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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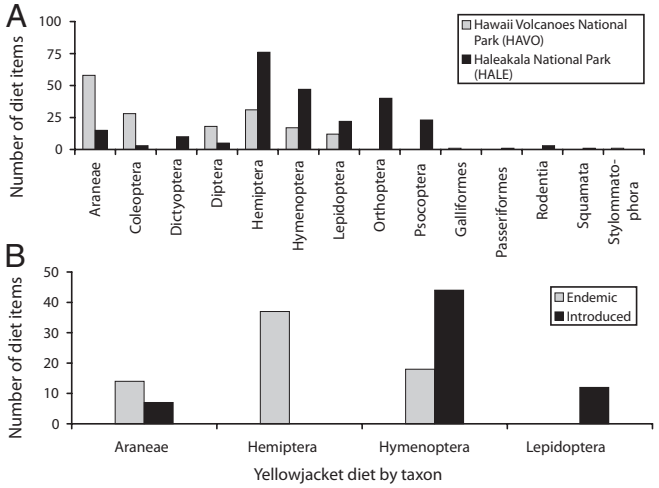

Fig. 1. (*A*) Molecular analysis of 412 diet items collected from foragers in 2 Hawaiian national parks. Invertebrates comprised the majority of the *Vespula* diet; vertebrate samples were scavenged carrion. (*B*) We classified diet items in the 4 most common orders of endemic arthropods at our field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

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.

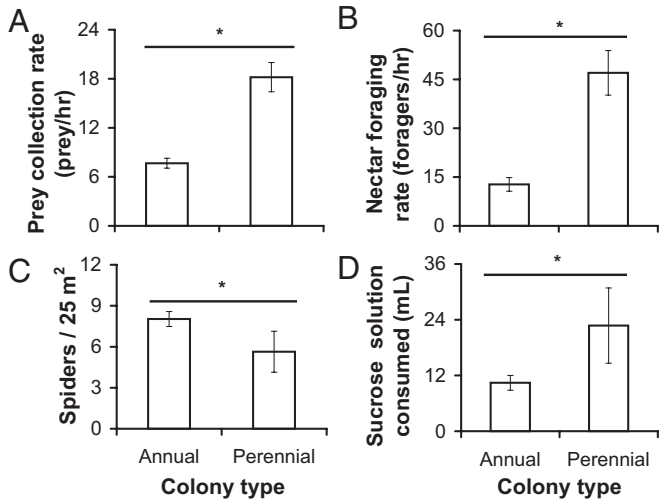

Fig. 3. Compared with annual yellowjacket colonies, perennial colonies exhibited higher rates of prey foraging ($t_{28} = 2.61$, $P = 0.014$) (*A*) and nectar foraging ($t_{21} = 4.79$, $P < 0.0001$) (*B*). Higher foraging rates translated into greater resource depletion: mean spider densities were lower 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*). *, $P < 0.05$.

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