula* nest, we established a 40 m X 40 m experimental plot, which was divided into 10 m X 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 approximately 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). PCR reactions were performed in a 15-μL volume on Eppendorf Mastercycler Gradient thermal cyclers. We used 2 μL of template DNA, 10X Taq Buffer (Eppendorf), 1.5 μL of 1.5mM $MgCl_2$, 1.5 μL of 10X BSA, 0.3 μL of 10μM dNTPs, 0.6 μL of each 10μM primer, and 0.2 μL 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°C - 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 searches, where BLAST scores > 400 and percent match > 95% were considered putative matches.

Mechanisms underlying displacement: predation versus 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 honeybees. We used post-mortem thoracic muscle pH to distinguish fresh-killed prey from decaying corpses (Wilson et al. Submitted). After death, pH of animal tissue decreases because muscle remains metabolically active and continues to produce lactic acid through irreversible anaerobic glycolysis (Lindahl et al. 2006). As lactic acid accumulates, pH drops until glycolytic enzymes become inactivated (Lawrie and Ledward 2006). Because muscle pH responds to stress and 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). 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. Submitted).

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. (Wilson et al. Submitted). 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. (Wilson et al. Submitted).

As an additional measure of the relative importance of predation versus 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 ≈ 40 m x 40 m plots, which lacked ants and other common diurnal scavengers. In three plots, we interspersed 10 honeybees and 10 yellowjackets, and in two plots, we distributed 15 honeybees and 10 yellow-faced bees. At each plot, we observed which corpses were scavenged by *V.*

pensylvanica. Data were pooled across homogenous trials (*Apis* versus *Vespula*: $X^2_2 = 2.92$, $p = 0.23$; *Apis* versus *Hylaeus*: $X^2_1 = 2.03$, $p = 0.15$). 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 honeybees 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 *Vespula* colonies (six trials each) indicated wasps do not distinguish bees killed in ethanol from those killed in water ($X^2_4 = 4.67$, $p = 0.32$). 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 honeybees.

At six colonies, we conducted an additional five trials in which we offered wasps 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 honeybees.

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 the diet of *Nesodynerus* wasps.

Each trapnest consisted of 3.8 cm X 3.8 cm X 10 cm piece of white pine dipped in paraffin wax. On one face, nine holes (diameter: 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. In October 2006-2008, traps were laid in the following areas: (1) sites where yellowjackets were absent or had been removed more than eight months previously (n = 400 traps), (2) sites where yellowjackets had been removed within two months (n = 108 traps), and (3) sites where yellowjacket nests were present (n = 127 traps). Trap nests were collected in spring (2007-2009). In April 2008, we laid an additional 29 traps, which were collected and dissected in August 2008. Trap occupancy was analyzed by plot treatment using a G-test.

To determine whether *Vespula* 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 LCO1490 and HCO2198 (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 *Vespula* 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. *Apis, Nesodynerus* and *Hylaeus* 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 *Hylaeus*: $F_{2,18} = 6.35$, $p = 0.022$). 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*: $F_{1,2} = 4.92$, $p = 0.038$; and *Hylaeus*: $F_{1,21} = 4.46$, $p = 0.040$).

Effect of *Vespula* removal on endemic Hymenoptera

Removal experiments demonstrated that yellowjackets exclude both *Hylaeus* and *Nesodynerus* (Fig. 2). *Hylaeus* 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 after removal ($F_{2,26} = 4.03$, $p = 0.029$) 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 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, *Hylaeus* and introduced *Apis mellifera* comprised 27% ($n = 18$) and 23% ($n = 14$)

respectively. Three species of *Hylaeus* 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 diet included braconid wasps (Braconidae) (*n* = 1), *Paratrechina bourbonica* (Formicidae) (*n* = 1), *Spilichneumon superbus* (Ichneumonid) (*n* = 2), and *V. pensylvanica* (*n* = 27).

Time of day and ambient temperature influenced the prevalence of Hymenoptera in the yellowjacket diet. *Hylaeus* 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 versus scavenging

Thoracic pH measurements indicate that while yellowjackets prey upon *Hylaeus, V. pensylvanica* both preys upon and scavenges *Apis.* We compared thoracic muscle pH from the diet items (*Apis*: *n* = 10, *Hylaeus*: *n* = 3) to standards of stressed and non-stressed bees; data for *Apis* standards originate from Wilson *et al.* (Wilson et al. Submitted). In Fig. 3, the low pH measurements of all three *Hylaeus* and those of six honeybees 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 *Hylaeus* but obtain *Apis* in part 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 honeybees.

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 = 9.14E^{-7}).

In addition to preying upon and scavenging honeybees in the field, yellowjackets rob honeybee 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, honeybees 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 items 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 *V. 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. *M. polymorpha*, *St. tameiameiae*) as *V. pensylvanica*, native bees and wasps avoid visiting plants that yellowjackets occupy. 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 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 sufficiently heat up to avoid attack. Consistent with this hypothesis, we collected *Hylaeus* from *V. pensylvanica* foragers predominantly in cool ambient temperatures. Under such environmental conditions, *Hylaeus* appear sluggish and will bask in the sun (E. Wilson, pers. obs.); this may be in part to utilize solar radiation to warm flight muscles (Larsson 1991; Stone et al. 1995; Stone and Willmer 1989). 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. Solitary wasps were also displaced but are not yellowjacket prey. Exploitative competition between 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 honeybees despite that a single *Apis* colony can harvest 10 – 60 kg yr^{-1} of pollen (Goulson 2003) and 17 – 414 kg yr^{-1} of nectar (Southwick and Pimentel 1981). Likewise, interference competition at nectar resources between honey bees and native solitary Hymenoptera was never observed. Taken together, these results indicate that yellow-faced bees and solitary wasps behaviorally avoid *V. pensylvanica*, a potential defense strategy against yellowjackets. 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. Interspecific competition seems likely given that invasive *Vespula* 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.

Honeybees as a resource subsidy for *Vespula*

Several lines of evidence suggest that honeybees play an important but underappreciated role in mediating interactions between native arthropods and invasive yellowjackets. *Vespula pensylvanica* often nests in proximity to perennial *Apis* colonies. At our study sites, more than 65% of *V. pensylvanica* colonies were within 600 m of at least one well-established honeybee colony and no *Vespula* colony was more than 1 km from a honeybee nest. Western yellowjackets mostly forage within 600 m of their nest (Akre et al. 1975) and molecular diet analyses reveal that yellowjackets commonly forage on honeybees (Wilson et al. 2009). Muscle pH analysis, scavenging plots and behavioral choice tests, all indicate that yellowjackets collect honeybees through a combination of predation and scavenging. Thus, honeybee colonies with their large, perennial workforce provide a reliable and abundant supply of invertebrate prey, carrion (Coelho and Hoagland 1995; Visscher 1983), and honey (De Jong 1990).

Honeybee-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 honeybee carrion. Moreover, *Nesodynerus* were never observed visiting or robbing honeybee colonies. For these reasons, the aggregated and constant production of protein and carbohydrate resources in honeybee 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 *Hylaeus* and *Nesodynerus* appear to exhibit substantial intra-generic 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: *Hylaeus* is displaced through a combination of behavioral avoidance and predation, whereas *Nesodyneus* must compete 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 honeybee, 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.

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Table 1. Scavenging of *Apis mellifera, Hylaeus* spp. and *Vespula pensylvanica* by *V. pensylvanica. Apis mellifera* and *V. pensylvanica* are scavenged equally, whereas all *Hylaeus* remain uncollected. ** $p < 0.0001$

Hymenopteran taxon	Number presented	Number scavenged	Proportion scavenged	X^2 value	Standardized Residuals
Apis mellifera	30	26	0.87	0.074	-0.19
Vespula pensylvanica	30	28	0.93		0.19
A. mellifera	30	25	0.83	25 **	3.54
Hylaeus spp.	20	0	0.00		-3.54

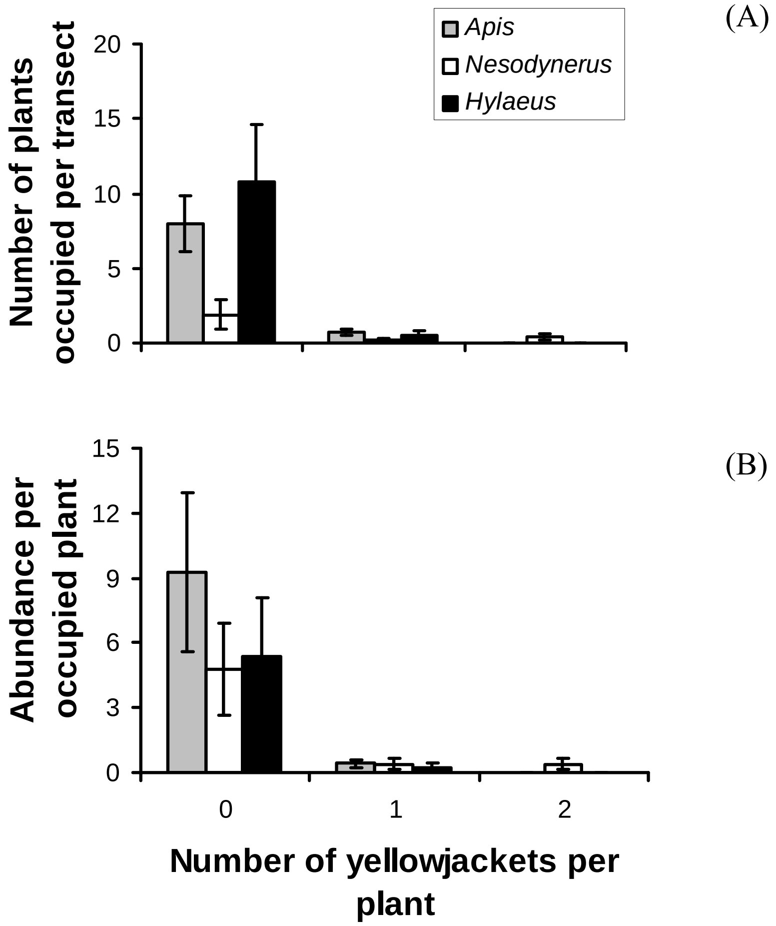

Figure 1. *Apis, Nesodynerus,* and *Hylaeus* abundances on floral resources versus yellowjacket density. Mean (± SE) **(A)** number of plants occupied per transect, and **(B)** abundance per occupied plant as a function of yellowjacket density per plant.

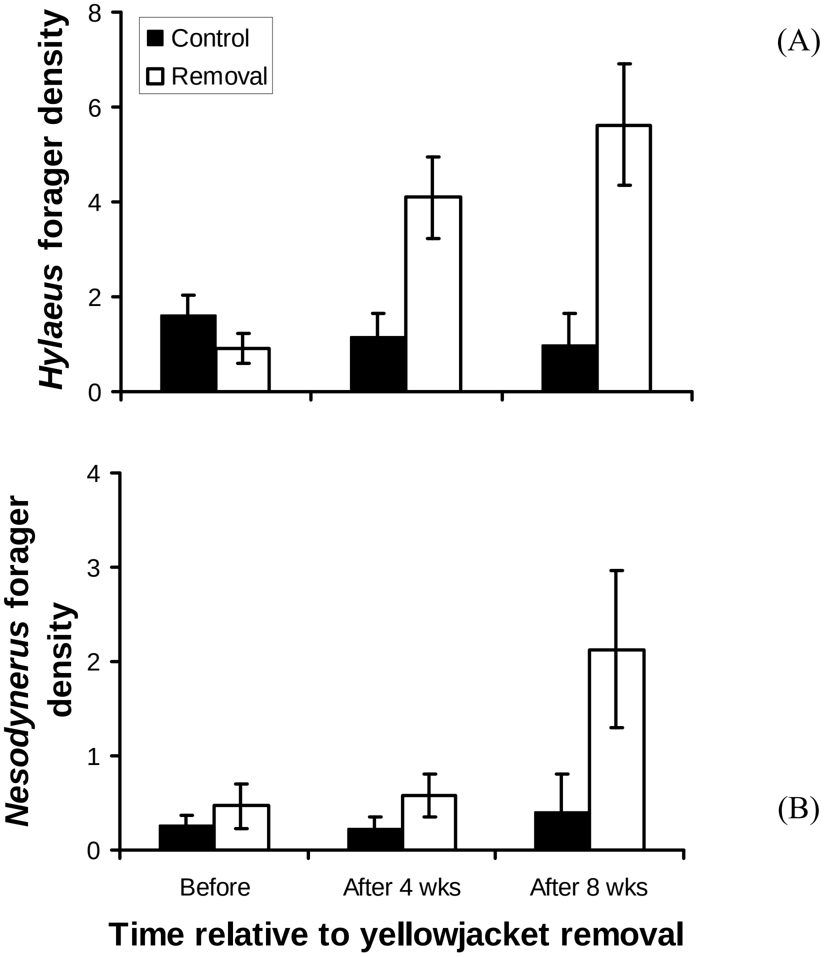

Figure 2. (A) *Hylaeus* densities (mean ± SE) before and after *Vespula* colony removal ($n = 27$ removal plots and 23 control plots). Different letters indicate significance from post-hoc t-tests. **(B)** *Nesodynerus* densities (mean ± SE) before and after *Vespula* colony removal ($n = 27$ removal plots and 23 control plots). Letters indicate patterns of significance as in (A).

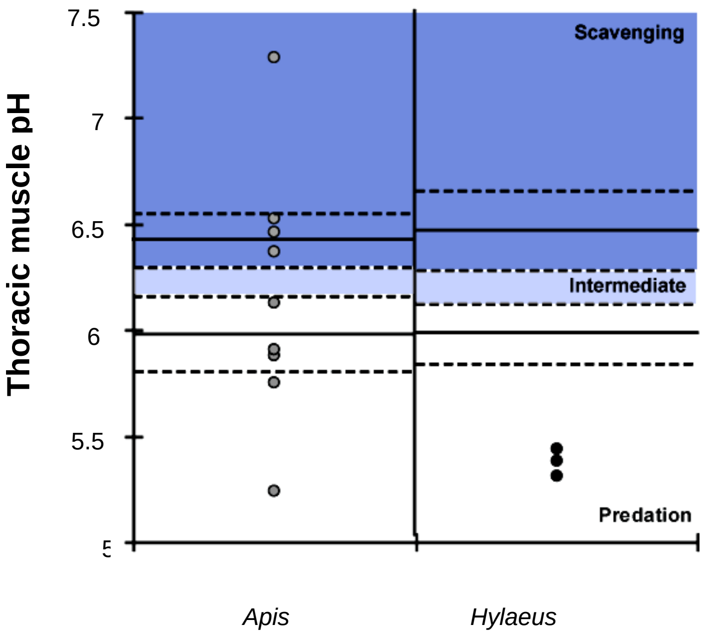

Figure 3. Diet items classified as carrion or prey based on pH measurements. Mean pH (solid lines) ± SD (dashed lines) by species and putative ecological mechanism. Dark blue shaded area encompasses scavenging and control pH measurements. White area encompasses predation and stress pH measurements. Light blue shaded area represents pH range between predation + SD and scavenging – SD.

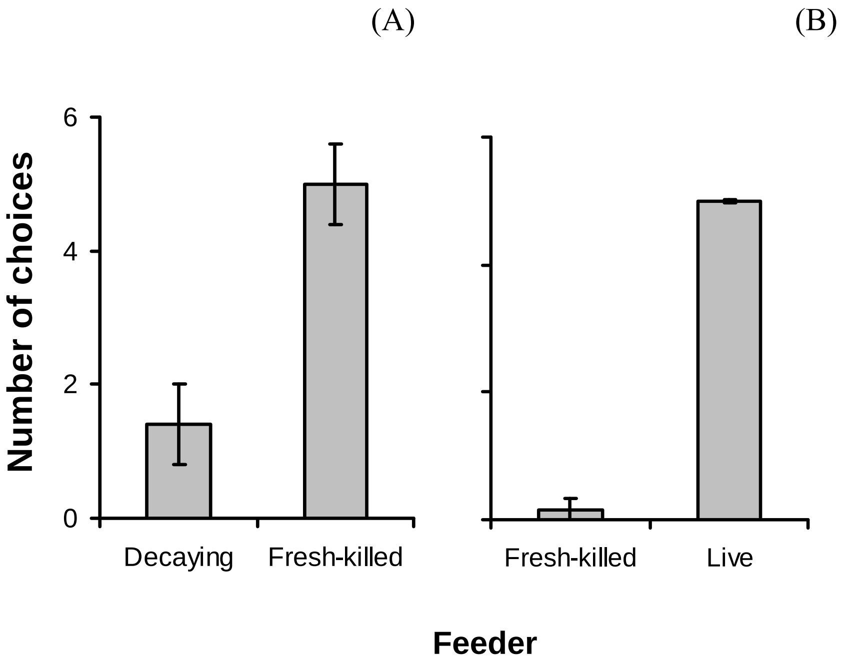

Figure 4. Choice tests of yellowjackets between **(A)** decaying and fresh-killed honeybees, and **(B)** fresh-killed and live honeybees.

Context-dependent recruitment behavior in the western yellowjacket

ABSTRACT

Eusocial vespid wasps remain the only eusocial insects where communication of resource information among nestmates is unresolved. We present evidence that yellowjacket foraging strategies depend on the assessment of resource size and persistence. The context dependency of foraging behavior by *Vespula pensylvanica* provides a likely explanation for the inconsistent reports of vespid wasp recruitment. Furthermore, life history traits influence foraging. Foragers from annual colonies routinely patrol near the nest and exhibit increased bait visitation in response to the return of successful foragers, whereas visitation by foragers of perennial colonies does not differ from discovery rates of naïve wasps. These behavioral disparities provide insight into how foraging strategies and search patterns change with colony size and longevity. In a series of experiments investigating the effects of bait dispersion and visual cues of conspecifics, the perception of demand by yellowjackets strongly affected subsequent foraging decisions. When competition for resources was assessed to be high, *V. pensylvanica* foragers quickly exploited the bait closest to their colony regardless of occupation by other wasps; however, foragers preferred visiting unoccupied baits when competition was perceived to be low. Context dependency in foraging appears widespread in the Vespidae, where recruitment behaviors change with urbanization and perceived resource competition. Such plastic foraging strategies may contribute to the success of some invasive vespid wasps.

INTRODUCTION

Social insects exploit carbohydrate and protein resources that are unpredictable in availability and quality (Anderson and Ratnieks 1999; Dornhaus et al. 2006). For such colony-level foraging to be efficient, colonies must achieve a high degree of organization and communication (Wilson 1965). One of the most sophisticated examples of social insect communication is recruitment, which is defined by Wilson (1971) as any mode of communication that brings nestmates to a place where work is required. Raveret-Richter (2000) refined this definition in the context of foraging and distinguished *nest-based* from *field-based* mechanisms. Recruitment at the *nest* occurs when a single forager communicates information to nestmates about available food resources, resulting in foragers subsequently departing the nest in search of a specific resource (Jeanne et al. 1995). Recruitment in the *field* occurs when incoming foragers are drawn to a food resource due to cues at the resource. Cues can encompass visual or odor information emanating from the resource, feeding wasps, or both. Local enhancement, a common form of recruitment in the *field*, occurs when foragers are attracted to aggregations of feeding conspecifics and thus distribute themselves nonrandomly at resources (Thorpe 1963).

Ecological advantages of recruitment are obvious: colonies can more quickly exploit aggregated resources and immediately respond to transient resources. However, sophisticated communication systems are costly to develop and may be adaptive only under particular social, behavioral and ecological constraints (Dornhaus et al. 2006). For instance, there may be a threshold colony size below which recruitment is not cost effective (Beekman et al. 2001). Moreover, the competitive environment may influence how communication evolves. Recruitment may be maladaptive for species that evolved with other species that eavesdrop and exploit communication systems (Nieh et al. 2004).

Primitive forms of recruitment occur in some vespid wasps (D'Adamo et al. 2003; Hrncir et al. 2007; Overmyer and Jeanne 1998). Given that wasps require carbohydrates and invertebrate prey, they tend to forage in environments with a few large resources and many small ones; such environments may select for opportunistic foraging strategies as opposed to recruitment (Richter 2000). Although highly-developed communication systems are likely absent in vespids, these wasps may display flexible behaviors in which individuals can learn to associate resources either with successful foraging sites (Lozada and D'Adamo 2006) or develop search images based on gustatory and olfactory information gathered from nestmates (Jandt and Jeanne 2005; Jeanne and Taylor 2009; Overmyer and Jeanne 1998).

One potential mechanism for social wasp recruitment is local enhancement, where foragers are attracted to the visual and odor cues of aggregations of feeding wasps (Slaa et al. 2003). Recent studies describe local enhancement in several vespids, including some of the most problematic invasive wasps (*e.g. Vespula germanica* and *V. vulgaris*) (D'Adamo and Lozada 2005; D'Adamo et al. 2003). By guiding new foragers to resources and by decreasing search time, local enhancement can lead to increased foraging efficiency.

Using a combination of experimental and observational approaches, we investigated the context dependency of recruitment to protein resources in the western yellowjacket, *Vespula pensylvanica*. The ability to convey information about resources to nestmates would allow the western yellowjacket to better exploit resources and to increase the number of workers foraging in response to food rewards. This study aims to demonstrate how yellowjackets forage in different contexts and to resolve inconsistent reports of local enhancement in the Vespidae.

MATERIALS AND METHODS

All experiments were performed along Hilina Pali Road and Crater Rim Trail (elevation 995 - 1160 m) in Hawaii Volcanoes National Park (HAVO). This park supports locally abundant populations of invasive *Vespula pensylvanica* that exhibit both annual and perennial colony types (Wilson et al. 2009). Perennial colonies can have orders of magnitude more wasps compared to annual colonies (Plunkett et al. 1989), which contain on average a few thousand individuals (Visscher and Vetter 2003). All experiments were carried out at isolated colonies during August-September 2007 (n = 6 colonies) and 2008 (n = 8 colonies), such that there were no nests within 100 m of each experimental colony.

Recruitment to protein

To test the hypothesis that *V. pensylvanica* recruits to protein, we examined how the experience level of foragers affects foraging patterns. At each of six colonies, we observed visitation to protein baits (14.8 cm^3 canned chicken) located 10 m upwind from each focal colony. We conducted two 60-min trials at each colony: (1) ‘naïve only’ where visitation was limited to new foragers arriving at the bait, and (2) ‘unrestricted’ where all incoming foragers were allowed to visit the bait. The order of the trial types was randomized for each colony and no colony participated in more than one trial per day. A forager is defined as a wasp that landed on and began to collect chicken. After an individual started to process the bait in ‘naïve only’ trials, she was captured and retained until the end of the trial. Thus, we prevented any communication about the food resource at the nest. For ‘naïve only’ trials, we noted the time of each forager’s visit. For ‘unrestricted’ trials, each forager was uniquely marked on the thorax and abdomen using enamel paint while the wasp collected bait (Hrncir et al. 2007). Marking *in situ* does not appear to disturb foragers because they continue to process chicken during and after being marked (Eckles et al. 2008). In this treatment, incoming wasps foraged freely on the bait; the time of each visit and the identity of each forager were noted.

We used paired t-tests to assess differences between trial types for (1) the numbers of foragers, and (2) rates of new forager arrival. Because two of the six colonies were perennial colonies, we also assessed the effect of colony type (annual or perennial) on the difference in rates of new forager arrival between trial types. For each time interval (n = 30), we calculated the difference in rates of new foragers arriving between ‘unrestricted’ and ‘naïve only’ trials by colony and used a two-sample t-test to examine the effect of colony type.

Effect of protein bait dispersion on local enhancement

Using isolated colonies and thus restricting bait visitation to nestmates, we examined how forager responses to conspecifics were influenced by the dispersion (clumped or dispersed) of a constant volume of bait (30 cm^3) in an artificial patch. We focused on how visual cues of conspecifics affect visitation to protein sources, because for scavenging predators the odor of carrion or meat baits may overpower any chemical cues emanating from foragers at a food source (Hrncir et al. 2007). Ten m upwind of each focal colony (n = 8 colonies), we placed a feeder station consisting of four Petri dishes (30-mm diameter) equally spaced at 12-cm intervals. Two feeders were occupied by 10 dead wasps, posed in aggregations around the Petri dishes. The feeder order was randomized for each trial to avoid spatial bias. Odors of wasp corpses were removed through extractions with hexane (Richter and Tisch 1999). The remaining two feeders were devoid of posed wasps (Fig. 1).

For the clumped treatment, two feeders (one occupied feeder and one unoccupied feeder) provided 15 cm^3 of canned chicken as (Fig. 1a). Dishes on unrewarding feeders contained cotton to provide visual cues of the feeding station, baits and aggregating wasps but no food. For the dispersed treatment, all four feeders contained 7.5 cm^3 chicken bait (Fig. 1b) although two feeders were devoid of wasp dummies, and two feeders had 10 wasp dummies each. In all experiments (clumped and dispersed), a total of 30 cm^3 chicken was available to control for bait odor among trials. During 60-min trials, we observed which feeders incoming wasps visited and immediately removed foragers once they had chosen a feeder. In this way, no live foragers were present at a feeder when a new forager arrived. To analyze the effect of conspecifics in different patches, we used t-tests to compare the number of foragers at each feeder within the treatment. Using paired t-tests, we analyzed the effect of bait dispersion on the mean difference in feeder visitation between the rewarded unoccupied and rewarded occupied feeders. Unrewarded feeders in the clumped treatment were excluded from analyses because they received no visits.

Effect of wasp density on local enhancement

Because visitation may increase with dummy wasp density (D'Adamo and Lozada 2005; Fowler 1992), we provided incoming wasps with a choice of four feeders, each stocked with 7.4 cm^3 chicken bait, and varied the density of wasp dummies at each feeder

(0, 5, 10 or 20 dummies). Experiments were conducted 10 m upwind of each of the five focal colonies. For each colony, we conducted three 60-min trials and observed each incoming wasp's choice of feeder. All wasps were removed once they selected a feeder. We analyzed forager visitation with a three-way ANOVA, in which dummy density and feeder position were fixed effects and colony was a random effect. Significant fixed effects were subsequently analyzed with Tukey HSD tests.

Trends from other studies on vespid foraging

To develop a more comprehensive understanding of the context dependency of social wasp foraging, we compiled 12 published studies on vespid wasp recruitment that examined local enhancement. The following data were summarized from each study: species, range, habitat, season, native status, number of colonies participating in a single trial, recruitment behavior, degree of bait dispersion, number of feeders occupied by wasps, dummy type, bait type, feeding behavior (predatory or scavenging), and heterospecific visitors. These data were examined for patterns associated with foraging behavior; Table 1 summarizes the most relevant attributes. Using a log-linear analysis for frequency tables, we examined relationships among foraging behavior (local enhancement, no preference, or local inhibition), habitat and native status (native or introduced). A second log-linear analysis was used to investigate associations among foraging behavior, native status, and number of participating colonies.

RESULTS

Recruitment to protein

Vespula pensylvanica clearly exhibited recruitment to protein. During trials, twice as many wasps foraged on chicken baits when all foragers were allowed to return (mean

± SE: 27 ± 4.5 wasps) compared to when visitation was restricted to naïve wasps (mean ± SE: 13.7 ± 2.9 wasps) (Fig 2a: $t_{12} = 2.53$, $p = 0.026$). This discrepancy resulted from a higher rate of new foragers arriving in unrestricted trials (0.42 new foragers/min) compared to trials with only naïve foragers (0.19 new foragers/min) (Fig 3a: $t_{12} = 2.76$, $p = 0.020$). While all colonies demonstrated their highest bait visitation in 'unrestricted' trials, forager accumulation differed between annual and perennial colonies (Fig 3b). Annual colonies exhibited up to an eight-fold greater increase between treatments compared to perennial colonies ($t_{29} = 2.51$, $p = 0.018$).

Rates of accumulation did not increase with colony activity and size. Perennial colonies exhibited higher entrance rates (wasps entering the nest/min) compared to annual colonies ($t_{12} = 3.38$, $p = 0.0054$). Using these traffic rates to estimate colony size (Malham et al. 1991), annual colonies in this study (n = 4 colonies) had 580 ± 71 workers (mean ± SE) whereas perennial colonies had 63,016 ± 47,000 workers (n = 2 colonies).

Effect of protein bait dispersion on local enhancement

Foraging behavior changed with dispersion of within-patch rewards. When wasps encountered a clumped patch, foragers only visited rewarded baits and visitation was split between the rewarded unoccupied (51%) and rewarded occupied (49%) baits (Fig 4a; $t_7 = 0.10$, $p = 0.92$). However, when patch rewards were more dispersed, foragers visited unoccupied feeders 71% of the time (Fig. 4a; $t_7 = 2.56$, $p = 0.037$). This local inhibition behavior results from an active avoidance of conspecifics (Fig. 4b; $t_{14} = 2.46$, $p = 0.028$).

Effect of wasp density on local enhancement

Avoidance of occupied feeders occurred only at low dummy densities. When the number of dummies increased in a dispersed four-feeder patch, incoming foragers visited the first bait encountered (Fig 5; $F_{3,39} = 3.86$, $p = 0.016$). There was no effect of trial ($F_{2,8} = 0.59$, $p = 0.58$) or the density of wasp dummies on bait visitation ($F_{3,39} = 1.16$, $p = 0.34$; no dummies: 18 ± 4.51 wasps; five dummies: 22.67 ± 5.40 wasps; 10 dummies: 19 ± 6.88 wasps; and 20 dummies: 25.33 ± 5.40 wasps).

Trends from other studies on vespid foraging

We compared experimental designs and findings across published studies of vespid local enhancement. Table 1 summarizes the results of 13 studies (including this one), which differ in study species, nestmate status among interacting wasps, bait type, dummies used, location and time of year. Examination of bait visitation data revealed several patterns. Log-linear analysis of the effect of native status and environment (urban, natural areas, etc.) on local enhancement indicates that (1) introduced vespids are more likely to be studied in urban/suburban areas than in other environments ($G^2 = 8.6$, df = 2, $p = 0.014$), and (2) local enhancement is more often observed in urban/suburban habitats than in natural areas, while local inhibition and no preference are most often observed in non-urban habitats ($G^2 = 12.28$, df = 4, $p = 0.015$).

Further analysis reveals that introduced and native populations of vespid wasps exhibit different behaviors in response to foraging with non-nestmates ($G^2 = 19.46$, df = 7, $p = 0.0069$). When multiple colonies participated in a single trial, local enhancement was most common in the introduced populations compared to the native range ($G^2 = 14.24$, df = 4, $p = 0.0066$). In fact, when multiple colonies within native populations participate in the same experiment, only local inhibition and no preference have been observed. These observations contrast with studies examining foragers from a single colony, where wasps encountered at the bait are likely nestmates ($G^2 = 11.8$, df = 4, p =

0.019). In fact, vespids exhibited no preference two-to-one over local inhibition and no local enhancement when visitation is restricted to nestmates. Polistines and Vespinines appear similarly influenced by environment and presence of non-nestmate conspecifics ($G^2 = 13.14$, df = 16, p = 0.10).

DISCUSSION

In the first explicit test of recruitment via local enhancement in *V. pensylvanica,* we show that the western yellowjacket exhibits moderate levels of recruitment and that local enhancement is not the mechanism. The results of this study underscore the importance of context dependency and plasticity of vespid foraging behavior. Successful *V. pensylvanica* foragers may activate nestmates to forage by passive communication about the presence of food in the environment, similar to the odor-only mechanisms used by bumblebees (Dornhaus and Chittka 2001), honeybees (Sherman and Visscher 2002), stingless bees (Esch et al. 1965) and *Polybia* wasps (Hrncir et al. 2007). The higher rate of newcomers to baits in “unrestricted” trials compared to “naïve only” demonstrates that some stimulation of foraging occurs when a wasp carrying protein returns to the nest. This agrees with reports that *Vespula* search for resources with the odor of food brought back to the nest (Jandt and Jeanne 2005).

The use of field-based recruitment has been difficult to generalize in social wasps. In this study, naïve *V. pensylvanica* avoids conspecifics (local inhibition) at dispersed baits. These results contrast with the clumped patch and the dummy density dependence experiments, in which naïve yellowjackets visited the first bait they encountered. Hence, *V. pensylvanica* shows local inhibition when there are multiple open (unoccupied) baits and exhibit no avoidance when there is only one open bait. Such behavior is consistent with naïve wasps engaging in scramble competition, where foragers locate food quickly, exploit it as individuals, and avoid aggression at a food source (Reid et al. 1995). When few baits are occupied, wasps may perceive that competition for resources is low and that there is little urgency to exploit resources. Wasps will thus try to minimize future agonistic interactions by choosing unoccupied feeders. When incoming wasps perceive that competition for resources is high (all but one feeder occupied), they land on the nearest bait and quickly collect it. This hypothesis is difficult to test by examining the literature because not all experimental designs addressed the potential for spatial bias or sufficiently describe the relatedness of foragers at baits.

Colony life history influences successful location of protein baits by *V. pensylvanica*. While the total number of foragers locating the bait in "unrestricted" trials did not differ between perennial (26 ± 10 wasps) and annual (27.4 ± 5.7 wasps) colonies, visitation increased in response to experienced foragers bringing chicken back to the nest. The disparity in newcomer arrivals between colony types may be explained in part by differences in colony size. In our study, perennial colonies produced approximately two orders of magnitude more workers compared to annual colonies. Because foragers from perennial colonies can quickly deplete protein and nectar resources near their nests (Wilson et al. 2009), strong predation creates zones of depletion around yellowjacket colonies that may expand with increasing colony size. Foragers from larger, perennial colonies resort to foraging at greater distances from the nest compared to those from annual colonies (pers. obs.). Thus, recruits from perennial nests may become activated by experienced wasps returning with chicken but overshoot baits because few natural protein resources remain within close proximity to perennial colonies. In order to explicitly demonstrate whether returning wasps in perennial colonies stimulate nestmates to forage, forager visitation to baits outside the zones of depletion should be investigated.

The degree of competition perceived by foragers can influence foraging behavior (Jeanne et al. 1995). Competition may be perceived if resources are limited or occupied by other wasps. In the context of competitive foraging, antagonistic behaviors can evolve to facilitate efficient resource collection (Parrish and Fowler 1983). In *Polybia*, intolerance was inversely related to prey size; wasps exhibit aggression toward newcomers when prey resources were limited such that a single forager can collect the entire item (Richter 1990). Although *V. pensylvanica* may have perceived competition for resources, we did not observe any agonistic interactions at the feeders and the amount of chicken available was too much for a single forager to carry. Further study is needed to fully understand if these foraging choices are responses to learning contexts or if wasps can instantaneously assess resource availability and profitability.

Context dependency of foraging behavior appears to be widespread within the Vespidae. Across the 13 published studies examined in Table 1, local enhancement is most often observed in urban/suburban habitats than in any other area. Recent work by D'Adamo and Lozada (2007) suggests that habitat characteristics affect yellowjacket foraging behavior. Such human-modified habitats may provide more regular opportunities for scavenging (Akre and Davis 1978; Akre and MacDonald 1985), thus resulting in high local densities of non-nestmate yellowjackets. Past interactions at these urban scavenging sites can lead to learned responses, such as attraction or avoidance of wasp aggregations at resources (Jeanne and Taylor 2009). Because learning in vespid wasps can occur after a single experience (Weiss et al. 2004), foragers may be able to respond quickly to changes in competition for resources. For example, local enhancement may be most common in urbanized environments because these wasps developed a search image for wasp aggregations. This may explain in part why studies in human-modified areas have found that the occupant at a bait has little influence on the forager's decision to land at the resource (Richter and Tisch 1999).

Recruitment can be very advantageous for species invading new environments, where benefits of enhanced and coordinated foraging promote invasion success (D'Adamo and Lozada 2007; Farji-Brener and Corley 1998). In their introduced ranges, several vespids recruit to aggregations of conspecific non-nestmates (Table 1). This is in direct contrast to native populations, where vespids mostly ignore or avoid non-nestmates at food resources. Furthermore, studies examining foragers from a single nest, where wasps encounter mostly if not exclusively nestmates at the bait, vespid wasps show no preference (66.7%) or exhibit local inhibition (33.3%). It is important to note that *no* local enhancement has been reported when visitation is restricted to *nestmates*. To date, no evidence indicates that wasps distinguish nestmates from non-nestmates at a food resource (Parrish 1984; Richter 1990), although such discrimination may occur at the nest (Starks et al. 1998). However, the presence of non-nestmates can be used as an indicator of wasp abundance or nest density; the more non-nestmates, the more likely an area will have a large wasp population and increased nest density. Because denser wasp populations often lead to increased resource competition (Parrish 1984), we expect competition increases with urbanization. While foraging behavior has been shown to have a genetic basis in some eusocial insects (Pankiw and Page 2001), we detected no difference attributed to species, genus or subfamily; all wasps were similarly influenced by environment and presence of non-nestmates.

Summary

Unlike the sophisticated communication and recruitment systems of eusocial ants (Cassill 2003) and bees (Dornhaus and Chittka 2001; Nieh 2004), yellowjackets only appear capable of more primitive forms of recruitment. These foraging behaviors in *V. pensylvanica* are influenced by colony size—where smaller colonies forage closer to their nests and larger colonies begin to search for resources farther from their nests. Furthermore, the perception of demand by yellowjackets may affect subsequent decisions to collect resources. Such context dependency is also observed in aggressive interactions amongst yellowjackets, where assessment of resource quantity (Richter 1990) and number of collecting wasps can predict the levels of aggression exhibited (Parrish 1984). When *V. pensylvanica* foragers perceive strong competition among nestmates for resources, yellowjackets will exploit the nearest bait and quickly leave; in contrast, foragers will avoid occupied meat baits when competition among nestmates is perceived to be minimal. Context dependency in carbohydrate and protein foraging appears to be widespread in the family Vespidae, where recruitment behaviors change with urbanized habitat structure and perceived resource competition. Local enhancement has only been observed when representatives from multiple nests are visiting the same resource (e.g. D'Adamo et al. 2003; Fowler 1992; Reid et al. 1995). Thus, local enhancement may be most common in urban/suburban habitats because wasps may be more likely to interact with multiple colonies than with nestmates under these circumstances. Flexibility in foraging behaviors may provide some invasive wasps with a competitive advantage and contribute to their success as biological invaders.

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Table 1. Prevalence of local enhancement at baits across vespid wasps. *Behavior* describes the type of recruitment activity demonstrated. LE: incoming foragers are attracted to the presence of conspecifics; NP: incoming foragers visit feeders regardless of occupation; LI: incoming foragers are repelled by the presence of conspecifics. Dummy type: L: live foragers; D: wasp dummies. *Dummy type* refers to the kind of wasp cues available for local enhancement. *Bait type* indicates the resource used in the study. *Other visitors* reference any species other than focal taxon that visited and could dominate the resource. *Habitat* indicates the type of environment in which each study was performed. *Status* describes whether the focal species is native or introduced in the area studied. *Participating colonies* indicate the number of colonies whose foragers may be participating and encountering each other in any one trial. * requires nest activation.

Sources: [1] (Fowler 1992); [2] (Jeanne et al. 1995); [3] (Richter and Tisch 1999); [4] (Reid et al. 1995); [5] (D'Adamo et al. 2000); [6] (D'Adamo et al. 2003); [7] (D'Adamo and Lozada 2005); [8] (Parrish and Fowler 1983); [9] (Kim et al. 2007); [10] (Jander 1998); [11] This study; [12] (Richter 1990); [13] (Hrncir et al. 2007);

Species	Behavior	Dummy type	Bait type	Other visitors	Habitat	Status	Participating colonies per trial	Sources
Agelaia pallipes	LE	D	Meat	Multiple ant spp	Urban/suburban	Native	Presumed multiple	[1]
A. hamiltoni	NP	L	Meat	*Angiopolybia paleens*	Ranch	Native	3	[2]
A. multipicta	NP	L	Meat	n/a	Disturbed secondary growth	Native	3	[2]
Vespula consobrina	LI	D	Carb	Multiple wasp spp	Urban/suburban	Native	Presumed multiple	[3]
V. flavopilosa	NP	D	Carb	Multiple wasp spp	Urban/suburban	Native	Presumed multiple	[3]
V. germanica	LE	L	Meat	n/a	Suburban & natural areas	Introduced	Presumed multiple	[4]
	LE	L	Meat	*V. maculifrons*	Suburban	Introduced	Presumed multiple	[5]
	LE	L	Meat	n/a	Suburban	Introduced	Presumed multiple	[6]
	LE	L	None	n/a	Suburban	Introduced	Presumed multiple	[7]
	LE	D	Carb	n/a	Urban/suburban	Introduced	Presumed multiple	[8]
	LE	D	Carb	n/a	Urban/suburban	Introduced	Presumed multiple	[3]
V. koreensis	NP	L	Carb	n/a	Urban/suburban	Native	1	[9]
V. maculifrons	LE	L	Meat	n/a	Suburban & natural areas	Native	Presumed multiple	[4]
	LI	D	Carb	Multiple wasp spp	Urban/suburban	Native	Presumed multiple	[3]
	LI	D	Carb	*V. germanica*	Urban/suburban	Native	Presumed multiple	[8]
	NP	L	Fruit	n/a	Partially wooded	Native	Presumed multiple	[10]
V. pensylvanica	LI	D	Meat	n/a	Natural areas	Introduced	1	[11]
	NP	D	Meat	n/a	Natural areas	Introduced	1	[11]
	NP	D	Meat	n/a	Natural areas	Introduced	1	[11]
V. vidua	NP	D	Carb	Multiple wasp spp	Urban/suburban	Native	Presumed multiple	[3]
Polistes fuscatus	LE	D	Carb	Multiple wasp spp	Urban/suburban	Native	Presumed multiple	[3]
Polybia diguetana	NP	D	Prey	*P. occidentalis*	Ranch/dry forest	Native	Presumed multiple	[12]
	NP	L	Prey	*P. occidentalis*	Ranch/dry forest	Native	Presumed multiple	[12]
P. occidentalis	LE *	L	Carb	n/a	Urban/suburban	Native	Presumed multiple	[13]
	LE	D	Prey	*P. diguetana*	Ranch/dry forest	Native	Presumed multiple	[12]
	LE	L	Prey	*P. diguetana*	Ranch/dry forest	Native	Presumed multiple	[12]

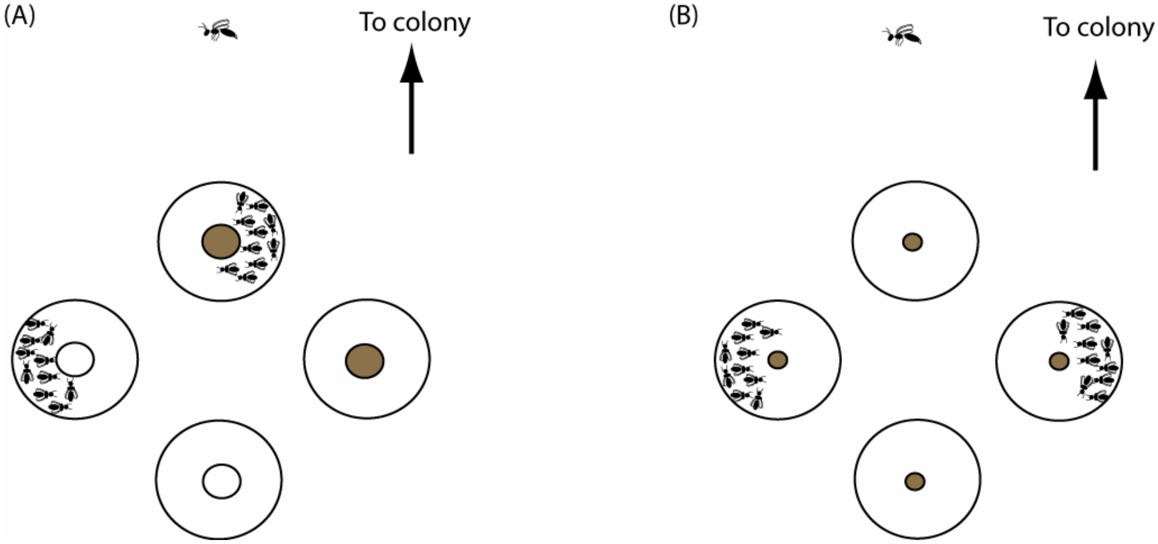

Figure 1. Experimental feeder design for (A) clumped patches where half of feeders have protein baits and (B) dispersed patches where all feeders have protein baits. Filled circles represent protein bait and open circles indicate cotton. The size of filled circles represents the proportional amount of bait provided per feeder. Wasp dummies occupy half of the feeders in both experiments; feeder orientation relative to the colony was randomized in each trial.

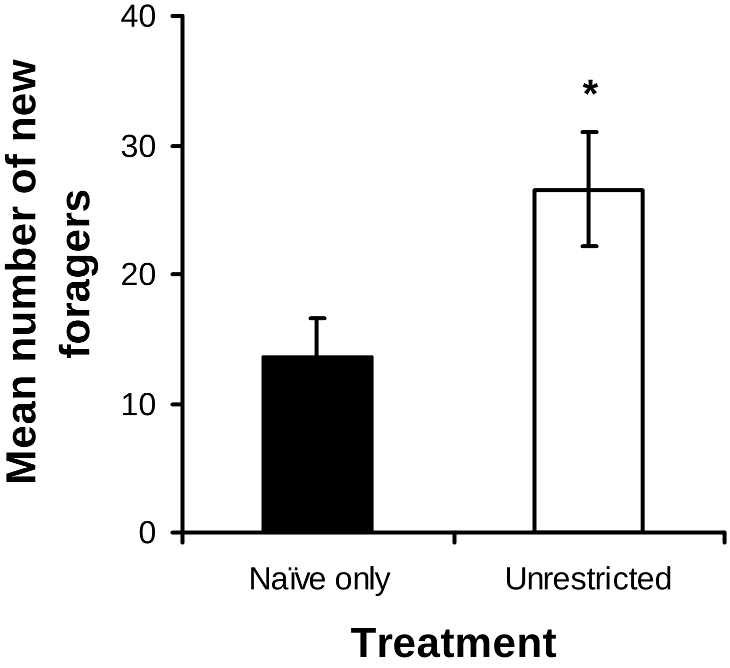

Figure 2. New forager visitation (mean ± SE) increases when successful, experienced wasps are allowed to continue foraging (n = 6 colonies) compared to "naïve only" trials. In "naïve only" trials, every forager is collected upon landing on baits thus excluding experienced foragers; in "unrestricted" trials, all incoming foragers are allowed to visit. * indicates significance $p < 0.05$.

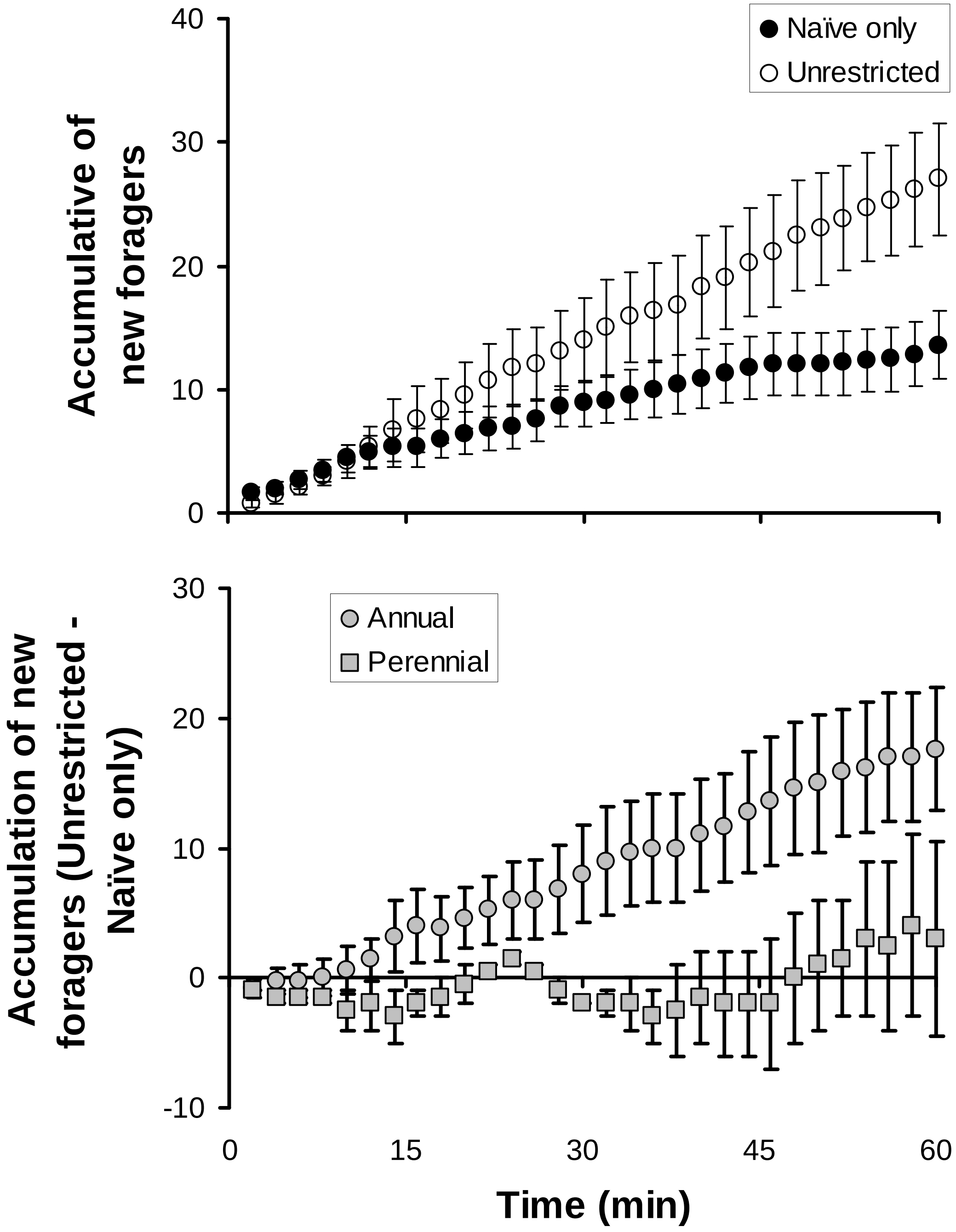

Figure 3. Rates of new forager visitation are influenced by the restriction of incoming foragers and by colony type. (A) Accumulation of naïve foragers (mean ± SE) during the trials is greater for the 'unrestricted' treatment relative to the 'naïve only' treatment. (B) Annual colonies have higher rates of new forager accumulation in "unrestricted" trials as compared to "naïve only" trials. Perennial colonies exhibited similar rates of new forager accumulation in both trial types.

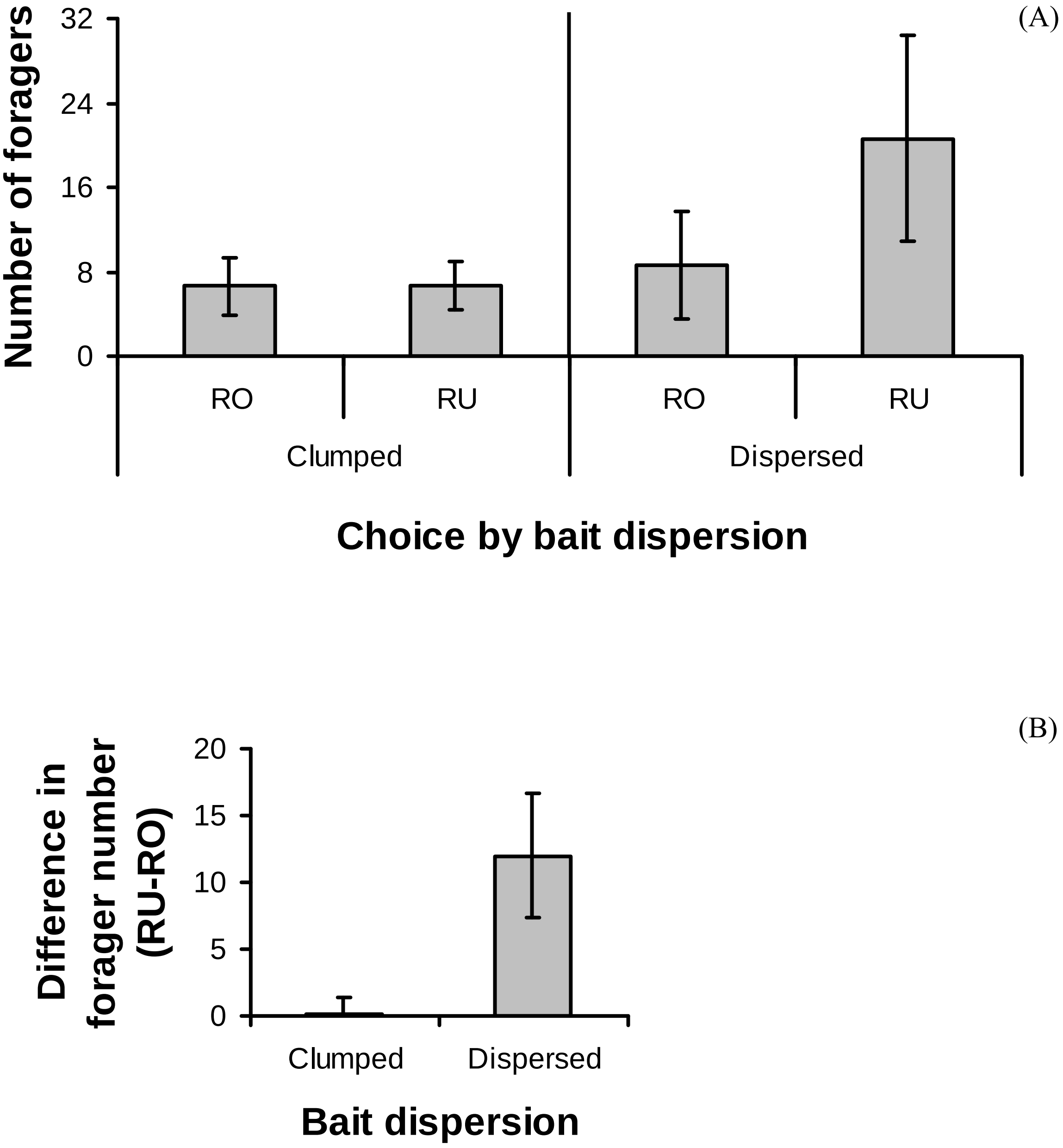

Figure 4. The presence of conspecifics influences the number of wasps (mean ± SE) foraging at clumped and dispersed baits. (A) No preference for wasp dummies is shown in clumped patches where two of four feeders provide meat; unoccupied rewarded (RU) and occupied rewarded (RO) feeders are equally visited. Unrewarded baits were not visited. In patches where baits are dispersed across four feeders, yellowjackets prefer RU over RO. (B) Forager visitation in clumped patches is equally split between RU and RO feeders. In patches with dispersed baits, visitation to RU feeders is greater than that to RO feeders. * indicates significance $p < 0.05$.

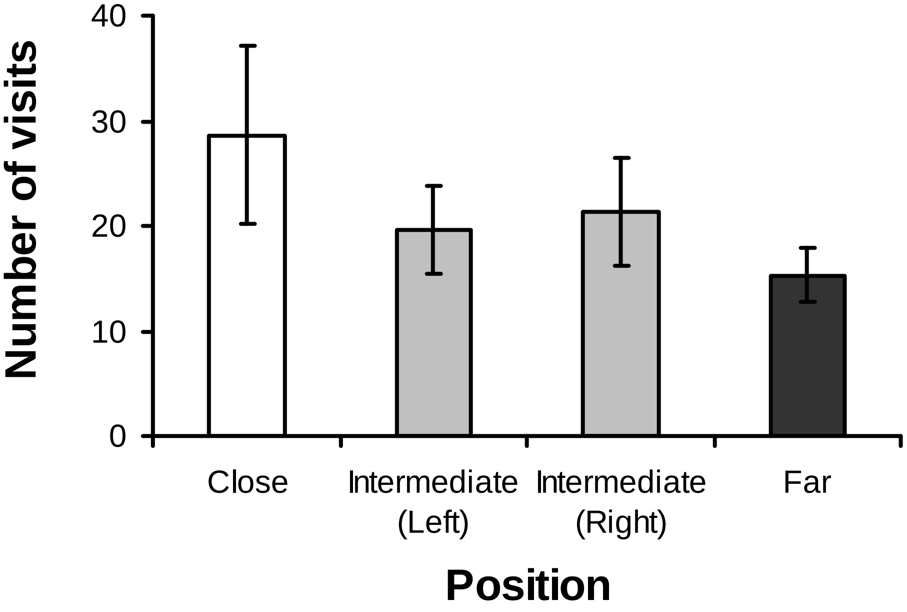

Figure 5. Number of incoming wasps (mean ± SE) show no discrimination for the number of dummies on a feeder but visit the first available feeder they encounter. Different letters indicate significance $p < 0.05$ in Tukey HSD tests.

Predation or scavenging? Thoracic muscle pH and rates of water loss reveal cause of death in arthropods

ABSTRACT

The difficulty of directly observing and quantifying predatory events hinders a complete understanding of how predation shapes the structure of food webs. For this reason, ecologists commonly infer the occurrence of predation through indirect approaches such as PCR-based and isotopic analyses. While these methods clarify aspects of resource consumption, they fail to distinguish predation from scavenging. Given that facultative scavenging is a ubiquitous and phylogenetically widespread foraging strategy, discriminating prey from carrion is essential for the accurate assessment of interactions among trophic levels. Drawing such distinctions remains critical for isolating the ecological mechanisms underlying energy fluxes and the demographic effects of consumption. Using physiological properties of muscle tissue—specifically pH and rate of water loss—we develop a novel and generally applicable method to discriminate prey from carrion in the diets of scavenging predators. These properties change in a quantifiable and deterministic manner post-mortem and can be used to estimate the time and putative cause of death. Applying this method in laboratory and field situations resulted in the correct identification of prey and carrion in 49 of 56 cases (88%). The approaches developed in this study can thus be used to separate predation from scavenging to provide a more definitive characterization of species interactions and food webs.

INTRODUCTION

Predation can play an important role in structuring ecological communities (Paine 1966; Post et al. 2008; Schmitz et al. 1997). Observing predatory events *in situ,* however, poses many logistical challenges (Miller et al. 2006; Retana et al. 1991). When the species involved are small or highly mobile, direct observation of predation becomes nearly impossible (Hagler et al. 2004). Furthermore, the time required to capture even a few direct observations of predation, which typically involve multiple species of predators (Heimpel et al. 1997; Rosenheim et al. 1999), makes obtaining sufficient sample sizes infeasible. For these reasons, ecologists rely heavily on PCR-based methods (Foltan et al. 2005; King et al. 2008; Sheppard et al. 2004; Symondson 2002) and stable isotope analyses (Fiedler et al. 2007; Hood-Nowotny and Knols 2007; Kelly 2000) to characterize species interactions and to infer trophic level. A major shortcoming of such methods, however, is this inability to differentiate killed prey from scavenged carrion for consumers that engage in both behaviors (Foltan et al. 2005; Juen and Traugott 2005; King et al. 2008; Morris et al. 1999).

Refining such distinctions will improve the interpretation of diet analyses because predation and scavenging differ in their ecological effects. Consumption does not necessitate direct demographic changes in the taxa consumed. While predation directly depresses prey populations (Schmitz et al. 1997), scavenging involves consuming individuals already removed from the population and consequently has no specific demographic effects on prey taxa (Abrams 1987). Diet analyses that fail to discriminate between carrion and prey can thus substantially overestimate predatory effects and lead to invalid assessments of trophic level (Calder et al. 2005). Distinguishing and quantifying the relative contribution of these ecological processes will provide more accurate characterizations of species interactions (King et al. 2008) and energy flow through food webs (DeVault et al. 2003).

Facultative scavenging is one of the most common foraging strategies of both vertebrates (DeVault et al. 2003; Hunter et al. 2007) and invertebrates (Foltan et al. 2005; Sunderland and Sutton 1980). Considering that invertebrates comprise much of the global terrestrial animal biomass (May 2000; Williams 1960), the importance of invertebrate carrion as a resource for scavenging predators has received surprisingly little attention. Many predatory invertebrates engage in facultative scavenging, including Amphipoda (Ide et al. 2006), Coleoptera (Foltan et al. 2005; Juen and Traugott 2005; Sunderland and Sutton 1980), Decapoda (Wolcott 1978), Dermaptera (Sunderland and Sutton 1980), Diptera (Foltan et al. 2005), Hemiptera (Foltan et al. 2005; Velasco and Millan 1998), Hymenoptera (Foltan et al. 2005), Isopoda (Barradas-Ortiz et al. 2003), Litobiomorpha (Sunderland and Sutton 1980), Neuroptera (Foltan et al. 2005), and Opiliones (Sunderland and Sutton 1980). Several studies have identified ants as key scavengers of small invertebrate carrion (Fellers and Fellers 1982; Fellers 1987; Retana et al. 1991). However, these observational studies capture only a fraction of scavenging dynamics because they used carrion baits that individual ant workers could carry by themselves, while much of insect diversity falls into larger size classes (Finlay et al. 2006). Just as larger prey require larger predators (Cohen et al. 1993), medium to large items of carrion often attract bigger scavengers (*e.g.* wasps or beetles) (Seastedt et al. 1981), or multiple individuals cooperating through nestmate recruitment or group retrieval (Hölldobler and Wilson 1990).

Differentiating prey from carrion may be most critical for ecosystems with high net primary productivity (NPP) that generate substantial amounts of arthropod biomass. Because higher NPP is associated with increased social insect abundance (Kaspari 2001; Kaspari et al. 2000), social insect colonies likely serve as important point sources of dead biomass in such environments. Reliable and abundant supplies of carrion, for example, are produced by the large, perennial colonies of *Apis mellifera* (Coelho and Hoagland 1995; Visscher 1983). Given an average honeybee colony of ≈ 14,000 bees (Free and Racey 1968) and a mean worker mass of 116 mg (Schmolz et al. 2005), a single colony annually produces more than 1.6 kg of dead biomass. With over 2.3 million managed colonies in the United States alone (USDA 2009), dead workers of this and other social insect species represent an important and underappreciated food source for scavenging predators. Moreover, the aggregated and constant production of dead individuals from social insect colonies may magnify top-down effects of predation as scavenging predators subsidize their diets with carrion (Polis and Strong 1996; Rand et al. 2006).

To distinguish between predation and scavenging in arthropods, we require quantitative information about time since death (TSD). Forensic pathology (Bate-Smith and Bendall 1949) and related fields have established how TSD and peri-mortem stress (stress that occurs at or near death) influence post-mortem muscle pH (Lawrie and Ledward 2006). Because animal muscles remain metabolically active after death, they continue to convert glycogen to lactic acid through irreversible anaerobic glycolysis (Lindahl et al. 2006). As lactic acid accumulates, muscle pH declines until it reaches the ultimate pH, the point at which enzymes involved in glycolysis become inactivated (Lawrie and Ledward 2006). Ultimate pH typically is achieved 24 hrs following death

(Linares et al. 2007), however, peri-mortem stress can accelerate this decline (Rees et al. 2003). Thus for any given TSD, the muscle pH of a stressed individual will be lower than that of a non-stressed individual. Furthermore, because predation is stressful to prey, we expect the pH of prey to be lower than the pH of carrion at any TSD within 24 hrs.

Here, we demonstrate that after estimating TSD from water loss rate (measured as mass loss), thoracic muscle pH and other physiological properties can be used to differentiate prey from carrion. Because pH of muscle tissue decreases predictably post-mortem and is sensitive to stress, we can evaluate the peri-mortem stress level experienced by diet items and distinguish prey from carrion. This study uses social insects as a model system, in part because ants and social wasps represent ecologically dominant scavenging predators in many terrestrial ecosystems (Hölldobler and Wilson 1990; Jeanne 1979; Snyder and Evans 2006; Wilson et al. 2009). Nonetheless, it often remains unclear whether these consumers are serving as predators or scavengers (Tillberg et al. 2007). Furthermore, our approach could be extended to a wide range of scavenging predators, perhaps especially those that exhibit central-place foraging and for which diet items can be obtained prior to consumption. Isolating specific mechanisms by which diet items are collected (predation or scavenging) will clarify the nature of species interactions and reveal the extent to which food webs are reticulate in structure.

MATERIALS AND METHODS

We used a series of physiological measures to determine whether insect diet items are prey or carrion. The western yellowjacket, *Vespula pensylvanica*, served as our model scavenging predator due to its broad diet, predatory ability and propensity for scavenging (Jacobson et al. 1978). Because yellowjackets are known to consume bees, which are of economic and ecological importance, and to cannibalize, we examine how the physiology of bumblebee (*Bombus impatiens*), honeybee (*Apis mellifera*), and yellowjacket carcasses changes post-mortem and in response to predation stress. To estimate TSD, we first identified measurable and predictable time-dependent parameters (Henssge and Madea 2007). We then developed generalizable approaches to discriminate prey from carrion by estimating TSD from rate of water loss (a time-dependent but stress-independent parameter) and by comparing observed pH (a time- and stress-dependent parameter) to estimated pH for a given TSD. Because higher ambient temperatures can lead to increased rates of water loss (Atmowidjojo et al. 1997) and rates of pH decline (Lawrie and Ledward 2006), we controlled ambient conditions in the laboratory to simulate common field temperatures (18 – 23 ˚C) in order to create reliable and accurate baseline curves.

Colony maintenance: Three *B. impatiens* (Hymenoptera: Apidae) colonies (Biobest Canada Ltd., Ontario, Canada) were maintained in the lab at constant temperature (mean ± SE: 26.7 ± 1.2 °C) and humidity (31.4 ± 1.0 % humidity) under a photoperiod of 12 L : 12 D. Each colony was provided with water, sucrose solution and pollen *ad libitum*. We also maintained two freely foraging colonies of *A. mellifera* (Hymenoptera: Apidae) at the University of California, San Diego Biology Field Station. All *V. pensylvanica* (Hymenoptera: Vespidae) used in this study were foragers captured from two feral colonies in Haleakala National Park, part of the introduced range of this species.

To prevent peri-mortem stress, female bees and wasps were captured, sedated on ice and then sacrificed by decapitation while anesthetized. In this way, all individuals experienced no stress at the time of death but still died by decapitation, which is a common killing behavior of predatory wasps. Each thorax was exposed to the ambient lab environment (22.6 ± 1.1 °C and 32.4 ± 1.0 % humidity). Changes in ambient temperature (T_a), thoracic temperature (T_{th}), body mass and thoracic pH were measured at discrete intervals after death (Table 1), except for *V. pensylvanica* where only T_a and thoracic pH were measured. In this study, we focused on thoracic tissue because it consists of concentrated and relatively homogenous muscle.

We measured surface T_{th} to the nearest 0.1°C with an infrared thermometer (Radio Shack™, spot size 5 mm). To control for minor variations in T_a, the difference between ambient and thoracic temperatures ($T_a - T_{th}$) was used in statistical analyses. We measured thoracic pH by inserting a pH probe (Oakton Eutech Instruments™, model #PHSPEAR, accuracy: 0.01 pH units) into the thorax of each decapitated bee or wasp. This pH device is designed for measuring pH of solids and semisolids. Each forager was only measured once.

Evaluating TSD and stress-level estimators in a blind, no-stress experiment

To evaluate how rates of water loss (mg hr^{-1}) change post-mortem, we measured the rate of mass loss at 34 time points ranging between 1-120 hrs after death for 35 *B. impatiens* foragers. This sampling allowed for the estimation of mass loss rates (mg hr^{-1}) in the first hour after a diet item had been collected. We used this approach because under field conditions information about the peri-mortem mass of diet items is unavailable. Ten bees were killed by decapitation to simulate death by predation (“prey” bees), and 25 bees were freeze-killed and decapitated within 2-31 hours after death to simulate death by natural causes (“carrion” bees). These measurements were taken under controlled conditions (23.4 ± 0.5 °C, 41.7 ± 2.0 % humidity). We described the exponential rate of mass loss over TSD for "prey" bees (Fig. 1) and time since decapitation (TS_{decap}) for "prey" and "carrion" bees.

To test the accuracy of water loss rate as a TSD estimator, we collected and sacrificed an additional 45 *B. impatiens* foragers as previously described. In a blind, no-stress experiment, each individual bee was assigned a time (0 - 18 hrs after death) to have its mass and thoracic pH measured. Referencing Fig. 1 and TS_{decap} of "carrion" bees, we estimated TSD and TS_{decap} from rates of water loss exhibited by the 45 *B. impatiens* foragers and then compared the two time estimates. Because TSD and TS_{decap} were equivalent for all bees, TSD was used in subsequent analyses. Using TSD and by referencing Fig. 2a, we then examined whether observed pH measurements fell along the no-stress baseline. To determine the accuracy and precision of both estimators, we compared estimates to actual values and then evaluated the percentage of bees that exhibited the following: (1) estimated and actual TSDs differed by no more than ± 1 and ± 4 hrs, and (2) observed pH fell with the 99% CI of the baseline pH curve.

Effect of stress on TSD estimates: pH as an indicator of cause of death

Peri-mortem stress depresses and truncates the pH curve such that pH at death is lower and ultimate pH is attained more quickly. Thus, muscle pH should indicate high peri-mortem stress levels when the observed pH falls below the no-stress baseline curves at the estimated TSD. To test this hypothesis under controlled conditions, we collected 21 *B. impatiens* foragers; eight were sacrificed as previously described in the no-stress conditions, and 13 were subjected to one minute of stress (e.g. aggressive prodding) prior to decapitation. This time period simulates natural predation by yellowjackets, where mean handling time is 106 ± 14 sec (*n* = 30 predation events). Changes in T_{th}, body mass and thoracic pH were measured immediately following death. To assess the extent to which stress reduced muscle pH in the field, we presented freshly-killed and live honeybee foragers in choice tests to free-foraging yellowjackets from six different wasp colonies. In the field, freshly-killed bees were killed in ethanol to minimize stress and then rinsed with water. All bees were restrained by pins through the thorax to prevent dead bees from blowing away and live bees from flying away. Live bees retained the ability to sting and fight with attacking yellowjackets. We retrieved the honeybee thoraces processed by *V. pensylvanica* in these trials and subsequently measured thoracic muscle pH to quantify the effect of predation stress (freshly-killed: *n* = 11 bees, live: *n* = 24 bees). This approach reasonably mimicked natural predatory events. Pinning live bees (*n* = 10) did not result in a decrease in pH relative to control bees (*n* = 10) ($x_{pinned} = 6.41 \pm 0.06$, $x_{control} = 6.42 \pm 0.05$ pH units, $t_{17} = 0.56$, p= 0.58).

Statistical analyses

All statistical analyses were performed with JMP v. 7.1 (SAS Institute). Models of pH change over time were evaluated by comparing AIC values (Bozdogan 1987); the best model was an exponential curve. For *B. impatiens* and *A. mellifera*, we performed multiple regressions to assess how (i) TSD (hr), (ii) T_a, and (iii) body mass changed with thoracic muscle pH. For *V. pensylvanica*, we performed a multiple regression to assess how (i) TSD (hr) and (ii) T_a affected thoracic pH. For linear regressions of pH over time, we calculated the 99% confidence intervals. To evaluate pH as an indicator of cause of death, we performed two-sample t-tests to determine the effect of stress on the thoracic pH of *B. impatiens* and *A. mellifera*.

RESULTS

Our results demonstrate that the rate of water loss and the pH of thoracic muscle decrease predictably post-mortem and can thus be used to infer time and cause of death. Figure 1 illustrates rates of evaporative water loss after death for bumblebees killed by decapitation. These bees exponentially lost water (Eq 1: rate of water loss (mg hr^{-1}) = -0.8443 * ln(TSD) + 3.9631, $R^2 = 0.80$). Rates of water loss of “prey” bees illustrated in Figure 1 are consistent with water loss observed in the no-stress baseline experiments: decapitated *B. impatiens* bees lost 1% of their body mass per hour, while decapitated *A. mellifera* lost 0.75% of their body mass per hour. Lower rates of water loss were observed in “carrion” bumblebees where TS_{decap} ranged between two and 31 hours after death; these “carrion” bees also lost water exponentially (Eq. 2: rate of water loss (mg hr^{-1}) = -0.5121 * $\ln(TS_{decap})$ + 2.4492, $R^2 = 0.87$). “Prey” and “carrion” bees exhibited different rates of mass loss for the first 10 hours following death or decapitation, after which time rates of mass loss converged.

In the no-stress baseline experiments, all species exhibited significant post-mortem decreases in pH (Table 2). In the absence of stress, the rate of change in thoracic pH varied by species (Fig. 2). Overall, bumblebees exhibited 0.024 pH decrease/hr (Fig. 2a), while thoracic muscle of honeybees declined at a higher rate of 0.050 pH decrease/hr (Fig. 2b). *Vespula* exhibited an intermediate rate of 0.037 pH decrease/hr (Fig. 2c).

Microscopic inspection of thoracic muscle demonstrated that post-mortem muscle changed qualitatively over time. Under laboratory conditions, thoracic muscle of bumblebees remained moist for 8 hrs following death and was characterized by a predictable sequence of changes in color (Fig. 3a-c). As time passed, thoracic muscle became increasingly dry and stringy, and its color deepened (Fig. 3d-e). After seven days, thoracic muscle was dry and completely brittle (Fig. 3f). The predictable sequence of muscle appearance provides additional confirmation of TSD.

Evaluating TSD and stress-level estimators in a blind, no-stress experiment

To confirm that water loss data provide a true metric of TSD and not just TS_{decap}, we took the two time estimates for each bee, determined the expected pH on the *Bombus* no-stress baseline (Fig. 2a) for each estimate, and calculated the difference in pH for the two estimates. Because the mean difference in pH (0.08 ± 0.03 pH units) was much lower than the CI around the baseline curve (± 0.24 pH units), any discrepancy between time estimates is unlikely to result in a misclassification of diet items as prey versus carrion. For all analyses, we compared TSD and TS_{decap}, however, we report only TSD for the remaining experiments because of the similarity of these time values to one another.

Using post-mortem rate of water loss (mg hr^{-1}) alone to estimate TSD, 87% of estimates were accurate to within ± 1 hr and 100% fell within ± 4 hrs of the actual TSD. If water loss data were combined with blind visual assessments of muscle quality, accuracy within ± 2 hrs of the actual TSD increased to 95% of estimates. As an indicator of stress, 82% of observed pH values fell within the 99% CI of the no-stress baseline curve. An additional 9% of observations could be classified as no-stress because they slightly exceeded the upper CI. Thus, 91% of pH measurements confirmed that no stress was experienced.

pH as an indicator of cause of death

We tested the hypothesis that muscle pH can indicate the level of peri-mortem stress experienced by putative prey. For all individuals in the stress experiment (n = 21 *B.*

impatiens), rates of water loss in the first hour after initial measurement were insensitive to stress and resulted in 86% of estimated TSD within ± 1 hr and 100% within ± 1.05 hrs of actual TSD. Visual assessment of muscle confirmed that measurements occurred shortly after death and before coloration changed for both *Bombus* stress experiment and *Apis* field predation trials.

Peri-mortem stress caused an immediate decrease in muscle pH. Bumblebees subject to intermittent stress exhibited a mean decrease of 0.2 pH units (Fig. 4a), a drop detectable within minutes of death (t = -2.25, df = 19, p = 0.036). Predation on *Apis* foragers caused a larger pH decrease of 0.4 pH units (Fig. 4b; t = -7.395, df = 33, p < 0.0001). Using TSD estimates derived from water loss rates and referencing the no-stress baseline pH curve (Fig. 2a), we established whether observed pH measurements fell along or below these curves for the *Bombus* stress experiment. Due to the sensitivity of pH to stress, observed pH values fell along no-stress baselines *only* when peri-mortem stress was low or absent (75% of estimates for control *Bombus,* and 89% of estimates for scavenged *Apis*). For bumblebees experiencing intermittent stress for one minute prior to decapitation, observed pH measurements fell below the no-stress baseline curve in Fig. 2a at TSDs estimated from the rate of water loss curve. Similarly, for honeybees killed by predatory yellowjackets, at TSD estimated from rates of water loss from Fig 1, 100% of observed pH values were below the no-stress baseline curve in Fig. 2b.

DISCUSSION

We provide the first evidence for how rate of water loss, pH of thoracic muscle, and muscle color can be used to distinguish fresh-killed prey from decomposing corpses. For scavenged carrion (low to no stress), observed pH values fall along no-stress baseline curves at the TSD estimated from baseline water loss rates; in this situation, diet items with a low pH have been dead for many hours or days (Fig. 5). For prey (high stress), observed pH lies well below no-stress baseline curve at the TSD estimated from baseline water loss rates. Thus, the responsiveness of pH to stress (Rees et al. 2003) can provide important information about peri-mortem conditions and can be used to distinguish prey from carrion (Fig. 5). Use of pH measurements alone to estimate TSD would lead to accurate estimates for non-stressed individuals but overestimates for individuals experiencing strong peri-mortem stress. By combining information derived from rates of water loss, muscle pH and no-stress baselines for these parameters as described in this study, one can examine diet items of scavenging predators and infer the ecological process at work.

In the absence of peri-mortem stress, muscle pH decreases predictably at species-specific rates within the first 24 hours after death. All three focal species differed in body size, but body size does not appear to predict rates of pH decline. Bumblebees, which had the lowest rate of pH decrease, were the largest of the species tested. Honeybees were of intermediate body size, however they exhibited the fastest rate of pH decrease. *Vespula* were the smallest Hymenoptera species measured but yellowjacket muscle pH declined at an intermediate rate compared to the bees. Species-specific rates of pH decrease may result from different physiological and metabolic responses to stress, which depend in part on the genetic background of the focal individual or species (Terlouw 2005; Terlouw and Rybarczyk 2008). Although further research is required to determine what factors influence the rate of post-mortem pH declines, our results illustrate in a general sense how muscle physiology can be used to discriminate predation from scavenging.

Applications of this approach to other taxa will require separate quantification of species-specific post-mortem pH responses.

We tested at a narrow range of environmental conditions, those that were suitable for the times of day when Hymenoptera are common in the diet of *V. pensylvanica.* However, if the microclimates experienced by diet items are beyond the ranges used in this study (e.g. hotter or drier), this approach can still be used to distinguish recent predatory events—prey that experienced peri-mortem stress and have little water loss regardless of the ambient microclimate. Furthermore, this approach can be tailored to specific environmental conditions by controlling the conditions under which baseline data are collected. Using post-mortem muscle pH to infer cause of death may be most useful when temperature and humidity fluctuations are moderate.

The importance of carrion in the diets of scavenging predators cannot be determined solely through gut content analysis. Although consumed carrion can be detected in gut contents (Foltan et al. 2005; Juen and Traugott 2005), these items are not distinguishable from prey using PCR-based methods. Quantifying carrion in a predator's diet would benefit from information about the availability of fresh carcasses in the field (Foltan et al. 2005; Juen and Traugott 2005). However, measuring predator number, carcass removal rates and carrion availability in the field is difficult (Foltan et al. 2005), and infeasible for small taxa such as arthropods. The approach developed in this study could indicate the relative frequency of scavenging versus predation by central place foragers (Kasper et al. 2004; Tillberg et al. 2007; Wilson et al. 2009) because diet items can be obtained from returning foragers.

Establishing how diet items enter a scavenging predator's diet has broad applications in food web studies, which require reliable information about who is eating whom, in what quantities, and by what mechanisms (Hagler et al. 2004; Wilson et al. 2009). Direct interactions, such as predation, often have large impacts on community dynamics (Menge 1997), however if predators respond numerically through consumption of both carrion and prey, subsidies from scavenging may disrupt predator-prey dynamics by disconnecting responses of predator populations from their prey (Roth 2003). Such decoupling can complicate attempts to quantify predation pressure and to predict the outcomes of species interactions. Resource subsidies, for example, can magnify predatory impacts of generalist predators (Rand et al. 2006). With appropriate baseline data, water loss rates and muscle pH of diet items can be used to gain insight into the relative roles of predation and scavenging in a generalist's diet and to create more accurate models of local food webs.

The ability to differentiate between ecological processes such as predation and scavenging will greatly enhance the value of diet analyses (King et al. 2008). Knowing whether a species is experiencing high levels of predation can be of vital importance when direct observation is impossible or when focal species are of conservation or economic importance, for example native or endangered prey or important pollinators. Coupled with ecological studies that quantify predator and prey populations, this method allows for the detection and evaluation of any carrion supplementing predator diets.

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Table 1. Post-mortem variables measured for each of three focal species. The number of individuals measured at each time interval is given. -- indicates no foragers were measured at that time interval. T_a = ambient temperature. Each forager was measured only once.

Species	Wet mass (mg)	Time since death (hr)											Variables measured
		0	1	2	4	6	8	12	14	16	18	24	
Bombus	134.2 ± 3.3 N = 120	7	12	11	17	--	15	16	15	17	10	--	T_a, mass, pH
Apis	106.4 ± 3.5 N = 89	12	--	--	10	11	12	13	10	10	11	--	T_a, mass, pH
Vespula	52.8 ± 2.0 N = 30	52	--	--	62	26	26	55	27	36	26	29	T_a, pH

Table 2. Multiple regression statistics for thoracic muscle pH of three hymenopteran species. For all species, pH decreased significantly with increasing time since death (TSD). Thoracic pH was unaffected by ambient temperature (T_a) and body mass.

	Bombus impatiens			*Apis mellifera*			*Vespula pensylvanica*		
	F	df	*p*	*F*	df	*p*	*F*	df	*p*
Time since death (TSD)	7.93	1,117	0.0057	12.01	1,83	0.0008	305.52	1,335	< 0.0001
T_a	2.33	1,117	0.13	0.085	1,83	0.77	0.39	1,335	0.53
Final mass	0.38	1,117	0.54	0.0516	1,83	0.82			
T_a * TSD	0.18	1,117	0.67	0.074	1,83	0.79	2.54	1,335	0.11
Final mass * TSD	1.34	1,117	0.25	2.41	1,83	0.12			
Overall model	$F_{5,117} = 4.14$, $p = 0.0017$			$F_{5,83} = 16.22$, $p < 0.0001$			$F_{3,335} = 103.0$, $p < 0.0001$		

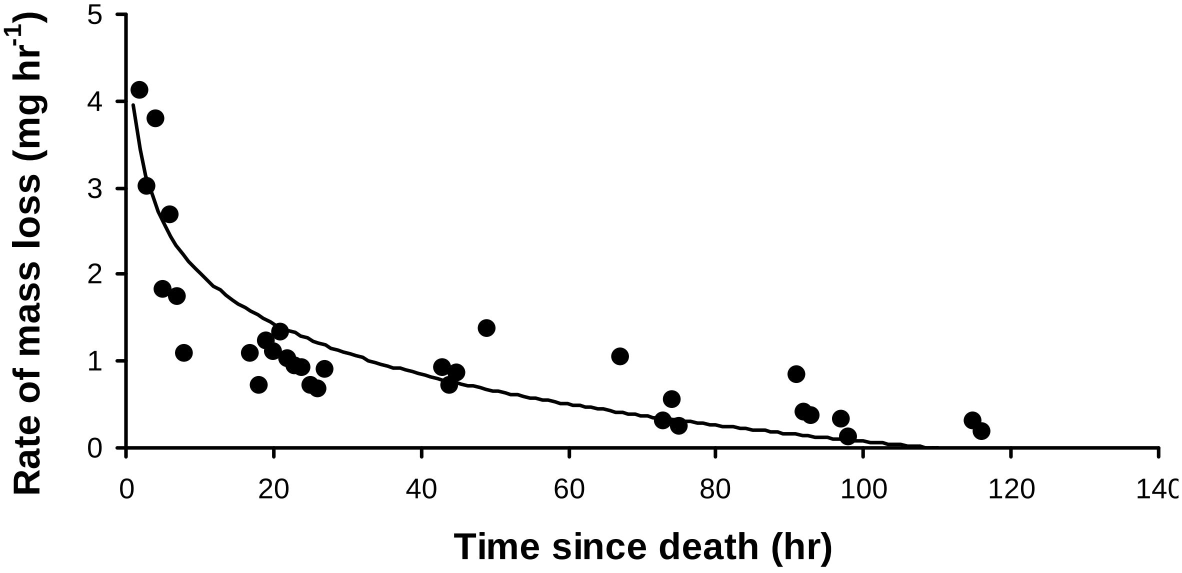

Figure 1. Rate of post-mortem water loss in *Bombus impatiens* bees killed by decapitation decreases exponentially. Each data point represents the mean rate of water loss for 10 bees.

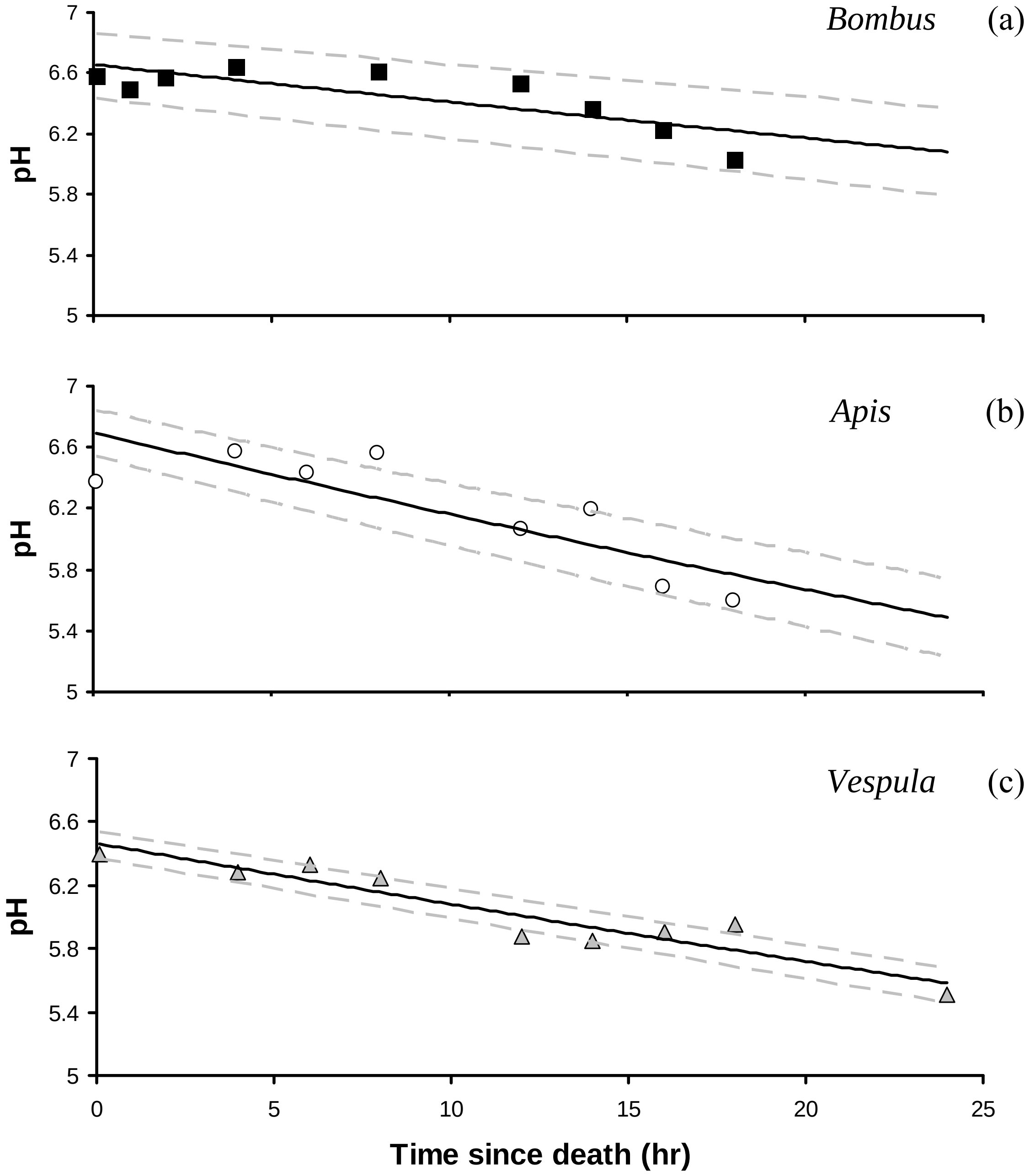

Figure 2. Thoracic muscle pH decreases predictably after death in three hymenopteran species in no-stress baselines. The rates of pH decrease vary among species as determined by exponential equations derived from multiple regression analysis. (a) *Bombus*: pH = $6.781e^{-0.00469*TSD(hr)}$; (b) *Apis*: pH = $6.6753e^{-0.008*TSD(hr)}$; (c) *Vespula*: pH = $6.458e^{-0.006162*TSD(hr)}$. Each data point represents the mean of multiple individuals (see methods for sample sizes).

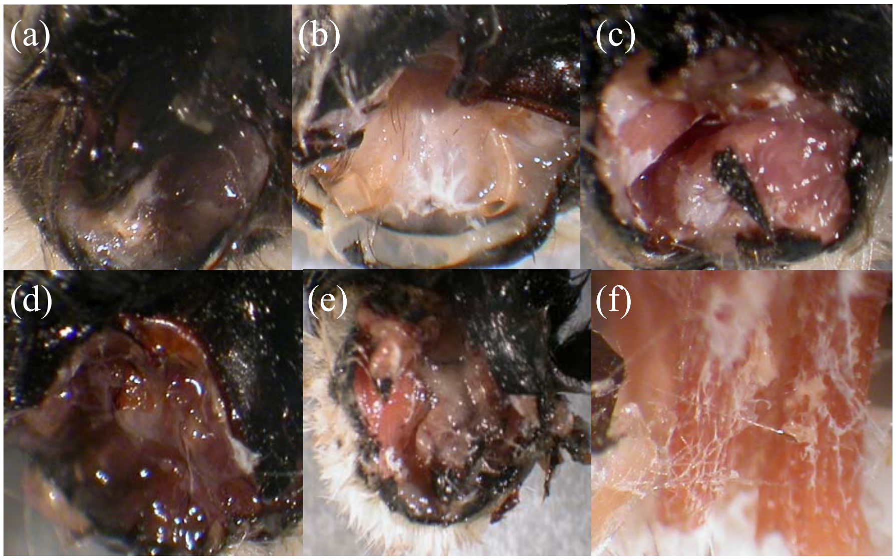

Figure 3. Post-mortem thoracic muscle characteristics in *Bombus* under laboratory conditions. (a) Immediately after death, muscle is moist and appears deep gray with pink undertones. (b) At 6 hrs after death, moist muscle changes color to white with pink undertones. (c) At 8 hrs after death, moist muscle begins to turn pink with white undertones. (d) At 18 hrs after death, muscle turns dark pink. (e) At 24 hrs after death, muscle begins to dry out and becomes increasingly brittle. (f) At 1 wk after death, muscle is completely dried out and appears fibrous.

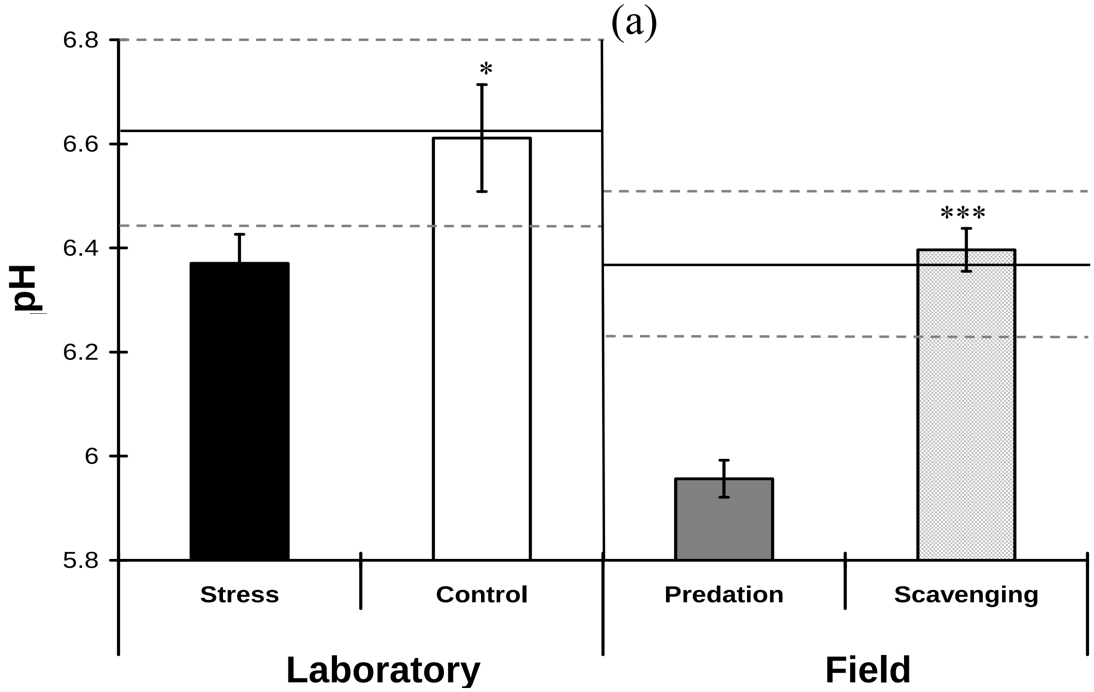

Figure 4. Peri-mortem stress lowers pH in laboratory and field situations, and these decreases become evident immediately after death. (a) *Bombus impatiens* foragers exhibit lower thoracic muscle pH after experiencing intermittent stress. Control measurements are comparable with baseline *Bombus* pH measurements (solid lines) and 99% CI (dashed lines) at TSD = 0 hr from Fig. 1. (b) *Apis mellifera* foragers exhibit significant drops in thoracic muscle pH as a result of predation. The pH values of scavenged bees are comparable with baseline *Apis* measurements at TSD = 0 hr from Fig. 1. * $p < 0.05$. *** $p < 0.0001$.

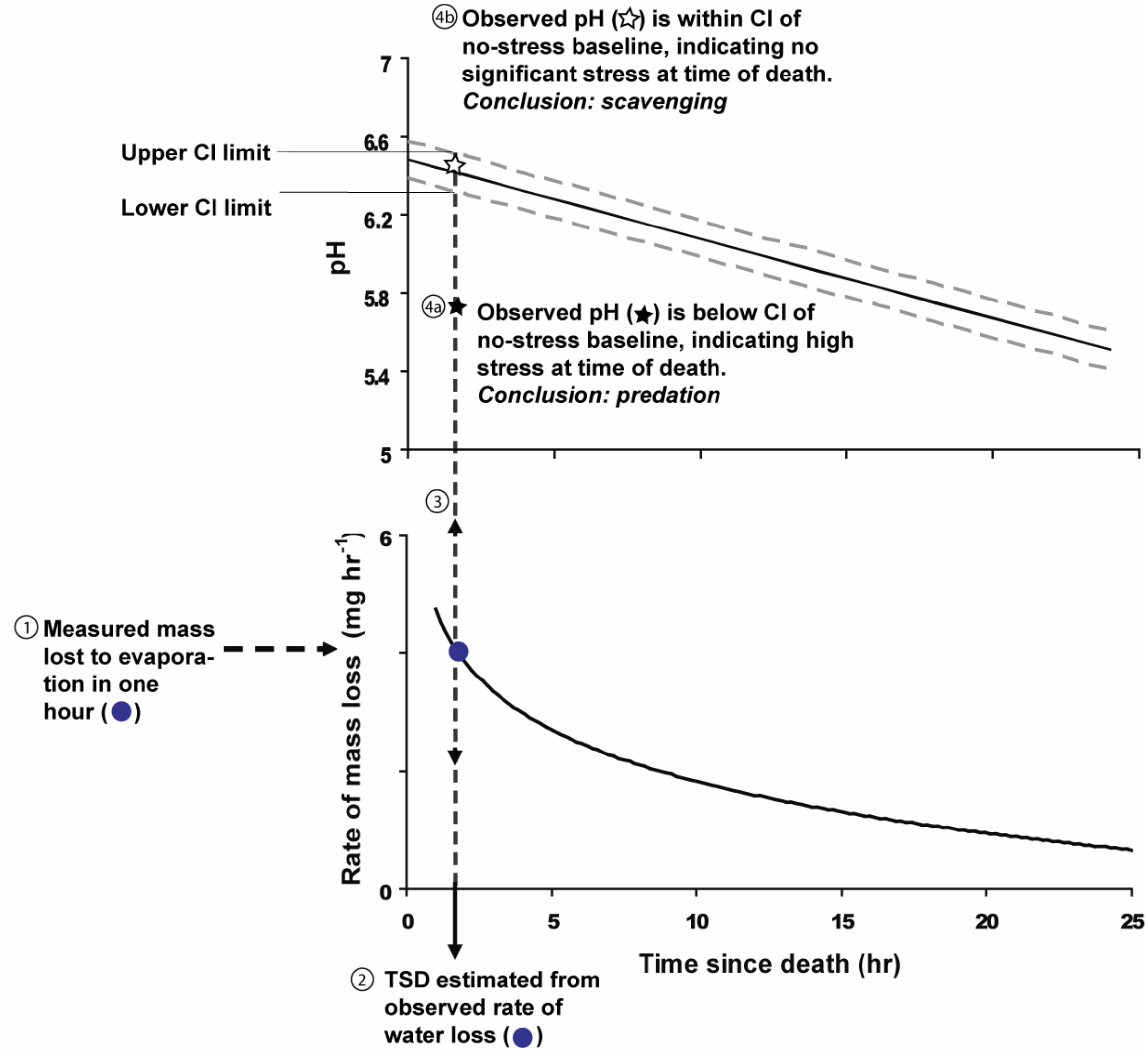

Figure 5. Conceptual diagram depicting how water loss and pH data can be used to classify diet items as prey or carrion. First, no-stress baseline curves are created for water loss and pH. When a diet item is collected, rate of water loss in one hour (blue dot) is determined and located on the no-stress water loss curve (1) to provide an estimate of TSD (2). Using this TSD estimate (3), we find the corresponding expected pH on the no-stress baseline. The observed thoracic muscle pH of the diet item (star) is plotted on the pH graph at estimated TSD and compared to baseline and its confidence intervals (CI). For the filled star (4a), the observed pH is well below the lower 99% CI. For open star (4b), the observed pH falls within the 99% CI of the baseline.