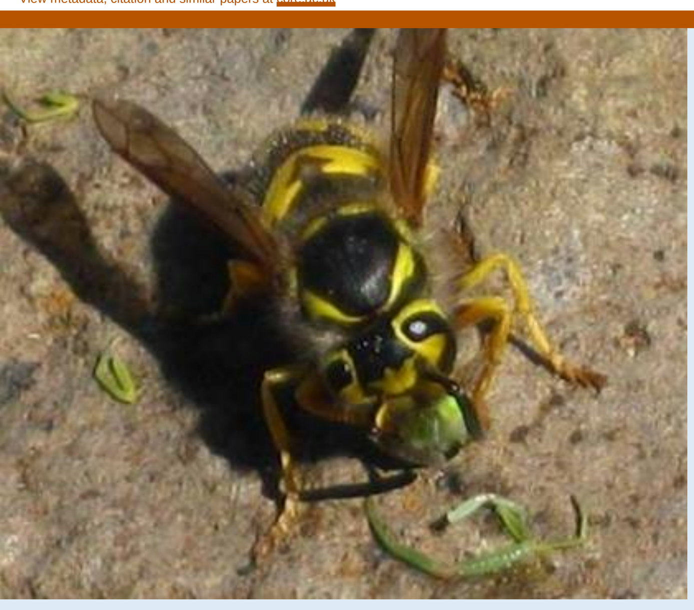

Diet subsidies and climate may contribute to *Vespula* invasion impacts

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Introduction

The introduction of non-native organisms is a leading threat to biodiversity. Oceanic islands like Hawaii may be especially sensitive to such introductions and thus serve as model systems for examining the ecological and evolutionary processes that underlie invasion dynamics.

Vespula (yellowjacket wasps) includes some of the most ecologically damaging invasive insects. Native to western North America, *Vespula pensylvanica* (western yellowjacket) became established over 30 years ago in Hawaii, where it reduces endemic arthropod densities. These wasps are opportunistic in their foraging behavior, quick to capitalize on rewarding resources. Similar to some other *Vespula*, these wasps exhibit plasticity in colony structure. While annual colonies are most typical of their native geographic range, up to 20% of colonies in the introduced range overwinter, producing perennial colonies that can reach sizes orders of magnitude larger than annual colonies **(Fig. 1)**. Such a shift in life history may greatly amplify net ecological effects.

Given the geographic distribution of *V. pensylvanica* perenniality—in Hawaii and, very rarely, southern California—factors associated with such climates may favor the expression of a perennial life history. Other invaders, such as the European honeybee (*Apis mellifera*), may promote yellowjacket survival by serving as diet subsidies. Here we examine how diet subsidies (in the form of honeybee colonies) and experimentally manipulated soil temperature may be involved in altering yellowjacket foraging behavior and colony phenology. Understanding the various factors affecting life history will help predict how trait evolution or plasticity may respond to future global change.

Objectives

- To examine how honey bees may affect yellowjacket foraging and life history traits through providing diet subsidies at times of seasonal dearth
- To examine how climate variables (such as temperature) may affect yellowjacket foraging and colony phenology

Methods

Honeybees and their products as diet subsidies
Honeybee colonies with their large, perennial workforce appear to provide reliable and abundant supplies of prey, carrion (Visscher 1983, Coelho & Hoagland 1995), and honey (De Jong 1990), potentially maintaining invasive *Vespula* populations at times of seasonal dearth. Our previous research documented the broad generalist diet of *V. pensylvanica* in Hawaii and revealed that honey bees comprise nearly a quarter of all Hymenoptera in the yellowjacket diet (3.5% of total diet) (Wilson & Holway 2010). First, we examined the physical proximity of yellowjacket nests to honeybee hives and assess how distance to honeybees influenced likelihood of overwintering, utilization of honeybees (or their products) and seasonal activity patterns using used GLMM or logistic regression as appropriate.

Effect of climate on *Vespula* life history
Abiotic conditions may directly contribute to this life history plasticity in *Vespula*. Given that brood and forager survival diminishes with decreasing nest temperatures (Gibo et al 1974), we test the hypothesis that maintaining warmer temperatures in late fall affects several *Vespula* life history traits, including increasing late season activity, delaying the production of gynes and delaying colony senescence. In the field, we can achieve warming using small (1-m diameter) open-topped Perspex chambers (OPCs) that passively increase soil temperatures inside the cone **(Fig. 2**Pilot experiments revealed passive heating through OPCs resulted in raising T_{min} by 4.8°C at depths of 15 cm as compared to temperatures in the absence of OPCs. **)**. We investigated how OPCs may be used to manipulate the temperatures of subterranean wasp nests. Using GLMM, we can compare forager activity rates, patterns of resource use and time of colony senescence between the warming and control treatments. Data from the warming experiments are preliminary.

All statistics were conducted in R (v. 3.1.0). Here, we present a preliminary analysis of foraging and phonological data. Data collection are ongoing.

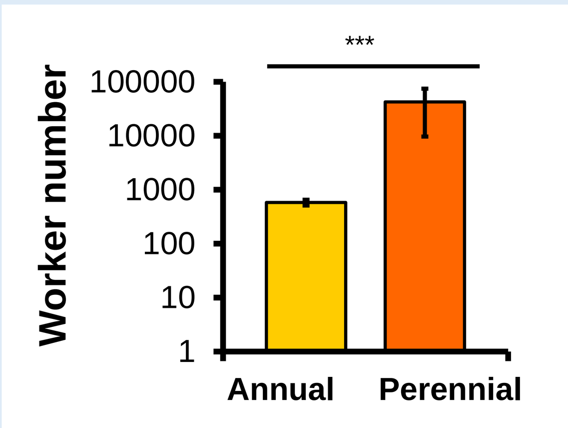

Figure 1. Mean number of workers from annual (N = 41) and perennial (N = 15) colonies of introduced *Vespula pensylvanica* in Hawaii.

Figure 2. Open top perspex cone used to passively heat ground-dwelling wasp nests. Based on design of Marion (1996). Photo: L. Yang

Results & Discussion: Honeybees as diet subsidies

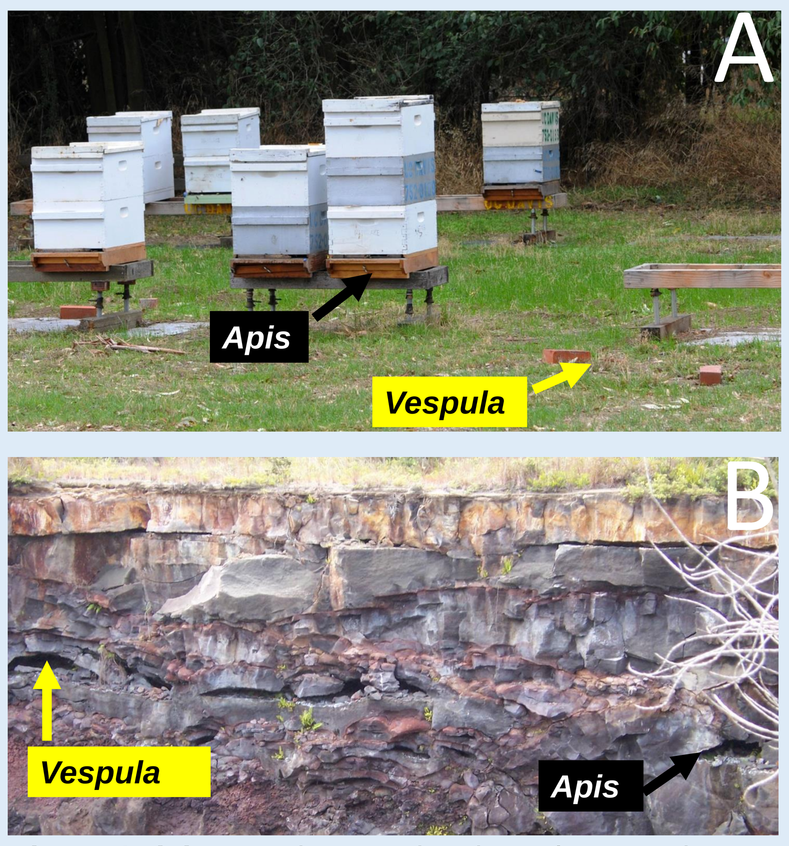

Figure 3. (A) *Vespula pensylvanica* colony nesting within meters of managed honey bees (Davis, CA) Photo: K. Garvey **(B)** Perennial *V. pensylvanica* colony within 50 meters of a honey bee colony (Hawaii Volcanoes National Park, HI).

- Western yellowjackets exhibit spatial associations with honey bees in both their native **(Fig. 3A)** and introduced ranges **(Fig 3B)**.
- Annual yellowjacket colonies disperse similar distances from a colony of either conspecifics and honey bees.
- Perennial colonies overdisperse from conspecifics colonies, and nest significantly closer to (<200m) honey bees **(Fig. 4)**. Because neither is limited for nest sites in Hawaii, this suggests that yellowjackets may be preferentially nesting near honey bees.

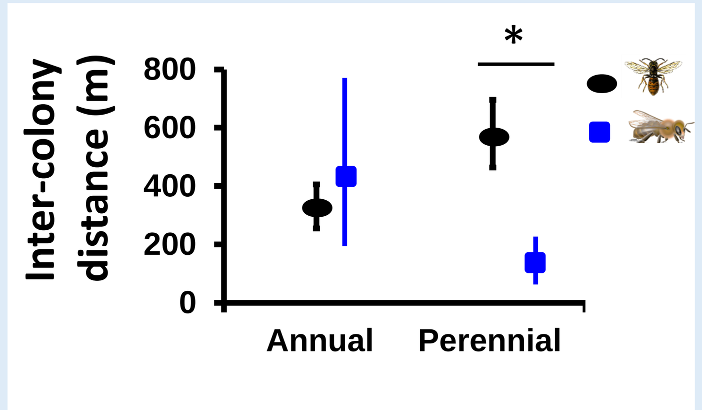

Figure 4. Annual *Vespula pensylvanica* colonies are equally dispersed from the nearest conspecific and honey bee nest (293 ± 53 m vs 312 ± 24 m respectively). N = 23 *Apis mellifera* colonies. N = 37 *V. pensylvanica* colonies.

Figure 4. Single western yellowjacket raiding feral honey bee hive. This forager was unchallenged by bees during her entire foraging trip inside the hive.

- *Vespula* wasps readily collect *Apis* foragers—live or dead. We have also observed very low levels of raiding behavior—where one wasp enters a bee hive unmolested and exits with a crop full of honey or larvae in their mandibles **(Fig. 4)**. This uncoordinated, individualized foraging strategy apparently fails to elicit honey bee defenses.
- Honey bees (and their products) may be particularly important to perennial yellowjacket colonies, which persist through the winter when other resources become scarce.
- Annual colonies closer to *Apis* hives exhibit 50% higher activity levels in October-December, when annual colonies typically senesce **(Fig. 5A)**.
- Honey bees are scavenged at a higher rate by yellowjacket foragers in late fall/winter—as annual colonies senesce but overwintering colonies persist **(Fig. 5B)**.
- Annual colonies closer to *Apis* hives delay senescing for an additional 75 ± 27 days per season **(Fig. 5C)**. Notably, 0% (0/22) annual colonies located > 200m from honey bees overwintered, 57% (8/14) annual colonies near honey bees did overwinter.

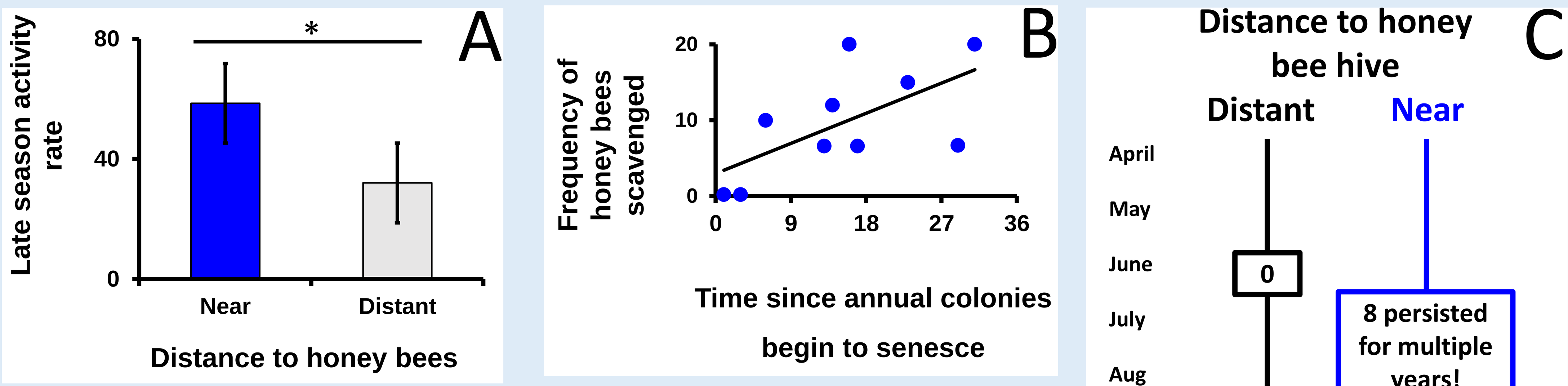

Figure 5. (A) Foraging activity at colonies late in the fall (in October through December) is significantly higher at *V. pensylvanica* colonies that are located within 200 m of an active honey bee hive ("near") as compared to activity levels at colonies that are located >200 m from an active bee hive ("far") (N = 62 *Vespula* colonies). **(B)** As the season progresses and annual colonies senesce, remaining colonies increase their utilization of honey bees as protein sources. This suggests that brood is still continuing to be present in these overwintering colonies. **(C)** Prolonged activity of annual colonies late in the fall is associated with proximity to honey bees. The foraging activity of annual colonies closer to *Apis* hives persists for an additional 74 days (± 29) per season. N = 22 and 14 *Vespula* colonies, respectively.

Results & Discussion: Climate effects

- Passively heating *Vespula* colonies in central California led to differences in T_{min} but not T_{max} or T_{avg} **(Fig. 6)**.
- Wasp forager entrance rates of colonies with OPCs were two-fold higher in the morning as compared to controls. Interestingly, colonies with OPCs persisted 15 days (± 5) longer than did control colonies (N = 5).

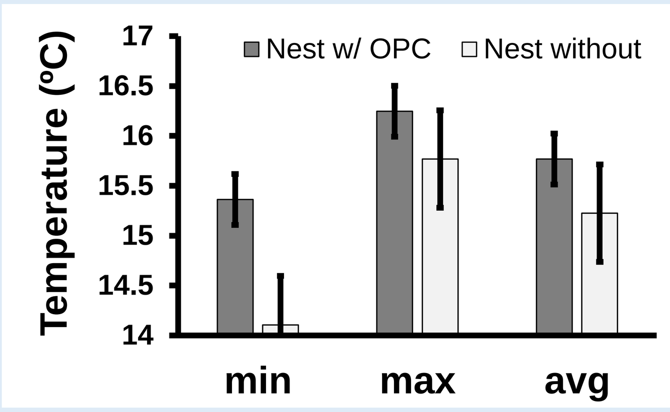

Figure 6. Minimum, maximum and average nest surface temperature with or without OPCs.

Conclusions

Multiple factors likely interact to led to the expression of the perennial phenotype. Our results suggest that honey bees and warm climates may both be interacting to influence overwintering. These data suggest that diet subsidies and mild climate contribute to invader life history shifts and ultimately will modify ecological impacts **(Fig. 7)**. While manipulative experiments are needed to determine if such factors are sufficient to induce overwintering, a better understanding what factors affect life history will help predict how trait evolution or plasticity may respond to global changes in the future.

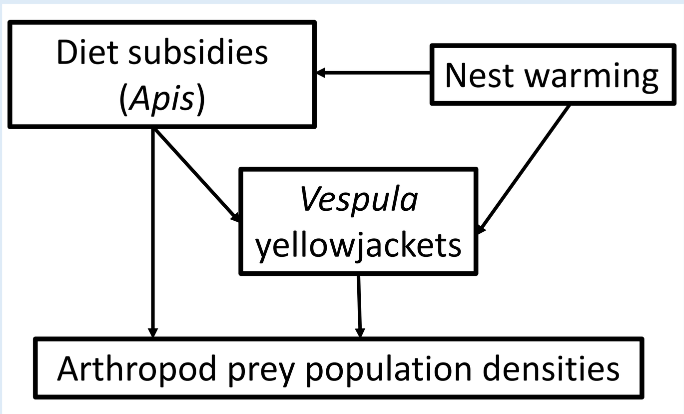

Figure 7. Conceptual diagram of how these ecological and climatic variables may affect invasive yellowjackets as well as net ecological impacts.

References and Acknowledgements

- Coelho, JR & J Hoagland. *Funct Ecol* **9**, 171-174 (1995).
- De Jong, D. 1990. in Honey bee pests, predators, and diseases, R. A. Morse, R. Nowogrodski, Eds. (Cornell University Press, Ithaca, NY), pp. 135-155.
- Gibo, DL, RM Yarascavitch, HE Dew. 1974. The Canadian Entomologist 106, 503-507.
- Marion, GM. 1996. Temperature enhancement experiments. *In:* ITEX Manual. U. Molau & P. Mølgaard (eds.). Danish Polar Center. Pp 17-22.
- Visscher, PK. 1983. *Anim Behav* 31, 1070-1076.
- Wilson, EE & DA Holway. 2010 *Ecology.* 91(11):3294-3302.

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