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Local dynamics of worker activity of the invasive *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae) wasps in Argentina

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Abstract. 1. The abundance of insects depends essentially on the reproductive success of individuals. In social insects, however, the abundance of sterile workers outside a nest depends on colony size but is also determined by ontogeny, nest demands, and local environmental factors. For invasive social wasps, the drivers of worker abundance are important because they determine the impact that these species have on the native systems, people, and their goods.

2. The aim of the present study was to understand the relative importance of endogenous and exogenous factors on the abundance of workers of populations of *Vespula* spp., by analysing 12 years of trap captures in NW Patagonia. This is the first attempt to model the activity levels of invasive *Vespula* spp. wasps over time in Argentina.

3. It was shown that between years, the worker activity of both vespids presents fluctuations, and that of *V. germanica* is determined by the spring mean temperatures. Within the flight season, *V. germanica* worker activity is affected by the relative abundance of workers in that year, whereas for *V. vulgaris*, activity it is affected by the relative abundance of both species that year. We found no relationship between individual weather variables and activity within a flight season for both wasps.

4. The patterns observed for Argentina are similar to those observed in all invaded temperate areas where *Vespula* spp. are established. This study provides useful information to understand the driving factors that affect *Vespula* spp. worker activity in Argentina. This could be a necessary step to develop plans to manage these invasive social insects.

Key words. Exotic wasps, Patagonia, social insects, *Vespula* spp., weather conditions, worker abundance.

Introduction

The study of fluctuations in animal numbers has attracted the attention of much ecological research since its early days (Elton, 1924; Andrewartha & Birch, 1964). This is in part because knowledge on when and how populations change through space and time has practical implications, for instance during the planning of conservations measures, or when exploiting natural populations, managing pests or even preventing the spread of invasive species. Also, understanding population fluctuations is central to our understanding of the fundamental issues such as, for example, population regulation, predator–prey and host–pathogen relationships, population extinction, and the success of animal invasions.

For insects, it is widely recognised that in many cases, fluctuations of their populations aside from being affected by endogenous, density-dependent processes related to life history traits, are strongly impacted by exogenous factors such as weather (Barlow *et al.*, 2002; Aukema *et al.*, 2005). Insects are typically small and ectothermic animals whose physiology, movement, and behavioural interactions with other species

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depend largely on temperature, winds, atmospheric pressure, and rainfall, among other factors. Population ecologists agree on the importance of the combined effects of exogenous and endogenous factors on the observed population behaviour of insects (Aukema *et al.*, 2005; Estay & Lima, 2010).

Essentially, for insect species, weather affects populations through its effects on survival and reproduction. However, how macro and micro weather variables affect insect activity – through insect populations that are commonly studied – is also important to fully understand population patterns (Willmer, 1982; Estay & Lima, 2010). Rarely one weather variable by itself affects animals, and rather the combined influence of several factors acting simultaneously may be responsible for the observed activity patterns for a given species. However, how much each factor contributes to the observed dynamics depends on the species and also on their habitat niches (e.g. territorial or aquatic, Kasper *et al.*, 2008). For example, for those insects in which vision is essential to lead their displacement, light availability and intensity can affect their activity significantly. Also, extreme temperatures can also affect the soil surface temperatures and refuge availability which determine how and when ground-dwelling insects such as ants, forage (Wehner *et al.*, 1992). Some studies have shown in turn, that air temperature is important to determine the activity for bees and wasps (Hilário *et al.*, 2000; Kasper *et al.*, 2008).

In social species, which establish colonies with distinguishable castes (i.e. workers, queens, and drones) and display some degree of division of labour, the abundance of individuals of a caste, in a given time and location, is explained by several factors such as the nest phenological stage, the number of colonies present in the area, and the numbers of insects of a given caste per colony (Spradbery, 1973; Beggs *et al.*, 1998). Wasp activity outside nests may be driven additionally, by several local environmental variables that can affect when sterile workers leave the nests to forage and for how long. While numerous studies have analysed the influence of endogenous and exogenous factors on insect population dynamics, including social insects (i.e. as number of colonies), the influence of such factors directly on worker activity, is less well understood (but see Archer, 1985; Barlow *et al.*, 2002).

Vespula germanica (Fabricius) and *V. vulgaris* (Linnaeus) (Hymenoptera: Vespidae) are invasive eusocial vespids, native to the Paleartic region. In the last century, *V. germanica* invaded New Zealand, Australia, South Africa, North America, Canada, Chile, and Argentina, whereas *V. vulgaris* is currently established in Australia, New Zealand, and South America (Beggs *et al.*, 2011). Since their first reports in Argentina, both species have become remarkably abundant in this region (*V. germanica* first report was in 1980, and *V. vulgaris* was in 2010; Farji-Brener & Corley, 1998; Masciocchi & Corley, 2013). Wasps in high numbers may negatively affect natural ecosystems and numerous economic activities such as beekeeping, horticulture, tourism, and cattle rearing. Also, the painful sting may interfere with human outdoor activities and affect residential areas (Akre & MacDonald, 1986; Rust & Su, 2012).

Vespula spp. in southern Argentina have an annual cycle, starting their colonies in October-November and ending in March-April. Each colony is composed by a single queen, thousands of workers and a few drones. Colonies are started by mated queens who lay the first worker eggs and build-up a sterile worker population progressively during the season, from a few hundred individuals to a peak between 3000 and 5000 workers in early autumn (Spradbery, 1973). As for other social insects, wasp worker labour through the season is known to be affected by the phenological development nest variations and colony demands. When the colony reaches peak abundance, activity outside the nest intensifies, also as a result of the greater number of larvae in the nest to feed and increasing investment in reproductives (future queens and drones, Spradbery, 1973). Also, daily foraging patterns (i.e. the number of foraging bouts, duration of the flight, and distance) are probably affected by local weather conditions. Past works have studied the effects of different factors on the population dynamics of *V. germanica* (nest numbers). Some of them have suggested that wasp population abundance is related to autumn and spring precipitation of the previous year (Madden, 1981; Archer, 2001). In the same way, a more recent study found a strong negative density dependence with an adverse effect of spring rainfall on wasp population size (Barlow *et al.*, 2002); and finally in the same line, others suggested that during warm springs followed by frost, the number of surviving queens may be significantly reduced (Spradbery, 1973). While population growth undoubtedly affects wasp numbers, fewer studies have focused on the environmental determinants of worker activity of *Vespula* spp. outside the nest (but see Akre *et al.,* 1981; Archer, 2001).

Our aim was to understand the activity of workers of *Vespula germanica* and *V. vulgaris* analysing the relative importance of endogenous and exogenous factors. We analysed worker activity levels, for each species, at two different time scales (within a flight season, and between years), to unravel the factors that may modulate each of these processes. We studied worker numbers in *V. germanica* and *V. vulgaris* in a given region over a 12-year-long period. As endogenous factors, we considered the wasp abundance during that period and the immediately previous one, and as exogenous factors, we examined different weather variables that generally relate to insect activity.

Methods

Study area

The study was carry out in the Natural Forest Reserve *Loma del Medio* which is located in the southwest of Río Negro province (41°40′ and 42°10′S to 71°42′ and 71°20′W), in NW Patagonia. *Loma del Medio* Forest Reserve is an area of approximately 2.400 ha, limited by high mountains on the West and Piedmont foothills in the East. The area is a nature reserve, inhabited by a few settlers. The weather in this area is long and sunny summer days and pleasant temperatures in autumn and spring. In winter, the temperature is moderate for Patagonian standards (−3 to 18 °C) with abundant precipitation. The flora of the area is dominated by forest of *Austrocedrus chilensis*, with some other woody plant species such as *Nothofagus dombeyi* and *Fitzroya cupressoides*. *Vespula* spp. are well established in this area since the 1980s being nowadays, probably the most abundant insects in the area.

Activity data

Sampling sites were established within the Natural Forest Reserve *Loma del Medio* and were characterised by having the lowest anthropogenic disturbance, to ensure that the collected data represented true wasp activity. Five sites were selected within the study area and in each one we placed two *Malaise* traps to estimate wasp activity. The minimum distance between sites was 1 km, to ensure sampling from different *Vespula* spp. colonies (workers fly on average 200 m from the nest; Spradbery, 1973). Traps were placed at the ground level, and to avoid the effects of local variation, similar micro-sites were selected. These micro-sites were wind protected and semi-shaded during daylight hours. In the collecting flask, a dichlorovinyl dimethyl phosphate tablet was placed to kill captured insects and hold them until their collection, at the end of the sampling period. Traps were placed in sampling sites during 1 week in each of the following months: December, January, February, March, and April. We sampled exactly the same sites from 2002 to 2013, the period in which this study was conducted. Because, *V. vulgaris* was detected for the first time in Argentina in 2010, all workers collected before that date (i.e. 2008 and 2009) were not sorted into species. Then, from 2010 onwards, collected workers were identified to species using keys (Buck *et al.*, 2008).

Weather data

Climate data for the 12 years were obtained from the Argentine National Weather Service. The meteorological station, referred to as 'El Bolsón Airport' (#87.800), is located approximately 3 km from the sampling sites (41°58′S–71°30′W).

While some weather variables can be recorded, we used for our analyses those that we considered having an influence on the *Vespula* spp. activity in Patagonia and are not correlated with them. For precipitation, for instance, we used the sum of days with rainfall, instead of the total millimetres fallen as it has been suggested that is the drop impact that affects *Vespula* spp. activity rather than water accumulation in a site (Kasper *et al.*, 2008). For temperature, in turn, we did not use the maximum temperature because *Vespula* spp. wasps are known to forage at temperatures greater than those reported in our study sites (Spradbery & Maywald, 1992); therefore, we used the mean temperature. Finally, we used the mean atmospheric pressure that is known to affect activity in several other insect species (Edwards, 1961; Ankney, 1984; Bergh, 1988; Anderson *et al.*, 1993).

Statistical analysis

We used generalised linear models to assess the relative importance of endogenous and exogenous factors on *V. germanica* and *V. vulgaris* activity levels. Given the different temporal dynamics of *V. germanica* and *V. vulgaris* wasps (Archer, 2001), and the different temporal scales of analysis, we proposed three models: one for flight season fluctuations of *V. germanica* workers, another for flight season fluctuations of *V. vulgaris* workers, and one for annual fluctuations of *V. germanica* workers. As a result of the recent detection of *V. vulgaris* in Argentina (Masciocchi *et al.*, 2010), we only analysed the annual fluctuations for *V. germanica* without taking into account the data collected in 2008 and 2009 because we cannot assure which species was caught then (i.e. a buffer interval). In each model, the weather variable temporal scale is the same as that of the wasp sampling (the weather variable of the same week of sample period, in the flight season model; and the same months of sample period, in annual model). The response variable for annual activity was the total number of *V. germanica* workers captured in a year (individual data are the sum of wasp captured in the two traps in the five sites during the 5 months), and for flight season activity, the total number of worker wasps captured in a month (individual data are the sum of wasps per two traps in five sites each month). As explanatory variables we used for the **annual fluctuation model**: *year*, optimum temperature days for foraging between December to April (*optimal foraging days*), mean temperature in spring months (*spring mean temp.*, October, November, and December), and the number of rainy days in spring months (*spring rainy days*); and for the **flight season fluctuation model**: *year, month*, *V. germanica worker abundance*$_{(t)}$, indicating the relative abundance of *V. germanica* wasps calculated as the ratio between the numbers of wasps captured per week and the total activity of wasps captured that year, *V. vulgaris worker abundance*$_{(t)}$, *V. germanica worker abundance*$_{(t-1)}$ same as above but for the previous year, *V. vulgaris worker abundance*$_{(t-1)}$, mean temperature in week sample *(mean temp.)*, mean atmospheric pressure in week sample (*mean atmosf. pressure*), number of rainy days in week sample (*rainy days*), and temperature of days outside the optimal foraging range in week sample (*non-optimal foraging days)*. The weather variables mentioned above that were not used in the models are those that show some degree of correlation with others variables. The initial models proposed were: **Annual activity of *V. germanica* workers ~ year + optimal foraging days + spring mean temp. + spring rainy days;** and **Flight season activity of *V. germanica/V. vulgaris* workers ~ year + month + *V. germanica* abundance$_{(t)}$ + *V. vulgaris* abundance$_{(t)}$ + *V. germanica* abundance$_{(t-1)}$ + *V. vulgaris* abundance$_{(t-1)}$ + mean temp. + mean atmosf. pressure + rainy days + non-optimal foraging days.**

To meet the model assumptions we transformed the flight season activity response variables [$x' = \log_{10}(x)$ for *V. germanica* model, and x' = square root (x) for *V. vulgaris* model], assuming for both models a normal distribution of residuals with the identity link function. A backward procedure was used to remove non-significant factors. Model comparisons were computed using the standard likelihood method and model selection was made using the Akaike Information Criterion (AIC): the best model having the lowest AIC value. Residuals were examined to confirm that the final model accurately fitted the data. All data analyses were performed using the R statistical environment (R Development Core Team, 2014).

Results

Vespula germanica and *V. vulgaris* workers were captured in all traps during the sampling period. *Vespula vulgaris* workers were

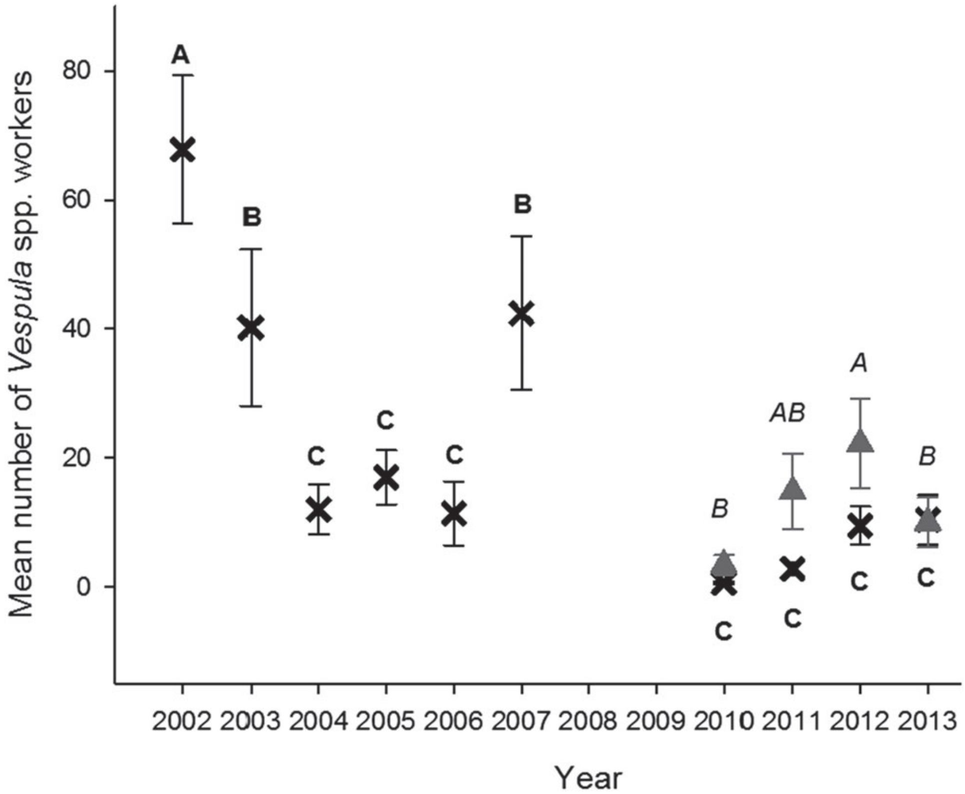

Fig. 1. The mean number of wasps captured per year. Each black cross represents the mean number of *Vespula germanica* workers in a given calendar year, and each grey triangle is the mean number of *V. vulgaris* workers in a given calendar year; the bars represent the SE. The **bold letters** indicate *V. germanica* significant differences between years; and the *italic letters* indicate *V. vulgaris* significant differences between years.

identified in samples as from 2010, as the species had not been previously reported in this region (Masciocchi *et al.*, 2010). Of the total worker wasp captures, *V. germanica* represented 35% of the sample.

The worker activity of *V. germanica* and *V. vulgaris* shows a clear fluctuating pattern with significant differences over the years ($P_{V.\ germanica} < 0.0001$, $n = 50$, $P_{V.\ vulgaris} = 0.03$, $n = 20$, Fig. 1). Previous to the arrival of *V. vulgaris*, the average number of *V. germanica* workers captures per year was 157.8 ± 112.9. However, since 2010 to 2013, when both species coexist, the amount of *V. germanica* workers captured per year was 37.7 ± 36.2 whereas *V. vulgaris* was 70 ± 36.2. Also, the average capture of wasps per month varied. In January, *V. germanica* worker captures were 3.8 ± 5.8, in February 6.3 ± 5.8, in March 22.3 ± 5.8, and in April 5.5 ± 5.8 wasps; whereas for *V. vulgaris* in the same months were 18 ± 6.8, 9.8 ± 6.8, 23 ± 6.8, and 19.3 ± 6.8 respectively (the mean ± SE in all cases, Fig. 2).

A constant annual pattern was observed when we broke down the data into a month-long time frame (Fig. 2). The colonies of both species reach a maximum activity in March, and then worker numbers fall until activity completely stops in late April.

Our models showed that the annual activity of *V. germanica* workers was influenced by year and the mean temperature of the spring months. Wasp activity decreases over the years; however, warm springs are accompanied by an increase in the activity levels of *V. germanica* workers (Table 1). In contrast, the *V. germanica* worker activity within a flight season is affected by year and the relative abundance of *V. germanica* workers that year. An increase in *V. germanica* worker abundance implies an increase in *V. germanica* worker activity. However, *V. vulgaris* worker activity is also affected by month and the relative abundance of *V. vulgaris* that year. Therefore, an increase in *V. vulgaris* worker abundance implies an increase in *V. vulgaris* workers that year, but this activity decreases if there is an increase in the abundance of *V. germanica* workers (Table 1). Moreover, the worker activity within a flight season of *V. germanica* wasps decreased over the years, whereas that of *V. vulgaris* increased.

Discussion

This is the first study to analyse the worker activity of *Vespula* spp. during 12 consecutive years in Argentina, an area invaded by these wasps. Worker activity showed a clear fluctuating pattern with significantly different abundance among years for both species. *Vespula germanica* annual activity was affected by the previous mean spring temperature, but within a flight season, worker numbers were affected by the relative abundance of *V. germanica* wasps in that year only. In contrast, *V. vulgaris* flight season worker activity was affected by the relative abundances of both species.

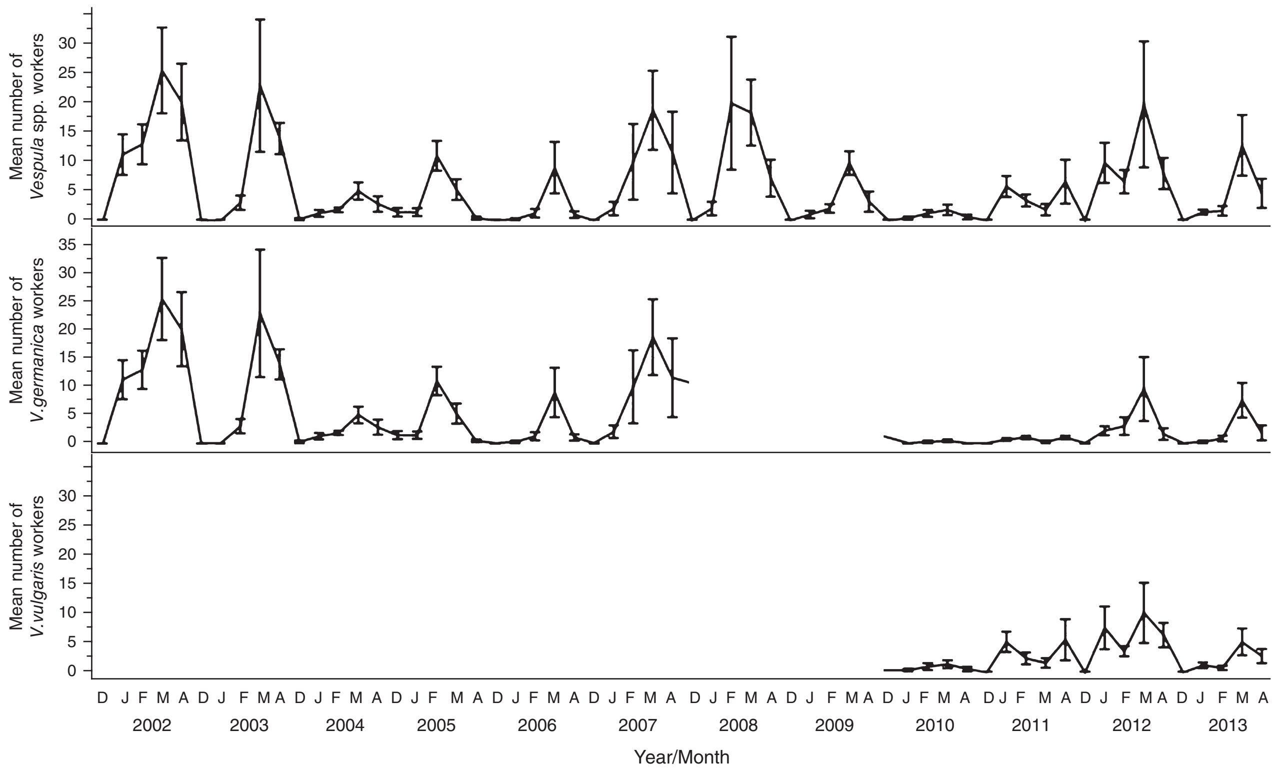

Fig. 2. The mean number of workers captured per month during the 12 years. Top graph represents *Vespula* spp. workers activity during the sample period. The middle graph represents *V. germanica* workers activity during the sample period. The graph below represents *V. vulgaris* workers activity during the sample period. Each point represents the mean number of workers captured per month, and bars represent the SE.

Since 2010 and until 2013, years where it is possible to confirm the coexistence of both species, the mean number of *V. germanica* workers decreased, and *V. vulgaris* wasps was always higher than that of *V. germanica* (65% to 35%, respectively). This could be suggesting that in Argentina, the process of invasion by *V. vulgaris* resembles that noted for other invaded regions: *V. vulgaris* arriving later than *V. germanica,* and reaching larger populations in only a few years (Beggs *et al.*, 2011). Further, comparative analysis of this observation could be interesting to know how this interaction evolves over time.

The annual activity of *V. germanica* workers is influenced by year and the mean temperature of the spring months. As noted previously (e.g., Long *et al.*, 1979; Akre *et al.*, 1981), weather conditions during colony establishment can play an important role in species success and population numbers. The queen begins nest construction during these months, on her own, and so colony vulnerability to environmental phenomena is highest at this stage. We show here that the mean temperature during the spring months can also have an effect on worker activity levels of *V. germanica* outside the nest during the following summer. Namely, we suggest that cooler spring temperatures diminish wasp activity expected in the forthcoming summer months, probably because of the reduced nest success during the early developmental stages.

Past work has also suggested that although spring temperatures are important during colony foundation, it is the combination of temperature with the precipitation what becomes critical to colony success (Akre *et al.*, 1981). Outbreaks in wasp abundances have been noted to occur during years when spring precipitation was low, coupled with high temperatures. Although here we could not find any effects of the amount of rainy days on wasp activity, we observed a negative correlation between the mean spring temperature and days with rain ($P = 0.0074$, $R^2 = 0.53$). We suggest that the precipitation of spring months in combination with the spring mean temperatures are important factors determining the expected activity of workers in the next summer. This finding confirms previous knowledge and is important to forecast 'wasp years' in southern Argentina.*Vespula* spp. showed similar flight season pattern fluctuations throughout the years. The maximum worker wasp activity was regularly reached in March, decreasing subsequently to disappear, in late April. This pattern is similar to that observed in all invaded temperate areas where *Vespula* spp. are established. The nest ontogeny is mainly affected by the time when the queens start egg laying and the temperature regulation inside the nest. So, it is likely that in all regions where the queens start the nest formation at the begging of spring months, a higher wasp activity will be in early autumn.

Vespula germanica worker activity within the flight season is affected by year and the relative abundance of *V. germanica* wasps that year; an increase in *V. germanica* wasp population naturally leads to an increase in *V. germanica* worker activity. However, *Vespula vulgaris* worker activity is affected by year, month, and the relative abundance of both *V. vulgaris* and *V.*

Table 1. Final general linear models for both *Vespula* spp. activity dynamics (i.e. annual and flight season activity) as a function of explanatory variables.

Effects	β	SE	Statistic	P
Annual activity of V. germanica workers				
Year	**−18.04**	**3.15**	$F_{(1,7)} = 30.3$	**0.001**
Spring mean temperature	**91.41**	**15.69**	$F_{(1,7)} = 33.9$	**0.001**
Optimal foraging days	−1.80	0.33	$F_{(1,7)} = 3.5$	0.1
Flight season activity				
V. germanica				
Year	**−0.07**	**0.02**	$F_{(1,37)} = 10.2$	**0.003**
***V. germanica* abundance$_{(t)}$**	**1.63**	**0.37**	$F_{(1,37)} = 18.9$	**0.0001**
V. vulgaris				
Year	**0.45**	**0.26**	$F_{(1,16)} = 10.9$	**0.005**
Month	**−0.12**	**0.1**	$F_{(1,16)} = 15.2$	**0.001**
***V. germanica* abundance$_{(t)}$**	**−1.28**	**2.56**	$F_{(1,16)} = 6.2$	**0.02**
***V. vulgaris* abundance$_{(t)}$**	**9.91**	**4.45**	$F_{(1,16)} = 4.9$	**0.04**

Initial models: Annual activity of *V. germanica* workers ~ year + optimal foraging days + spring mean temp. + spring rainy days; and flight season activity of *V. germanica/V. vulgaris* workers ~ year + month + *V. germanica* abundance$_{(t-1)}$ + *V. vulgaris* abundance$_{(t-1)}$ + *V. germanica* abundance$_{(t)}$ + *V. vulgaris* abundance$_{(t)}$ + mean temp. + mean atmosf. pressure + rainy days + not optimal foraging days. Comparison of model fit parameters supported the following final reduced models: annual activity of *V. germanica* workers ~ year + optimal foraging days + spring mean temp.; and flight season activity of *V. germanica* workers ~ year + *V. germanica* abundance$_{(t)}$; flight season activity of *V. vulgaris* workers ~ year + month + *V. germanica* abundance$_{(t)}$ + *V. vulgaris* abundance$_{(t)}$. Significant parameters are in bold. $N_{(\text{annual activity})} = 10$; $N_{(V.\ germanica\ \text{flight season activity})} = 50$, $N_{(V.\ vulgaris\ \text{flight season activity})} = 20$. '*F*' represents the statistical used in this test ('F Fisher'); the d.f. are shown in parentheses.

germanica wasps of that year. Again, an increase in *V. vulgaris* worker abundance implies an increase in *V. vulgaris* worker activity, but this activity decreases if there is an increase in the abundance of *V. germanica* workers. This is an interesting finding that could be suggesting that *V. germanica* workers interfere with the activities of *V. vulgaris*. In New Zealand, another area invaded by both vespids, conflicts between *V. germanica* and *V. vulgaris* workers have been observed, resulting in victory for the *V. germanica* worker; however, despite this, *V. vulgaris* has displaced the *V. germanica* wasp of that area (Harris *et al.*, 1991). How both species interact in invaded regions deserves careful mechanistic studies.

We found no relationship between individual weather variables and activity within a flight season for both *V. germanica* and *V. vulgaris*. This result could be suggesting, as previously noted for other *Vespula* spp., that weather affects *V. germanica* colonies at the critical stage of colony foundation, but once this period is passed, colonies are relatively unaffected by local weather conditions (Akre *et al.*, 1981). Another explanation could be that the weather during the sampling months, in our study area, falls within the tolerance range for *Vespula* spp. workers (Spradbery & Maywald, 1992; Kasper *et al.*, 2008). The temperature, air atmospheric pressure, and precipitation during the summer months in NW Patagonia appear not to be a limiting factor for *Vespula* spp. wasp activity.

In contrast with other insects, in social species, activity may not be linearly related to population abundance. This is likely why much past work that has studied the population dynamics of *Vespula* spp. have used nest density as an estimate of wasp abundance, rather than captures of workers in traps (Archer, 1981; Barlow *et al.*, 2002; Estay & Lima, 2010). Although there is evidence of a correlation between *V. vulgaris* activity with nest numbers (Beggs *et al.*, 1998), this is only one study carried out in New Zealand. While inter-annual activity may be affected by competing species (other native or invasive wasp species), within season activity is closely related to colony development. Both of these aspects warrant local, specific studies.

To understand the impact caused by an invasive social wasp and predict peak abundance of noxious individuals, it is not only important to understand the drivers of their population dynamics, but in parallel determine those that affect worker activity levels. This is because it is foraging workers at a given place and time, who pose a risk to human health or impact on given economic activities. Our study is the first to quantify the activity of workers of *V. germanica* and *V. vulgaris* in a recently invaded area, exploring the main drivers. Such information may prove useful to establish more precise control measures. Note that these are to a large extent, limited to the application of toxic baits that are carried by foraging workers to their nests (Sackmann & Corley, 2007; Beggs *et al.*, 2011). In contrast, it is also useful to know that once the colony is established, local weather variables seem to have little influence on wasp activity in a given year. Possibly, the weather conditions within this invasion area are less rigorous than those found in native or even other invaded areas.

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