

Density-dependent effects of an invasive wasp on the morphology of an endemic New Zealand ant

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Abstract Invasive species can cause extinction, but perhaps more commonly they compete for resources, resulting in subtle life history modification in native species. Changes in food quantity and quality as a result of biological invasions have the potential to influence the size and morphology of native species. The invasive wasp *Vespula vulgaris* reaches its highest known population densities in the honeydew beech forests of New Zealand, where it competes with native ants (*Prolasius advenus*) for food. We tested the hypothesis that this competition would reduce ant worker size in areas of high wasp density. A significant reduction in worker size was found with increasing invasive wasp density, after accounting for site and environmental covariate effects. However, this significant average reduction in size was small. For example, an increase of 10 wasp nests ha⁻¹ was associated with an average decrease of only 1.2 % in the Weber's length of native ant workers. We also examined scaling of morphological relationships in ants to test the hypothesis that scaling would vary between ant populations at differing wasp densities.

Scaling relationships for six out of eight measured morphological characters significantly differed in ants when subject to high wasp densities, relative to areas of low wasp abundance. These results indicate that invasive wasps can potentially reduce native ant size, and alter scaling relationships, likely by limiting resource availability during ant development. Such subtle effects of an invasive species may be common in situations where invasive species exert strong competitive pressure.

Keywords Competition · *Prolasius advenus* · Relative growth · Allometric scaling · *Vespula vulgaris*

Introduction

The detrimental impact of invasive species on native biota is widely viewed as being second in magnitude only to habitat destruction (Vitousek et al. 1996). While predation by introduced organisms can result in extinction, the effects of competition on recipient taxa are typically considered to be sub-lethal and often much less apparent than predation (Davis 2003). Resource exploitation or interference competition by invasive species can result in a reduction in fitness, survival or growth in native species (Lockwood et al. 2007). For example, Vogel and Pechmann (2010) found competition between native and invasive

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tadpoles resulted in a decrease in body size measures and a lower rate of survival to metamorphosis for the native species. Furthermore, the effect of interspecific competition on larval size was found to be density dependent in a study of four anuran species. Increasing larval density was accompanied by a reduction in larval size at metamorphosis. However, these decreases in anuran size were not associated with a decrease in survivorship (Boone 2005).

The quantity and quality of food resources available during larval development can be a major contributing factor to adult size in holometabolous insects (Emlen and Nijhout 2000; Mirth and Riddiford 2007). The size of the final larval instar prior to pupation is directly correlated with adult size (Wheeler 1991). Numerous studies have indicated that a reduction in the availability of food resources at the juvenile stage results in the production of smaller adult offspring in holometabolous insects (Wheeler and Buck 1992; Emlen and Nijhout 2000; Mirth and Riddiford 2007; Sorvari and Hakkarainen 2009). By contrast, adult shape, or the relative proportion of one body part to another, is dictated after pupation has been initiated. An individual's body parts, such as the structures of the head, thorax and the appendages, develop from the imaginal discs (Emlen and Allen 2004). This developmental process occurs in a closed system during the pre-pupal and pupal stages, when feeding has ceased (Nijhout and Wheeler 1996) and is entirely reliant on reserves accumulated by the larva.

Social insect colonies are often composed of different castes or specialised adult forms. According to caste ratio theory (Oster and Wilson 1978), colonies of species such as ants should be able to alter the proportion of each morph produced in response to environmental change. Allometries, or size independent growth rates, in holometabolous insects have been shown to change rapidly (Emlen and Nijhout 2000). For example increased competition has been shown to upregulate soldier production in *Pheidole pallidula* (Passera et al. 1996). In other ant species, variation in the availability of food has been shown to increase colonies' relative investment in soldiers (McGlynn and Owen 2002), alates (Sorvari and Hakkarainen 2009) and workers (Ode and Rissing 2002).

The common wasp *Vespula vulgaris* (L.) is an invasive species distributed throughout New Zealand. The New Zealand population of common wasps are

likely to have originated in England or western Europe, and with several introductions since the 1920s (Lester et al. In press). After becoming widespread and abundant in the 1970s, this species' highest population densities have been recorded in the *Fuscospora* beech forests of the Nelson Lakes area (Thomas et al. 1990; Barlow et al. 2002). Their success has been attributed to the presence of abundant honeydew resources (Barlow et al. 2002), which are a sugary exudate excreted from the anal filament of the juvenile scale insect *Ultracoelastoma assimile* (Maskell) that infests the *Fuscospora* beech forest (Morales et al. 1988). The wasps' consumption of honeydew is so great that it has been found to reduce both the quality and quantity of the resource to the detriment of native bird species (Moller and Tilley 1989; Beggs and Wilson 1991; Moller et al. 1991) and insects (Moller and Tilley 1989). In addition, *V. vulgaris* is a voracious predator of many invertebrate orders (Harris 1991; Harris and Oliver 1993; Toft and Beggs 1995) and likely competes for invertebrate prey with insectivorous birds (Moller and Tilley 1989) and predatory invertebrates (Thomas et al. 1990).

The endemic small brown bush ant *Prolasius advenus* (Fr. Smith) is the most abundant ant species in these forests (McColl 1975; Grangier and Lester 2011; Duthie and Lester 2013). This ant has no distinct worker sub-castes (e.g. worker and soldier castes), but varies in total length from approximately 2.9–3.5 mm (Don 2007). It feeds on macro-invertebrate prey and is dependent on honeydew as a source of carbohydrate (Smith 1896; Smith 1969; Don 2007). The diet of the common wasp displays significant overlap with that of *P. advenus* (Don 2007; Duthie 2011; Grangier and Lester 2011). The wasp therefore represents a significant competitor that appears to exert a density-dependent restriction of both carbohydrate (Moller and Tilley 1989) and protein (Harris 1991) resource availability to native species such as ants. These wasps are not known to eat worker ants, though will consume reproductive stages of *P. advenus* (Harris 1991; Harris and Oliver 1993). Here we use a collection of morphological measurements to test the hypothesis that ant (*P. advenus*) workers are smaller in areas where wasps maintain high population densities, compared to areas where wasps are less abundant. As caste ratio theory (Oster and Wilson 1978) posits that colonies should be able to increase the relative abundance of particular worker morphs according to

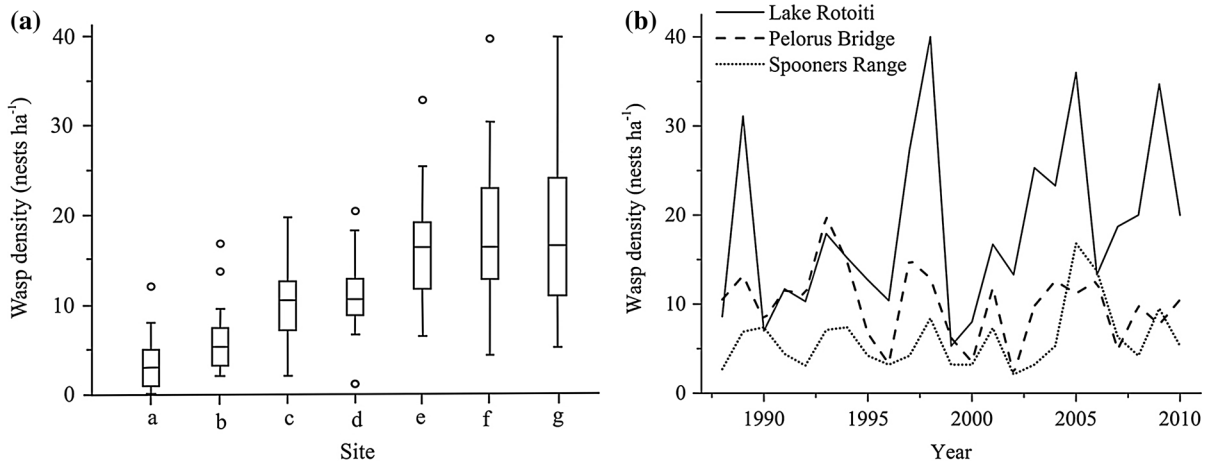


Fig. 1 **a** Range of annual wasp densities (nests ha⁻¹) at each of seven South Island *Fuscopora* beech forest sites: *a* Graham Valley, *b* Spooner’s Range, *c* Pelorus Bridge, *d* Matakītaki, *e* Tiraumea, *f* Mt. Misery and *g* Lake Rotoiti between 1988 and 2010. Boxes represent the 25th percentile, mean (not median)

and 75th percentile. Whiskers represent sample minimum and maximum values per site. Outliers are represented by open circles; **b** variation in annual wasp density (nests ha⁻¹) at three sites: Spooner’s Range (dotted line), Pelorus Bridge (broken line) and Lake Rotoiti (solid line) between 1988 and 2010

environmental pressure, we also compared scaling relationships of *P. advenus* at high and low wasp densities to test the hypothesis that morphological development was altered where wasps were more abundant.

Materials and methods

Study sites and specimen collection

Between 1988 and 2008 annual surveys of wasp nest densities were conducted by Landcare Research Nelson [for methods see Beggs et al. (1998) and Barlow et al. (2002)] in seven Nelson Lakes honeydew beech forest sites: Graham Valley (41°09’S, 173°31’E); Lake Rotoiti (41°49’S, 172°50’E); Matakītaki (42°58’S, 172°20’E); Mt. Misery (41°54’S, 172°39’E); Pelorus Bridge (41°18’S, 173°34’E); Spooner’s Range (41°27’S, 172°55’E); and Tiraumea (41°54’S, 172°37’E). A reduced survey was conducted in 2009 and 2010 measuring densities at only four of the sites: Lake Rotoiti, Mt. Misery, Pelorus Bridge and Spooner’s Range. The data collected provide a historical record of annual variation in wasp density and delineate sites with consistently higher and consistently lower levels of wasp infestation (Fig. 1).

Our assumption was that ant morphology in any 1 year of examination would likely have been influenced by several prior years of wasp densities, given that most ant colonies exist for several years. The wasp nest densities for each site in 2008 and 2009, respectively, were: 5.0 (wasps were not sampled in 2009) in Graham Valley, 20.0 and 34.7 in Lake Rotoiti, 9.4 (wasps were not sampled in 2009) in Matakītaki, 21.0 and 39.8 in Mt. Misery, 7.7 and 9.8 in Pelorus Bridge, 4.2 and 9.5 in Spooner’s Range, and 25.5 (wasps were not sampled in 2009) in Tiraumea. Environmental data on the yearly mean daily temperature and yearly mean daily minimum air temperature (°C), and total annual rainfall (mm year⁻¹), were obtained for each site from New Zealand’s National Climate Database. Weather stations were located between 3 and 29 km from each site. Given the proximity of sites and stations, some station data were used for multiple sites.

Prolasius advenus worker specimens were collected between summer 2008 and 2009 from the seven sites monitored for wasp density. Samples collected in 2008 were taken from four nests collected *in toto* along the Landcare transect line at each of the seven long term survey sites, with the exception of Graham Valley and Tiraumea where two and one nests were collected, respectively. Approximately 30 workers were randomly sampled from each nest. A further 30

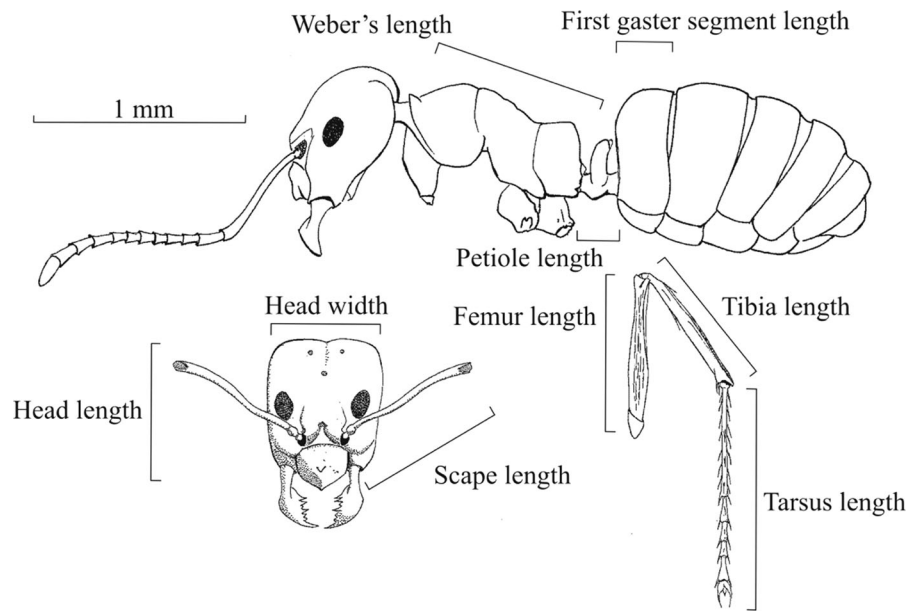


Fig. 2 Nine character measurements taken from *P. advenus* workers: head length, head width, scape length, Weber's length, petiole length, first gaster segment length, femur length, tibia length, and tarsus length

workers were sampled randomly by mouth aspirator from each of three nests per site opened along the transect lines at Lake Rotoiti, Mt. Misery, Pelorus Bridge and Spooner's Range in 2009. In addition between 23 and 152 further specimens per site were collected from pitfall traps. The traps were randomly placed in three 10×10 m quadrats set at all sites except Graham Valley and Tiraumea, which were omitted due to logistical problems associated with reaching the sites. The total number of ants sampled ranged between 30 and 271 per site.

Effects of increasing wasp density on ant worker size and morphology

Measurements (mm) were taken from a total of 1,068 *P. advenus* workers collected from the seven long term wasp density survey sites described above, to test the hypothesis that worker size decreased with increasing wasp density. Weber's length, which represents a lateral diagonal view of the distance between the anterior margin of the pronotum to the posterior margin of the metapleural bulla, was used as a standard measure of ant size (Fig. 2). This measurement was taken using a Nikon SMZ1500 microscope at between 80 and $110\times$ magnification, as were the

other measurements described below. We analyzed the data using the *avp* function for permutation testing of linear models in the R package *lmPerm* (R Development Core Team 2014). Ants may vary between sites due to genetic and environmental factors. Consequently we used a nested design, with random permutations performed only within sites. Weber's length was taken as the dependent variable, with the site-specific annual wasp density plus rainfall as covariates, using 10,000 within-site permutations of the data. Rainfall was used as the only environmental covariate to avoid multicollinearity issues, since we observed highly significant negative correlations ($P < 0.001$) between rainfall and the two temperature variables, which themselves were highly positively correlated ($P < 0.001$).

To further test the hypothesis that ant morphology varied with wasp density, measurements of eight additional variables were taken. These variables were head length (measured dorsally from the anterior tip of the clypeus to the occiput); head width (measured dorsally immediately posterior to the eyes); scape length (measured from the margin of the basal condyle to the margin of the first antennal segment); petiole length (viewed ventrally, the distance from the anterior to the posterior margin of the petiole); the

first gaster segment length (viewed laterally, the distance from the anterior-most point of the first gaster segment to its posterior margin); femur length (linear distance from the margin with the trochanter to the margin of the tibia); tibia length (linear distance from the junction with the femur to the junction with the first tarsal segment); and tarsus length (linear distance from the first tarsal segment to the tip of the tarsal claw) (Fig. 2). All leg measurements were taken from the right hind leg. An ant's gaster tends to vary in length depending on how much it has ingested so only the first segment, which cannot expand, was measured in this study. This gaster measurement is a commonly used proxy for total length of the abdomen (Tschinkel et al. 2003). To test the hypothesis that ant morphology varied with wasp density we used the *adonis* function for permutational MANCOVA in the R package *vegan* (R Development Core Team 2014). As before, a nested design was used with random permutations performed only within sites. Wasp density and rainfall were used as covariates, taking 10,000 within-site permutations of the data.

Scaling relationships in ants and the effect of high wasp densities

To examine the influence of wasp densities on the scaling relationships among body parts, we grouped sites into either high or low wasp densities. The low-density sites had nest densities <10 nests ha^{-1} (Graham Valley, Matakaitaki, Pelorus Bridge and Spooner's Range). The high-density sites had nest densities ≥ 20 nests ha^{-1} (Lake Rotoiti, Mt. Misery and Tiraumea). We chose to examine the scaling relationship between Weber's length, as a standard measure of ant size, and each of the other eight measured variables in all 1,068 specimens using standardised major axis regression (SMA; Warton et al. 2006). Scaling relationships were estimated on log transformed data, grouped by site according to low and high wasp densities, using the *sma* function in the R package *smatr* (R Development Core Team 2014). Confidence intervals (95 %) of the regression slope coefficients for low and high wasp densities were compared. Where no overlap of the confidence intervals of the two slopes was observed the scaling relationships were considered to be significantly different.

Results

Wasp densities

Boxplots of wasp density over the 20-year period show that some sites were consistently infested with wasps at high densities (Lake Rotoiti, Mt. Misery and Tiraumea), while others had consistently lower densities (Graham Valley, Matakaitaki, Pelorus Bridge and Spooner's Range) (Fig. 1a). Despite some within-site wasp density variation from year to year (Fig. 1b), in our sampling period of 2008–2009 the low-density sites all had <10 nests ha^{-1} , with the remaining high-density sites having ≥ 20 nests ha^{-1} (see “Materials and methods” section for the detail on wasp density estimates at each site).

Effects of increasing wasp density on ant worker size and morphology

Prolasius advenus workers decreased in size with increasing wasp density. We found workers were variable in size. The Weber's length (Fig. 2) of worker ants ranged between 0.71 and 1.08 mm, indicating that some workers were up to 1.5 times the size of others. To test the hypothesis that ant workers were smaller in areas where wasps maintain high population densities, we analyzed the data using the *aovp* function for permutation testing of linear models (R Development Core Team 2014). The permutational ANCOVA indicated a significant within-site decrease in mean Weber's length with increasing wasp densities ($\beta = -1.129\text{E}-3$; $P < 0.001$). The environmental covariate of rainfall had no statistically significant within-site effect on Weber's length ($\beta = 4.714\text{E}-5$; $P < 1.000$).

To test the hypothesis that ant morphology varied with wasp density we used the *adonis* function for permutational MANCOVA (R Development Core Team 2014). All nine characters measured decreased in size with increasing wasp density, with the exception of petiole length and the length of the first gaster segment, which each increased with increasing wasp densities (Table 1). A single within-site P value was calculated by permutation for the effects of wasp density ($P = 0.008$) and rainfall ($P < 0.001$). Despite the statistical significance, the effect sizes were generally small. For example, an increase of 10 wasp nests ha^{-1} was associated with an average

Table 1 Permutational MANCOVA results showing the within-site effects of wasp density and rainfall on the size of nine morphological characters measured in ant workers

Character	$\beta_{\text{wasp density}}$	β_{rainfall}
Head length	-1.166E-03	5.877E-05
Head width	-4.028E-04	7.098E-05
Scape length	-1.089E-03	-6.865E-05
Weber's length	-1.129E-03	4.714E-05
Petiole length	3.565E-04	-1.943E-04
First gaster segment length	2.928E-05	-2.037E-04
Femur length	-6.491E-04	-4.266E-05
Tibia length	-6.936E-04	-1.926E-05
Tarsus length	-7.359E-04	-8.563E-05

Beta (β) values indicate the direction and slope of the relationship. A single within-site P value was calculated using 10,000 permutations for the effects of wasp density ($P = 0.008$) and rainfall ($P < 0.001$)

decrease of only 0.011 mm (1.2 %) in the Weber's length of ant workers, *ceteris paribus* (all other things being equal or held constant). For comparison, the overall mean Weber's length was 0.934 mm.

Scaling relationships in ants and the effect of high wasp densities

We compared scaling relationships of *P. advenus* at high and low wasp densities to test the hypothesis that morphological development was altered where wasps were more abundant. Six of the eight morphological characters displayed a different scaling relationship with Weber's length in low and high wasp density sites, as indicated by non-overlapping 95 % confidence intervals of slope coefficients (Table 2). Some scaling relationships differed substantially. For example, the slope of the scaling relationship between the first gaster segment and Weber's length was approximately twice as steep in low than in high wasp density sites. The only characters that did not display different scaling relationships with Weber's length in different wasp density sites were head length and head width. We note that the effects of increasing wasp density from Table 1 apparently differ from those reported in Table 2. However, the effects in Table 1 are direct effects, estimated holding other factors in the model constant, while the relationships in Table 2 are all bivariate analyses involving only two variables, as is standard in the estimation of scaling relationships

using standardised major axis regression (Warton et al. 2006).

Discussion

This study indicates that invasive species can modify the size and morphology of native taxa. We observed a significant decrease in mean worker size of the native ant *P. advenus* with increasing density of the invasive common wasp *V. vulgaris*, after accounting for site and environmental covariate effects. Our results are consistent with studies of other ant species, which have demonstrated that a restriction of food resources results in production of smaller workers (Wheeler and Buck 1992; Mirth and Riddiford 2007; Sorvari and Hakkarainen 2009).

The common wasp has been demonstrated to exert significant interference competition pressure on *P. advenus* (Duthie 2011; Grangier and Lester 2011). Given the wasp's documented consumption of honeydew (Moller and Tilley 1989; Moller et al. 1991; Beggs et al. 1998) and invertebrate prey (Harris 1991; Harris and Oliver 1993), it likely exerts considerable exploitative competition pressure on the small brown bush ant by reducing both the quality and quantity of these resources. This hypothesis is supported by data that indicates a substantial increase in ant foraging where wasps are in high abundance, relative to areas where wasps have been experimentally controlled (Duthie and Lester 2013). We suggest that the observed reduction in worker size with increasing wasp density reflects a reduction in larval growth due to restricted resources mediated by competition with wasps. Such a conclusion is consistent with the findings of numerous other studies which have reported reduced adult size resulting from competition with invasive species in a diverse range of native taxa including perennial herbs (Miller and Gorchoff 2004), anurans (Vogel and Pechmann 2010) and cyprinid fishes (Mills et al. 2004).

An examination of scaling relationships in *P. advenus* workers found evidence of modified scaling relationships in areas of high wasp abundance. Scaling relationships for six out of eight morphological characters significantly differed in ants when subject to high wasp densities, relative to areas of low wasp abundance. For example, the estimated slope coefficient for first gaster length was twice as high in areas

Table 2 Slope coefficients from SMA regressions to estimate scaling relationships of eight ant morphological characters with Weber's length, all estimated on log transformed data, in low (<10 nests ha^{-1}) and high (≥ 20 nests ha^{-1}) wasp density sites

Morphological character	Low wasp density (<10 nests ha^{-1}) β (95 % CI)		High wasp density (≥ 20 nests ha^{-1}) β (95 % CI)
Head length	0.990 (0.942, 1.040)	=	1.061 (0.992, 1.135)
Head width	1.107 (1.056, 1.160)	=	1.054 (0.985, 1.128)
Scape length	1.610 (1.510, 1.716)	\neq	0.964 (0.898, 1.034)
Petiole length	3.277 (3.057, 3.512)	\neq	1.890 (1.696, 2.107)
First gaster segment length	3.738 (3.491, 4.003)	\neq	1.731 (1.573, 1.906)
Femur length	1.152 (1.089, 1.220)	\neq	0.977 (0.916, 1.043)
Tibia length	1.109 (1.047, 1.173)	\neq	0.955 (0.895, 1.020)
Tarsus length	1.187 (1.119, 1.259)	\neq	0.988 (0.916, 1.066)

with low wasp nest densities. The ecological significance of this result, if any, is uncertain. In these beech forests, the main source of carbohydrate is honeydew (Moller and Tilley 1989). Workers transport the liquid back to the nest in their crop and the gaster may swell to nearly twice its usual size (Smith 1969). An isometric relationship between worker size and nectar feeding rate has been demonstrated in the genus *Camponotus* (Medan and Josens 2005). It is possible that larger *P. advenus* workers with disproportionately larger gasters may be more efficient carriers of liquid resources such as honeydew. There may be selection for individuals with a better capacity for carrying honeydew. Such selection induced by invasive species has been reported in other taxa including snakes (Phillips and Shine 2004), lizards (Langkilde 2009), fishes (Robinson and Parsons 2002) and plants (reviewed in Strauss, Strauss et al. 2006). However, where wasps are more abundant honeydew availability is significantly reduced (Moller and Tilley 1989). Perhaps the competitive advantage of a larger gaster does not outweigh the developmental trade-off against other structures where wasps reduce the available honeydew resources. As noted above, the ecological significance of changes to scaling relationships in areas of high wasp abundance is uncertain. Allocation of resources to morphological characters during developmental growth is complex. Resources may be redistributed to other structures according to the hypothesis of competition among developing imaginal structures for limiting resources within the pupa, as proposed by Nijhout and Wheeler (1996) and Emlen (2001). Finally, we note that two of the eight characters measured scaled isometrically and also did not differ significantly in

their scaling relationships between high and low wasp density sites. This result would be expected, as authors such as Brown and Wilson (1956) also found that characters in the ant genus *Lasius* can scale in an independent fashion.

Increasing wasp densities were associated with significantly decreasing ant size. However, the decrease in size was small. With other climate variables such as rainfall held constant, an increase of 10 wasp nests ha^{-1} was associated with an average decrease of only 1.2 % in the Weber's length of native ant workers. While it might be statistically significant, we doubt that a 1.2 % decrease in size is biologically or ecologically meaningful for the life history of this ant. Nevertheless, the decrease in size may be a form of ecological character displacement (Brown and Wilson 1956) in its early stages, given the only recent introduction of common wasps to this area over the last ~ 50 years. Competitive effects of introduced wasps are likely to be considerably slower than for effects of predation or direct mortality, such as for the selection of longer limbs in lizards after invasion by fire ants (Langkilde 2009).

Invasive species can exert considerable influence on recipient taxa. The effects of competition with invasive species are typically sub-lethal (Davis 2003), but are usually reported in terms of displacement or reduction in abundance of native taxa. The results of this study appear to show a sub-lethal density-dependent effect of an invasive wasp on worker size and morphology of a native ant. Other studies have shown that worker size is positively correlated with foraging efficiency and survivorship (McGlynn 1999). Size related trade-offs, however, also exist between

discovery and dominance abilities in ants (Tanner 2008). Whether the variation in size and morphology of *P. advenus* workers with increasing density of *V. vulgaris* observed in this study reflects the slow erosion of a native species' fitness or a plastic response to a novel invader is uncertain. However, our findings indicate that the effects of competition with invasive species on native organisms may be more subtle than generally reported. We expect that such effects may be widespread, especially in systems where invasive species exert strong competitive effects with native organisms.

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References

- Barlow ND, Beggs JR, Barron MC (2002) Dynamics of common wasps in New Zealand beech forests: a model of density dependence and weather. *J Anim Ecol* 71:663–671
- Beggs JR, Wilson PR (1991) The kaka *Nestor meridionalis*, a New Zealand parrot endangered by introduced wasps and possums. *Biol Conserv* 56:23–38
- Beggs JR, Toft RJ, Malham JP, Rees JS, Tilley JAV, Moller H, Alspach P (1998) The difficulty of reducing introduced wasp (*Vespula vulgaris*) populations for conservation gains. *NZ J Ecol* 22:55–63
- Boone MD (2005) Juvenile frogs compensate for small metamorph size with terrestrial growth: overcoming the effects of larval density and insecticide exposure. *J Herpetol* 39:416–423
- Brown WL, Wilson EO (1956) Character displacement. *Syst Zool* 5:49–64
- Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53:481–489
- Don W (2007) *Ants of New Zealand*. Otago University Press, Dunedin
- Duthie C (2011) Factors promoting coexistence between endemic ants and invasive wasps. PhD thesis. Victoria University of Wellington, Wellington, New Zealand
- Duthie C, Lester PJ (2013) Reduced densities of the invasive wasp, *Vespula vulgaris* (Hymenoptera: Vespidae), did not alter the invertebrate community composition of *Nothofagus* forests in New Zealand. *Environ Entomol* 42:223–230
- Emlen DJ (2001) Costs and the diversification of animal structures. *Science* 291:1534–1536
- Emlen DJ, Allen CE (2004) Genotype to phenotype: physiological control of trait size and scaling in insects. *Integr Comp Biol* 43:617–674
- Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. *Annu Rev Entomol* 45:661–708
- Grangier J, Lester PJ (2011) A novel interference behaviour: invasive wasps remove ants from resources and drop them from a height. *Biol Lett* 7:664–667
- Harris R (1991) Diet of the wasps *Vespula vulgaris* and *V. germanica* in honeydew beech forest of the South Island, New Zealand. *NZ J Zool* 18:159–169
- Harris RJ, Oliver EH (1993) Prey diets and population densities of wasps *Vespula vulgaris* and *Vespula germanica* in a scrubland–pasture. *NZ J Ecol* 15:5–12
- Langkilde T (2009) Invasive fire ants alter behavior and morphology of native lizards. *Ecology* 90:208–217
- Lester PJ, Gruber MAM, Brenton-Rule EC, Archer M, Corley JC, Dvořák L, Masciocchi M, Van Oystaeyen A (In Press) Determining the origin of invasions and demonstrating a lack of enemy release from microsporidian pathogens in common wasps (*Vespula vulgaris*). *Divers Distrib*. doi:10.1111/ddi.12223
- Lockwood JL, Hoopes MF, Marchetti MP (2007) *Invasion ecology*. Blackwell, Oxford
- McColl HP (1975) The invertebrate fauna of the litter surface of a *Nothofagus truncata* forest floor, and the effect of microclimate on activity. *NZ J Zool* 2:15–34
- McGlynn TP (1999) Non-native ants are smaller than related native ants. *Am Nat* 154:690–699
- McGlynn TP, Owen JP (2002) Food supplementation alters caste allocation in a natural population of *Pheidole flavens*, a dimorphic leaf-litter dwelling ant. *Insectes Soc* 14:8–14
- Medan V, Josens RB (2005) Nectar foraging behaviour is affected by ant body size in *Camponotus mus*. *J Insect Physiol* 51:853–860
- Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii* reduces growth and fecundity of perennial forest herbs. *Oecologia* 139:359–375
- Mills MD, Rader RB, Belk MC (2004) Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. *Oecologia* 141:713–721
- Mirth CK, Riddiford LM (2007) Size assessment and growth control: how adult size is determined in insects. *BioEssays* 29:344–355
- Moller H, Tilley JAV (1989) Beech honeydew: seasonal variation and use by wasps, honey bees, and other insects. *NZ J Zool* 16:289–302
- Moller H, Tilley JAV, Thomas BW, Gaze PD (1991) Effect of introduced social wasps on standing crop of honeydew in New Zealand beech forests. *NZ J Zool* 18:171–179
- Morales CF, Hill MG, Walker AK (1988) Life history of the sooty beech scale (*Ultracoelostoma assimile*) (Maskell), (Hemiptera: Margarodidae) in New Zealand *Nothofagus* forests. *NZ Entomol* 11:24–38
- Nijhout HF, Wheeler DE (1996) Growth models of complex allometries in holometabolous insects. *Am Nat* 148:40–56
- Ode PJ, Rissing SW (2002) Resource abundance and sex allocation by queen and workers in the harvester ant, *Messor pergandei*. *Behav Ecol Sociobiol* 51:548–556

- Oster GE, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton
- Passera L, Roncin E, Kaufmann B, Keller L (1996) Increased soldier production in ant colonies exposed to intraspecific competition. *Nature* 379:630–631
- Phillips BL, Shine R (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proc Natl Acad Sci USA* 101:17150–17155
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>
- Robinson BW, Parsons KJ (2002) Changing times, spaces and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Can J Fish Aquat Sci* 59:1819–1833
- Smith CE (1969). A morphological and behavioural study of the ants *Amblyopone saundersi* Forel and *Prolasius advena* Fr. Smith (*Hymenoptera: Formicidae*). BSc (Hons) thesis. University of Otago, Dunedin, New Zealand
- Smith WW (1896) On the habits of New Zealand ants. *Trans Proc NZ Inst* 29:468–479
- Sorvari J, Hakkarainen H (2009) Forest clear-cutting causes small workers in the polydomous wood ant *Formica aquilonia*. *Ann Zool Fenn* 46:431–438
- Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol Lett* 9:357–374
- Tanner C (2008) Resource characteristics and competition affect colony and individual foraging strategies of the wood ant *Formica integroides*. *Ecol Entomol* 33:127–136
- Thomas CD, Moller H, Plunkett GM, Harris RJ (1990) The prevalence of introduced *Vespula vulgaris* wasps in a New Zealand beech forest community. *NZ J Ecol* 13:63–72
- Toft RJ, Beggs JR (1995) Seasonality of crane flies (Diptera: Tipulidae) in South Island beech forest in relation to the abundance of *Vespula* wasps (*Hymenoptera: Vespidae*). *NZ Entomol* 18:37–43
- Tschinkel WR, Mikheyev AS, Storz SR (2003) Allometry of workers of the fire ant *Solenopsis invicta*. *J Insect Sci* 3:1–11
- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. *Am Sci* 84:468–478
- Vogel LS, Pechmann HK (2010) Response of Fowler's Toad (*Anaxyrus fowleri*) to competition and hydroperiod in the presence of the invasive Coastal Plain Toad (*Incilius nebulifer*). *J Herpetol* 44:382–389
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Wheeler DE (1991) The developmental basis of worker caste polymorphism in ants. *Am Nat* 138:1218–1238
- Wheeler DE, Buck NA (1992) Protein lipid and carbohydrate use during metamorphosis in the ant *Solenopsis xyloni*. *Physiol Entomol* 17:397–403