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Invasion Success and Management Strategies for Social *Vespula* Wasps

Philip J. Lester¹ and Jacqueline R. Beggs²

¹School of Biological Sciences, Victoria University of Wellington, Wellington 6140, New Zealand; email: phil.lester@vuw.ac.nz

²Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, Auckland 1072, New Zealand; email: j.beggs@auckland.ac.nz

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Abstract

Three species of *Vespula* have become invasive in Australia, Hawai'i, New Zealand, and North and South America and continue to spread. These social wasp species can achieve high nest densities, and their behavioral plasticity has led to substantial impacts on recipient communities. Ecologically, they affect all trophic levels, restructuring communities and altering resource flows. Economically, their main negative effect is associated with pollination and the apicultural industry. Climate change is likely to exacerbate their impacts in many regions. Introduced *Vespula* spp. likely experience some degree of enemy release from predators or parasites, although they are exposed to a wide range of microbial pathogens in both their native and introduced range. Toxic baits have been significantly improved over the last decade, enabling effective landscape-level control. Although investigated extensively, no effective biological control agents have yet been found. Emerging technologies such as gene drives are under consideration.

1. INTRODUCTION

Social insects are very successful invaders (111) and are difficult to eradicate or control at the landscape level (19, 85). Eusociality has evolved independently twice in the family Vespidae (9) and includes 23 species in the eusocial genus *Vespula* (Vespidae: Vespinae) with a native Holarctic distribution (7). Three of these species have established outside of their native range to become pests: the German wasp or yellowjacket (*Vespula germanica*), the western yellowjacket (*V. pensylvanica*), and the common wasp (*V. vulgaris*) (14).

The typical life cycle of *Vespula* wasps involves the production of new queens and males each autumn. Queens leave the nest to mate with one to several males and then find an overwintering site to hibernate. In spring, the queens emerge to establish a colony. Colonies grow from the single queen to nests consisting often of several thousand workers over the summer (52, 133) (**Figure 1**). The movement and introduction of the three invasive species to new regions has been via human traffic and the movement of goods such as saw timber (134) containing mated hibernating queens (14). These species appear to have a preference for hibernation sites associated with humans, resulting in multiple introduction events (24, 99). Other *Vespula* species could potentially establish in new regions if they are similarly moved around the globe and find suitable environments.

Here, we review the invasion history and the ecological, economic, and human health effects of these three *Vespula* species. We then discuss approaches to management of these invasive species populations, as well as the application of emerging control or eradication technologies.

2. INVASION HISTORY

Both *V. germanica* and *V. vulgaris* are widespread and abundant throughout their native range of Eurasia (5, 134) (**Figure 2**). Both wasps have been introduced to the Southern Hemisphere on multiple occasions over the last century. *V. pensylvanica* is native to temperate western North America and has been introduced into Hawai'i (26).

For a population to establish, introduced queens need to initiate nests in the receiving environment during spring. The physical condition of the wasps after transport is important, as successful queens appear to be those with substantial energy reserves of fat (78). The queen must disperse to establish a nest, find food, resist competitors (including other *Vespula* spp.), and survive any predators and parasites as well as the climate of its new environment. This stage of the life cycle naturally incurs the highest mortality (4, 10) and is likely a major bottleneck in the establishment of a new population.

Of the invasive species, *V. germanica* is the most widespread. It was first reported as having established outside of its native range in 1945, in New Zealand (139), and is now widespread and abundant on both islands (35). Intraspecific genetic variation in the mitochondrial DNA of *V. germanica* suggests there has been an introduction to New Zealand with a haplotype similar to that found in populations in the United Kingdom and a more recent incursion of a haplotype from southern mainland Europe (24, 99) (**Figure 3**). The Australian populations of *V. germanica* were first seen in 1959 in Tasmania and on the mainland in 1976 (36, 134). The most common haplotype sampled in Australia was identical to the most common haplotype in both the United Kingdom and New Zealand, consistent with a successful secondary incursion from New Zealand, although it could have been a direct invasion from the United Kingdom (24). One of the other two haplotypes suggests an incursion directly from the United Kingdom, while the third haplotype in southwestern Western Australia matched central Europe and likely represents a separate incursion (24).

Figure 1

A time line showing the population dynamics of common wasps (*Vespula vulgaris*) in an invaded range (Lake Rotoroa, New Zealand) and in their native range (York, England). Three phases of the wasps' life cycle are shown. In England, a year of relatively low wasp abundance was followed by a year of higher densities. The differences in abundance for the New Zealand data were achieved by pesticides. The milder climate of New Zealand results in a much longer wasp season of around six months, compared with four in England. In particularly mild or warm conditions, the nest may survive the winter, becoming large and perennial. Figure adapted from Reference 100, and photos courtesy of Colin McDiarmid.

The South African population of *V. germanica* occupies a small range (153) perhaps limited by suboptimal climate in the receiving environment (38, 143). The South African haplotype is distinct from the other introduced populations and appears to represent a separate introduction from central mainland Europe (24). In South America, *V. germanica* was first observed in Chile in 1974, though initially misidentified as *V. maculifrons* (114). Its southward spread into and across Argentina was almost four times faster (40.9 ± 2.0 km per year) than that of its northward movement (12.0 ± 0.9 km per year) (106), and it has spread as far south as Tierra del Fuego (130). The Argentine populations cluster with French and Spanish haplotypes (24), which is unsurprising given historical trade between France, Spain, and Argentina. *Vespula germanica* has been reported as

Figure 2

The global distribution of both (a) *Vespula germanica* and (b) *V. vulgaris*, obtained from published records (see **Supplemental Table 1**). Green symbols represent the presumed native range, and red the invaded range. North American samples of *V. vulgaris* are now thought to be *V. alascensis*, though it is still possible that this wasp has been introduced to North America and has not been sampled. The Hawaiian *V. vulgaris* is presumed extinct but may also have been *V. alascensis*. Inset is a graph showing the latitude range occupied by these species, with *V. vulgaris* having a significantly higher average latitude (one-way ANOVA: $F = 154.8$, $df = 1,911$, $P < 0.001$). Box plots show the mean and the 25th and 75th percentiles, with whiskers extending from the hinge to the highest or lowest value that is within $1.5 \times$ of the interquartile range of the hinge.

Supplemental Material >

established on several islands and more isolated regions, including the Ascension Islands, Madeira, the Canary Islands, and Iceland (14). It was reported in Missouri, United States, in 1974 and has since spread to California and the eastern United States and into Canada (1). The origins of these populations have not yet been identified.

Vespula vulgaris was first observed outside of its native range in 1921, again in New Zealand (8). However, individuals were collected only occasionally between then and 1945, and populations

Figure 3

The number of successful introductions of *Vespula* can be estimated by the diversity of mitochondrial haplotypes in the introduced range. These rarefaction analyses indicate that as little as two introductions and successful establishments have been made into New Zealand for *Vespula germanica*, with at least six for *V. vulgaris* (though the slope of the curve indicates more are likely to be found here with increased sampling). Argentina appears to have low genetic diversity, indicating a low number of introductions, for both species. Left panel adapted with permission from Reference 24, right panel adapted from Reference 99, and photos courtesy of George Novak.

became established in the late 1970s, although they then rapidly became widespread and abundant (35). There appears to have been several separate, successful introduction events, all likely originating from western Europe or the United Kingdom (99). This species was first observed in mainland Australia in 1958 and Tasmania in 1995 (2). Australian populations of this wasp have previously not been classified as invasive (14) and in recent years may have declined substantially. In 2016/2017, entomologists and pest control companies attempted to collect *V. vulgaris* from multiple sites in Tasmania and mainland Australia, where they had previously been recorded. But none were found, and it was suggested that it had been superseded by *V. germanica* (99). If true, this would contrast with New Zealand, where *V. vulgaris* replaced *V. germanica* in some habitats (81). Similarly, *V. vulgaris* was reported in Hawai'i in 1975, but it has not been seen since 1991 (31) even though *Vespula* populations have been extensively studied there (74, 75, 154, 156). It appears that at least two separate incursions of *V. vulgaris* have occurred in South America. Both of these are haplotypes observed in New Zealand and western Europe, indicating the South American populations could be a secondary invasion from New Zealand or directly from Europe (99). Populations have spread as far south as the Cape Horn Biosphere Reserve on Navarino Island in southern Chile (28). Finally, there are records of *V. vulgaris* establishing on the remote island of Saint Helena and in Iceland (12).

Vespula pensylvanica, by comparison, has a much-reduced distribution outside its native range. It has so far been recorded as established only in Hawai'i. Populations were first observed in 1921 (26). They are now especially abundant in upper elevations, where populations can successfully overwinter and attain large numbers (48).

CLIMATE CHANGE WILL ALTER *VESPULA* DISTRIBUTIONS AND DYNAMICS

Climate change can facilitate the establishment of invasive insect populations (119), although predicting the distribution and performance of invasive species under climate change is particularly challenging because large-scale, spatial, and temporal data sets are lacking (27). There is accumulating evidence that climate change is influencing *Vespula* distribution and dynamics. Milder temperatures are associated with *Vespula* extending their distribution northward in Finland (132). Colony development is occurring earlier in spring for *V. germanica* in Poland (144). At Rothamsted in England, the average abundance of *V. vulgaris* increased by two orders of magnitude, as temperatures increased and rainfall declined (100). Milder climates will also facilitate large perennial nests, increasing the production of queens and their predation pressure (77). In many temperate areas that experience warmer, drier conditions (10, 100), we expect to see wasps increase their distribution, become more abundant, and have greater impacts. Not all areas will be similarly affected by climate change; extreme-weather events (e.g., flash flooding) will negatively affect wasp abundance. Furthermore, some areas may become too hot for *Vespula* spp., which may stop foraging if temperatures exceed 40°C (89). Further research on climate change effects on *Vespula* populations will help guide management.

Vespula species are relatively difficult to distinguish from one another, leading to several instances where species have been misidentified or overlooked by researchers. *Vespula vulgaris* was incorrectly recorded as being on the mainland United States, and it was not until 2010 that it was documented that these populations were actually the cryptic *V. alascensis* (32). Although these two species are distinctive at the molecular level, the only reliable diagnostic morphological characters are of the male genitalia. Similarly, because *V. vulgaris* morphologically resembles the already established *V. germanica*, *V. vulgaris* had likely been established in New Zealand for at least five years before it was detected in the 1980s (44). South American populations of *V. vulgaris* were first discovered in 2010 (105), but their arrival was also initially overlooked by researchers. The cryptic markings and high densities of introduced populations make it probable that further incursions could occur without detection if at least one species of *Vespula* is already present.

It seems likely that *V. vulgaris* and *V. germanica* will continue to expand their ranges both nationally and internationally as human populations and trade increases. Within countries, their rate of human-mediated spread frequently exceeds 30 km per year (106, 107), while most queens probably disperse only a few hundred meters naturally to find nest sites (30, 75). Anthropogenic environmental change is also likely to facilitate their increasing distribution. Irrigation may increase the range of wasps in South Africa (38). Other invasive species may facilitate populations and the distribution of wasps, such as with the addition of large quantities of extra sugar resource (honeydew) with the invasion of the giant willow aphid (*Tuberolachnus salicis*) in New Zealand (131). Climate change is likely to alter the abundance and distribution of wasps (100, 132). (See the sidebar titled Climate Change Will Alter *Vespula* Distributions and Dynamics.)

3. FORAGING PRESSURE AND EFFECTS ON ECOLOGICAL COMMUNITIES

High resource levels and availability in the invaded range have dramatically influenced *Vespula* abundance and ecological effects (13). *Vespula* spp. typically have a broad, omnivorous, and opportunistic diet that includes honeydew, nectar, insect prey, vertebrates, and carrion (121). Between 0.8 and 4.8 million loads of prey items per hectare per season were estimated to enter *Vespula*

nests in New Zealand, with carbohydrate intake ranging from 78 to 343 L per hectare per season (76). The highest known wasp densities globally are in New Zealand beech forest (*Fuscospora* spp.), driven by the availability of honeydew produced by endemic scale insects *Ultracoelostoma assimile* and *U. brittini* (Hemiptera: Margarodidae). Honeydew beech forest represents about 15% of the indigenous forest cover in New Zealand (13), with high densities of scale insect producing 6–1,200 L of honeydew per hectare per year (20). Densities of wasps of up to 370 individuals per square meter of tree trunk have been observed foraging on this honeydew (83), with up to 40 wasp nests per hectare (72). One study in New Zealand estimated the peak annual *Vespula* biomass in a New Zealand honeydew beech forest (with mean estimate at peak of 3,761 g per hectare) was in some years four times greater than the combined biomasses of birds and introduced rodents and stoats (*Mustela erminea*) (138).

Vespula wasps utilize honeydew from a range of sources, although the carbohydrate and amino acid composition of honeydew varies with the insect species producing it (41). In New Zealand, *Vespula* were the dominant foragers on honeydew produced by an endemic scale insect species, *Coelostomidia wairoensis* (Coccoidea: Coelostomidiidae), on the endemic tree host kanuka, *Kunzea ericoides* (Myrtaceae) (64). Even though *Vespula* are primarily diurnal foragers, they can be the most abundant insect on honeydew-infested branches at night (mostly not feeding), and their presence could disrupt other nocturnal foragers (65). Wasps quickly learned to harvest honeydew from the giant willow aphid that was found in New Zealand in 2013, attaining high densities and interfering with beekeeping and stinging people (92). Nevertheless, *Vespula* abundance in non-honeydew beech habitat is an order of magnitude lower than in honeydew beech forest because of a much lower abundance of scale insects in the former (148), highlighting the importance of honeydew availability in supporting high wasp densities. Other forms of sugar, such as nectar, can also be influential in the invasion success of *Vespula*. In Hawai'i, *V. pensylvanica* forage on the floral nectar of *Metrosideros polymorpha* (Myrtaceae), which is a widespread endemic tree species that provides an abundant, readily available sugar resource (75).

Vespula also forage for protein resources throughout their life cycle, although their specific diet varies between study sites, probably owing to variation in the availability of honeydew, nectar, and prey, as well as the individual *Vespula* species preference and foraging ability. In both their native and introduced range, *V. vulgaris* and *V. germanica* prey on a broad range of arthropods (mostly lepidopteran larvae, spiders, Orthoptera, and Diptera), as well as vertebrates and carrion (76, 88, 126, 133). Similarly, in Hawai'i, the diet of *V. pensylvanica* was found to be primarily Hemiptera, spiders, Hymenoptera [including other wasps and honey bees (*Apis mellifera*)], and Orthoptera, as well as carrion from birds, rodents, and geckos (156).

Vespula wasps are efficient predators with effects on recipient communities that are density dependent. These wasps are largely absent for much of winter until early summer but become abundant over summer and especially in autumn. Most likely to suffer wasp attack are resident species that produce vulnerable life stages in times of peak *Vespula* abundance, such as tipulids (94) or lepidopteran larvae, which occur in autumn. When wasps reach their peak densities, caterpillars would have almost no chance of survival (probability of 10^{-78} to 10^{-40}) (16). Only 10% of experimentally placed kowhai moth caterpillars, *Uresiphita maoralis*, survived after 4 h under high wasp abundance in New Zealand honeydew beech forest. Spring-occurring caterpillars or autumn caterpillars in areas of wasp control had a much higher chance of survival (16). Similarly, the probability of the orb web spider (*Eriophora pustulosa*) surviving until the end of a wasp season in the same habitat was virtually nil (142). Not surprisingly, naturally occurring native orb web spiders were at low density. Spider and caterpillar abundance in Hawai'i were also found to significantly increase after *V. pensylvanica* colony removal (156). Wasps appear to markedly reduce the abundance of invertebrates and even remove food items cached by native birds (12). *Vespula*

germanica has been observed killing bird chicks in nests in New Zealand, with wasp attack probably initiated by the scent of albumen from the recently hatched eggs (110). *Vespula* are implicated in the long-term decline of common native birds in New Zealand honeydew beech forest (55).

Wasps exert sublethal effects on many species and communities. *Vespula* can deplete resources, forcing birds out of preferred habitat (21), and cause large numbers of other social insects such as honey bees to guard their hives, diverting the workforce away from food collection. Some vespid wasps demonstrate well-coordinated efforts to rob ants of food, with some wasps stopping ants from leaving their nest while other wasp nestmates harvest food uninhibited (93). Other sublethal effects can include a significantly reduced size and morphology of native ant species (28). Some herbivorous caterpillars can learn to avoid vespid predation by changing their foraging behavior to feed on cooler and less-profitable parts of the plant, which in turn lowers their fitness (136).

Overall, the presence of invasive *Vespula* influences communities by a combination of predation and competition: a multi-trophic combination of species displacement through behavioral avoidance and predation (21, 75, 154). The effects on communities and ecosystem function can be widespread. The altered communities after wasp invasion in New Zealand extend to below-ground decomposers. Wasp harvesting of honeydew can promote a bacteria and bacterial-feeding community at the expense of a fungus and fungal-feeding fauna, resulting in a dramatically higher rate of carbon sequestration (150). Pollinating communities and plants are also affected. For example, invasive *V. pensylvanica* dominates nectar resources through both superior interference and exploitative competition (75). It both displaces and consumes native and nonnative pollinators decreasing overall pollinator effectiveness and the fruit set of *M. polymorpha* (74). We do note, however, that in some cases, introduced insects can provide important ecosystem services (137); there are occasions when *V. germanica* and *V. vulgaris* are effective pollinators (87) and *Vespula* foraging pressure may replace that of native species that have been lost from the system (20).

4. CHANGES IN BIOLOGY BETWEEN NATIVE AND INTRODUCED RANGES

The role of climate in insect population dynamics has long been debated, including for *Vespula* populations. Wetter and colder conditions in spring have often been related to relatively lower wasp abundances (2, 10, 108), though others have failed to find any such relationship (4, 61). Some 59–66% of the interannual variation in abundance of *V. vulgaris* in their native and introduced ranges was due to climate and density dependence (the abundance of wasps from the previous year) (100). Warm and dry spring weather conditions increase wasp abundance, and no evidence of population cycling was observed. The milder climate in New Zealand influences the emergence and population density in *V. vulgaris*: In England, wasps are abundant for four months of the year, compared to six in New Zealand (100) (**Figure 1**). The milder climate and longer active season in the invaded range has also enabled perennial colonies to develop in Australia, Hawai'i, and New Zealand for *V. germanica* (77), *V. pensylvanica* (156), and *V. vulgaris* (95). These perennial colonies can grow extremely large and exert substantial predation pressure. A perennial colony of *V. vulgaris* had ~230,000 workers, with 593,489 in a large *V. pensylvanica* nest (115). Harris (77) estimated that one large perennial *V. germanica* nest in New Zealand consumed 99 kg of prey in a year, compared to just 1.8 kg for an annual colony. One factor in the widespread invasion success of *Vespula* is their ability to have these post-introduction phenotypic changes in life history (156).

Behavioral plasticity and cognitive abilities have contributed to the predatory success of invasive *Vespula*. Visual, auditory, and olfactory stimuli are all used in the location of prey items, with wasps even learning to follow pheromone plumes to find prey items (84). They quickly learn to associate spatial cues with rewarding food resources (37, 121), appearing to integrate multiple cues to return

to resources even if obvious cues are moved (155). Information previously or simultaneously provided by experienced nestmates can influence food choice and resource discovery by naive foragers (128). They have the ability to resolve complex tasks that include the recognition of different human faces (8). Their adaptive and plastic foraging behavior has led to the development of novel interactions within their invaded range. For example, wasps were observed to remove competing ants from food items (71). The wasps would carefully pick up the workers in their mandibles, quickly flying backward, and dropping them apparently unharmed several centimeters away from the food. The efficiency and the frequency of this behavior significantly increased with the abundance of ants.

5. ECONOMIC AND HUMAN HEALTH IMPACTS

Wasps affect human health as a result of their venomous sting, causing both allergic reactions and accidents as people take evasive action to prevent being stung. Because of uncertainty of the venom origin, statistics on stings from both bees and wasps are often combined, and the rate due to *Vespula* alone is undetermined. The frequency of different species stinging people appears to vary between regions. Populations of central and northern Europe experience a prevalence of vespids (mainly *Vespula* spp.) and honey bee stings, whereas people in the Mediterranean area are stung by *Polistes* and *Vespula* more frequently than honey bees (22). Anaphylaxis from insect stings is thought to occur in approximately 3% of adults and may be fatal even on the first sting (68). Human mortality rates from hymenopteran stings have historically been estimated at 0.09–0.45 deaths per year per million people (33). A more recent Australian analysis estimated a crude death rate attributable to wasps of 0.1 per million people (152). Of the 199 per 100,000 people admitted to hospital for envenomation over the 12-year study, 31% were caused by contact with wasps or bees (152). More human males seem to be stung than females (113, 152). Many of the statistics associated with mortality attributed to wasps are subject to error: More heart attacks (myocardial infarctions) due to wasps occur than are likely recorded (22), and “wasps” include a range of species other than *Vespula* spp. (22, 68, 152).

Estimating the economic costs of introduced *Vespula* spp. is challenging. There are direct costs that are easily quantifiable (e.g., honey bee hive mortality) but also indirect costs that are difficult to assess (e.g., loss of honey bee productivity and pollination due to enforced hive guarding). Although *Vespula* may affect honey bees, *Vespula* themselves can be effective pollinators, and in one study in Californian coastal scrub, they were more effective pollinators than honey bees (140). MacIntyre & Hellstrom (102) assessed the economic impact of *V. germanica* and *V. vulgaris* across industries, society, and the natural environment in New Zealand. They estimated that these wasps cause an annual cost of NZ\$133 million to the economy (**Figure 4**). The vast majority of this impact was from the effect of wasps on bee survival and abundance, with flow-on effects to pastoral farming. They estimated that removing wasps would increase the pollination rate of clover (*Trifolium* spp.) by 2.5%. That small increase would reduce the need for fertilizer use and the reseeded of clover fields, resulting in a NZ\$62 million increase per year to the pastoral sector (**Figure 4**). The other major effects of *Vespula* in New Zealand were on the honey bee industry. About 1 million hectares of *Fuscospora* beech forests (13) provide honeydew that could be utilized by the apicultural industry to an annual value of NZ\$57.8 million per year. Wasps attack bees, destroy hives (34, 116), and cause management costs. Furthermore, wasps had direct impacts on animal health, forestry, arable farming, horticulture, human health, and traffic accidents, although the annual cost of these was less, at ≤NZ\$1.4 million per year (**Figure 4**) (102).

Wasps have a range of similar and additional effects in other countries. For example, in South Africa, *V. germanica* attack bee hives and damage fruit. In addition, these wasps cause a significant

Figure 4

A summary of estimated annual economic impact of invasive German (*Vespula germanica*) and common (*V. vulgaris*) wasps on the New Zealand economy, from a 2015 evaluation (102). The inset photograph is of a wasp threatening a honey bee that is guarding the entrance to her bee hive. Figure adapted from Reference 96, and photo courtesy of Chris Robins.

loss of productivity in vineyards because workers refuse to pick grapes in areas with large numbers of aggressive wasps. They also chew on the sores or scabs of cattle, causing knopvelsiekte (a hide condition) (83). In Israel, *V. germanica* were recorded inflicting lesions on the teats of dairy cows (*Bos taurus*), causing mastitis and *Streptococcus* infections (157). *Vespula* can also promote plant disease after feeding on crops such as grapes (103). Although the vast majority of the literature on invasive social wasps has focused on negative effects of these animals as pests, it is possible that they also exert some economic benefit in invaded ecosystems. *Vespula* spp. have long been known as voracious predators of pestiferous flies (133) and may even have had a role in limiting the establishment and spread of other invasive species (102). Several authors (70, 94) have suggested that members of another vespid genus, *Polistes*, could be used as biological control agents, and one author (46) even suggested that *Vespula* spp. wasps could be cultured for biological control in New Zealand.

6. COMPETITOR AND ENEMY RELEASE HYPOTHESIS

The enemy release hypothesis proposes that an introduced species will become abundant in a novel range because of the absence of its coevolved natural enemies (90). Classical biological control programs rely on the importation of these coevolved pathogens, predators, and parasitoids to regulate pest populations. The role of competitor release as a factor contributing to the success of invasive species has also been highlighted (90).

A developing *Vespula* nest is particularly vulnerable to competitors and predators. This queen colony phase (6) is when the queen must find a nest site, build a small nest, forage, and produce and feed larvae. Other *Vespula* wasps are a major limiting factor for successful development. There can be substantial inter- and intraspecific competition for nesting sites among wasps, involving gladiatorial battles between queens in spring (109). Some nests have been observed containing 25 corpses of queen wasps from two different species. Usurpers within the native range of many *Vespula* include some obligate social parasite species such as *V. austriaca*, which invade nests and kill the queen and many workers before dominating the remaining workers into rearing new queens for the parasite wasp (117). Estimated usurpation rates by parasitic vespids wasps range between 23% and 65% in various states of the United States (6). The presence of these parasites and competitors would likely limit the probability of a newly introduced queen establishing in a new location.

Mature *Vespula* nests that contain hundreds or thousands of workers are much more resilient and seldom fail (133). In areas such as Europe and North America, small mammals may exert high predation pressure on young nests (149) and larger animals like badgers and bears will attack and consume mature nests (69, 149). Predatory birds such as the Oriental honey buzzard (*Pernis ptilorhynchus*) in Japan specialize in social wasp predation (86). These vertebrate predators are absent from much of the introduced range, with only limited evidence that mammals such as mice occasionally attack nests in New Zealand (48). Twenty-four common bird species have been listed as occasionally eating wasps, including blackbirds (*Turdus merula*), crows (*Corvus* spp.), and starlings (*Sturnus vulgaris*) (133), but are unlikely to have any significant effect on wasp populations.

The native range of *Vespula* wasps also contains invertebrate predators or parasitoids that can be found in mature nests. Spradbery (133) described approximately 137 insect species and several mites that are found in wasp nests. Mites, such as *Pneumolaelaps niutirani*, are found in and on *V. germanica* (60), possibly transmitting disease. The wasp nest beetle *Metoecus paradoxus* (Coleoptera: Ripiphoridae) is widespread but mostly found only in low abundance in 20–80% of nests (133). There are several species of *Volucella* hoverflies that attack wasps, including species that are obligate ectoparasitoids of vespids. Other parasitoids include the trigonayid wasp *Bareogonolus canadensis*, which has been considered as a biocontrol agent for *V. vulgaris* in New Zealand (30). Attempts at introducing some species for biological control are described in the next section.

Wasps carry a diverse array of potential pathogens. This includes many fungal, bacterial, nematode, protozoan, and viral species associated with *Vespula* (59, 97, 99, 122). Nest collapse due to disease in *Vespula* has been observed (133). Archer (3) found nest irregularities, including atypical brood development, in approximately half of 214 *V. vulgaris* nests in England. Similarly, out of six *V. vulgaris* nests in New Zealand, every wasp examined was infected with *Kashmir bee virus*, with an increasing viral load associated with significantly higher immune response (43). Nest viral loads and immune gene expression in these wasps were significant predictors of nest size and queen production (43). These results are indicative of prevalent microbial disease on wasp populations.

It is possible that some pathogens could be utilized for biological control (67, 80). A key problem with these pathogens, however, is that they are typically generalists affecting a wide range of related insects, including invasive ants and honey bees (72, 101). Spatial patterns of increasing pathogen infections in one bee host species have been observed to correlate with infection in others (62). There is likely to be spillover of pathogens from invasive to native species, which can be of major conservation concern in hymenopteran communities (29). Any future attempts to use pathogens for wasp control may have unintended nontarget effects unless host-specific pathogens can be found.

Overall, do invasive *Vespula* benefit from competitor or enemy release? There were few or no related competing vespids present for the first introductions of *Vespula* spp. into many areas, including Hawai'i and New Zealand. The absence of competitors or parasitic usurpers in recipient communities must be a considerable advantage for queens establishing a nest. It is clear

that predators and pathogens can destroy nests and limit productivity, but whether these natural enemies exert significant population regulation even in the native range of *Vespula* is still uncertain. Wasps seem unlikely to experience substantial pathogen release, although there may be variation between areas in their microbial communities (97).

7. CONTROL

Edwards (52) recognized nine principal ways by which social wasp control has been attempted, each with varying levels of efficacy. These methods include the killing of hibernating spring queens, destroying nests, insecticidal baiting, trapping, electric grid devices, contact insecticides, preventative measures, biological control, and integrated pest management. Some of these are useful only at local scales or the immediate area of application. Methods of population level control and more recently proposed novel control methods are discussed below.

Biological control offers the potential for efficient, self-sustaining *Vespula* control over large areas. One Holarctic parasitoid that has been used in biological control attempts against *Vespula* is *Sphecophaga vesparum vesparum* (Hymenoptera: Ichneumonidae) (48). These parasitoids were released throughout New Zealand and established in several locations (15). The *Sphecophaga* life cycle is complex, with winged females entering nests and ovipositing eggs onto late-fifth-instar larvae or pupae, from which three types of cocoons are produced. One cocoon produces brachypterous females within two weeks, the second produces winged females and possibly males, and the third cocoon produces overwintering adults that may live for up to four years as cocoons (141). The brachypterous cocoons are essential for successful wasp biological control, because these females do not disperse and instead parasitize large numbers of wasps within their natal nest. Beggs et al. (18) found that biocontrol against *Vespula* using *S. v. vesparum* had not achieved a measurable reduction in the wasp population in New Zealand. Although the number of parasitoids per parasitized nest was initially high, this was not sustained and subsequent nests typically had very few brachypterous *Sphecophaga*. These poor results could be due to the low genetic variability of the released parasitoids (15) and/or a mismatch between the origin of the parasitoid and the wasp host (24, 99). However, they may just be reflective of actual parasitism rates; one study in the native range found *S. v. vesparum* was rare and a maximum of only 0.4% of brood was parasitized (3). Barlow et al. (11) concluded that this or any other potential parasitoid would need a much higher effective rate of increase to control wasp populations and that alternative biological control agents are also likely to be ineffective. Two other parasitoids, *S. v. burra* from the state of Washington in the United States and *S. orientalis* from Israel, were also released in New Zealand (45, 47); however, there has been no evidence that either established (17). This may be because of parasitoid-host incompatibility since it was later discovered that the host in the United States was *V. alascensis* and not *V. vulgaris* (32).

There are a range of other organisms currently under consideration for biological control of invasive *Vespula*. These include the brood parasites *Volucella inanis* (Diptera: Syrphidae) and *M. paradoxus* (Coleoptera: Ripiphoridae), and *Leopoldius* spp. (Diptera: Conopidae). In New Zealand, additional strains of *S. v. vesparum* are being sought in the hope of overcoming any issues with genetic diversity. Nematodes (63, 104) and pathogens (67, 80) have also been proposed or tested as biological control agents. Although these natural enemies could potentially provide cost-effective control, there are nontarget issues to consider first, and others have not been optimistic for success. Edwards (52) was especially pessimistic, suggesting that biological control was unlikely to be effective and further research was unwarranted.

Another potential control option is the use of artificial pheromones, in either mating disruption or attractant forms. Mating disruption could be accomplished by saturating areas with sex

pheromones to confuse the males' ability to find receptive females, but it would likely be expensive to achieve this at a large scale. Sex pheromones could also be employed in the male lure-and-kill approach (54). *Vespula vulgaris* was found to use sex pheromones (25), although no evidence was observed for such pheromones in a study on sex attraction responses for *V. pennsylvanica*, *V. alascensis*, and *V. squamosa* (40). Derstine et al. (40) did find that males may be attracted to gyne-produced pheromones in different contexts, an observation that is supported by previous work in wind tunnels with *V. squamosa* (118). The discovery and description of any specific compounds used as sex pheromones has remained elusive but will be needed before pheromones can be used for wasp control.

Attractive, insecticidal baits offer the potential of a broader geographic scale for wasp control and currently appear to be the most effective method to reduce populations of *Vespula* and most social insects (42). This method relies on an attractive bait matrix mixed with an insecticide that will not deter collection that workers then feed to the colony. Volatiles from a range of natural carbohydrates or proteins can attract social wasps (26, 50, 135, 145, 151). A wide variety of synthetic compounds have also been shown to attract *Vespula*, including acetic acid, butyl butyrate, isobutanol, heptyl butyrate, octyl butyrate, 2,4-hexadienyl butyrate, and 2-methyl-1-butanol, or mixtures of these different chemicals (53, 91, 92). Combinations of volatiles may be better attractants than individual sources, although results vary between species (91, 146). Nontarget effects can be reduced if the baits have limited carbohydrate content (and are thus not attractive to bees) and if they are deployed when wasps are abundant and dominating preferred food resources.

Currently, the most effective toxin is fipronil, a phenylpyrazole, but a range of chemicals have been tested, including chlorpyrifos, hydramethylnon, permethrin, sodium fluoroacetate, and sulfluramid (79, 124, 125). Insecticidal baits have been successfully used against *V. germanica*, *V. pennsylvanica*, and *V. vulgaris* to reduce wasp activity by up to 99.7% (19, 73, 79, 124, 127). Perhaps the largest known area for wasp control using toxic baits has been with the use of a protein-based bait in New Zealand. Edwards et al. (51) placed bait stations on a grid at 300 × 50 m apart in areas of up to 2,000 hectares, using one application of Vespex containing 0.1% fipronil. Wasp traffic declined by up to 97% 20–38 days after baiting (51). Thus, baiting can be effective over relatively large areas, although reinvasion is likely from queens in the following autumn and spring. Eradication is currently unlikely to be feasible where wasps are widespread, but insecticidal baits may be an option for eradicating isolated pockets of *Vespula*.

New, emerging techniques are being developed for the widespread control or eradication of insect pests. For example, Blackwood et al. (23) proposed that the intracellular bacteria *Wolbachia* could be introduced into pest populations to capitalize on preexisting Allee effects and eradicate insect pests. Trojan female techniques that rely on maternally inherited mitochondrial DNA mutations that affect male but not female reproductive fitness are an emerging technique for pest control (66). Gene drives are also an emerging approach with potential for pest eradication and are under discussion for their use on *Vespula* in New Zealand (39) (see the sidebar titled Gene Drives as a Potential Method for Wasp Control). As nearly all the biological requirements and logistical parameters for a gene drive (e.g., high gene flow, high fecundity, short generation time) (112) are satisfied for *Vespula* spp., this technology may be a viable management option in countries such as New Zealand.

8. CONCLUSIONS

Vespula spp. can be major pests in many areas of their invaded range, especially where there are abundant carbohydrate resources. They are recognized as a critical issue in countries such as

GENE DRIVES AS A POTENTIAL METHOD FOR WASP CONTROL

RNA-guided gene drives based on CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9) are being proposed as tools to reduce or eradicate pests (82, 112), including *Vespula* wasps (39). Vespine wasps have a haplodiploid sex-determining system, with successful mating needed for new workers to be produced the following spring and summer. A CRISPR/Cas9 gene drive system will fail if modified queens do not spread their genes via the production of new queens in the following autumn. Male-specific traits are a logical CRISPR/Cas9 target; for example, the *boule* gene could be manipulated for nonviable sperm production (129). A queen mating with infertile males would result in nest failure, but modified queens mating with heterozygous males would allow the CRISPR/Cas9 modification to persist and spread. Given the limited genetic diversity of *Vespula* in their introduced range (**Figure 3**), and by designing guide RNAs specific to invasive populations, implementing a gene drive system that does not function for all genotypes in the native range (precision drives) should be possible (58). Limited genetic diversity in the introduced range would mean that variation enabling resistance (49) would be unlikely. A so-called social license to operate is essential prior to the release of any gene drive (39).

New Zealand (98), where the public also identify these wasps as a priority for pest management (123). They and related social wasps, such as Asian yellow-legged hornet, *Vespa velutina*, continue to be introduced and spread via human trade (14). For invasive *Vespula*, there has been some progress toward achieving the Convention on Biological Diversity's Aichi Target 9, that "by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment" (147). We have identified and prioritized species and can control local populations using pesticides, but considerable work is needed to slow further introductions, improve the effectiveness of widespread control, and/or achieve eradication.

FUTURE ISSUES

1. Detecting and preventing *Vespula* from invading new areas remains a challenge. New tools and strategies are needed to improve the ability to detect and manage new incursions (56, 120).
2. Substantial advances have been made over the last decade in the ability to attract wasps to toxic bait for nest control (51, 73, 91, 124). Methods of attraction and control should be further advanced for species-specific toxicants (e.g., gene silencing or RNA interference technologies) (158). Eradication at local or small scales may now be possible using these technologies.
3. Effective and safe methods for control are needed at large spatial scales. Next-generation technologies are being proposed, such as gene drives (39, 82) and *Wolbachia* infections combined with Allee effects (23), which may offer cost-effective control. Eradication at larger scales may be possible using these developing techniques. Biological control may provide population suppression, although no attempts to date have been effective.
4. *Vespula* spp. host and are infected by a range of diseases that are shared with honey bees and other insects (43, 59, 97, 101, 122). The frequent high abundance of *Vespula* spp.

in their invaded range may prove to be a significant disease reservoir and a hidden nonpredatory effect of these wasps.

5. Climate change will continue to alter the distribution, abundance, and population dynamics of invasive social wasps (57, 100, 132). Milder climates in some areas may see more perennial nests and substantially more wasps. These effects, combined with the continued range expansion of wasps into South America and other regions, will lead to new conservation issues.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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**74. Management of
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increase native and
introduced bee
visitation, increasing
pollination and fruiting.**

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156. Shifting from small annual colonies to large perennial colonies in *Vespula pensylvanica* intensifies the colonies' impact.