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ORIGINAL PAPER

Better colony performance, not natural enemy release, explains numerical dominance of the exotic *Polistes dominula* wasp over a native congener in South Africa

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Abstract The European paper wasp *Polistes dominula* has invaded many parts of the globe and often displaces similar native species. Factors contributing to this remain unclear but may include longer seasonal activity period, natural enemy release, greater colony productivity and smaller body size. Since its discovery in South Africa in 2008, the local abundance of *P. dominula* has increased greatly. In invaded habitats, it is now much more common than the native *P. marginalis*. Here we determine some of the factors that enable dominance of *P. dominula* over the native congener during early stages of the invasion process. The activity of both species was monitored in four habitat types (urban, rural, fringe and natural) to determine differences in abundance, seasonal activity period, and habitat preference. Nests and individuals of both species were collected and compared for colony productivity (nest size), parasitism levels, and size of individuals. Both species preferred anthropogenically altered habitats, with *P. dominula* significantly more abundant than *P. marginalis*. Contrary to expectation, the exotic species suffered significantly higher parasitism than the native species. However, *P. dominula* had a substantially longer activity period and greater colony productivity than *P. marginalis*. *P. dominula* is therefore able to reach much greater population size than *P. marginalis* despite higher parasitoid pressure and similar individual size due to better colony performance. This has implications for future biological control initiatives.

Keywords Hymenoptera · Invasion biology · Interspecies competition · Parasitism · Social insects

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Introduction

The European paper wasp *Polistes dominula* is a highly invasive species recently recorded in South Africa (Eardley et al. 2009; Veldtman et al. 2012; Benadé et al. 2014). Its native range includes parts of Europe, Asia, Russia and northern Africa, but it has now successfully spread to every continent except Antarctica (Cervo et al. 2000; Miller et al. 2013) via human mediated introductions (Buck et al. 2008; Miller et al. 2013). On many of these continents, it is intruding into the niche of native paper wasp species (Gamboa et al. 2002, 2004) which leads to direct competition for food, foraging habitat and nesting sites (Gamboa et al. 2002, 2004; Benadé et al. 2014). In

South Africa, *P. dominula* was first recorded in 2008 (Eardley et al. 2009), but has rapidly expanded its range (Veldtman et al. 2012; Benadé et al. 2014). It shares this invaded distribution range with the native *P. marginalis*, but has become much more abundant than the native species (Veldtman et al. 2012; Benadé et al. 2014). Determining the specific traits that make *P. dominula* successful over the ecologically and taxonomically similar *P. marginalis* in its newly acquired habitat may provide vital information for its control and for the prevention of future invasions (Jones and Lawton 1995).

The success of *P. dominula* over native congener species in North America has been attributed to multiple factors including shorter brood development times, natural enemy release, and greater reproductive abilities (Cervo et al. 2000; Gamboa et al. 2004). Determining the success of this same exotic species over a different native congener, and on a different continent, provides opportunity to identify the most important factors that explain its success in general. Invasive success is often attributed to lack of regulation by natural enemies (Jeffries and Lawton 1984; Liebert et al. 2006), hence the drive behind biological control efforts are usually to reconnect exotic species with their natural predators and parasites, i.e. classical biological control (Irvin and Hoddle 2010). Recently, Madden et al. (2010), Miller et al. (2013) and Benadé et al. (2014) reported parasitism of *P. dominula* outside of its native range in North America and South Africa respectively. In North America, *P. dominula* is parasitized by *Dibrachys cavus* (Hymenoptera: Pteromalidae), *Chalcoela iphitalis* (Lepidoptera: Pyralidae) and a *Sarcophaga* sp. (Diptera: Sarcophagidae) (Miller et al. 2013). In South Africa, nests often contain larvae and puparia of the parasitic fly *Anacamptomyia* sp. (Tachinidae) (Benadé et al. 2014). This fly probably moved onto *P. dominula* from the native *P. marginalis* (Benadé et al. 2014). This provides the opportunity to assess parasite loads on colonies of both wasp taxa, and to evaluate the biotic release hypothesis (Jeffries and Lawton 1984; Liebert et al. 2006) as explanation for successful invasion by *P. dominula* (i.e. parasite load is expected to be much lower on the novel exotic species than the native species).

A smaller body size of an exotic competitor wasp can contribute to its invasive success, as it requires less energy to maintain a smaller body than a larger one (Armstrong and Stamp 2003). For social Hymenoptera, a smaller body size denotes a greater number of individuals produced and maintained (e.g. workers in ant colonies) for the same amount of energy consumed (e.g. a limited food resource) when compared to larger counterparts (Bourke and Franks 1995). This results in superiority through numbers, and a greater degree of colony productivity (McGlynn 1999). The advantages of greater numbers include better foraging efficacy, better brood care, and more success against competitors (Bourke and Franks 1995).

In North America, *P. dominula* has multiple advantages over the best studied of the native congener species *P. fuscatus* (Armstrong and Stamp 2003), including smaller body size, greater foraging efficacy, and a much higher reproduction rate. *P. dominula* has a shorter brood development time than *P. fuscatus*, allowing for greater colony productivity, and as a result, greater competitive fitness (Cervo et al. 2000; Gamboa et al. 2002; Armstrong and Stamp 2003). The greater colony productivity manifests as nests that contain three times as many cells in the case of *P. dominula* compared to *P. fuscatus* (Gamboa et al. 2002). This link between smaller body size, greater number of nest cells, greater nest productivity, and consequently, increased fitness of *P. dominula* over *P. fuscatus* (Gamboa et al. 2002) may also explain the apparent competitive advantage of *P. dominula* over *P. marginalis* in South Africa.

Here we determine whether the exotic *P. dominula* has characteristics that result in a performance advantage over the native congener *P. marginalis* in South Africa. We specifically compare these two species in terms of (1) overlap in foraging habitat, (2) differences in seasonal activity periods, (3) possible role of natural enemy release (i.e. parasitism rates by shared parasitoid species), (4) differences in body size, and (5) differences in colony productivity (in terms of cell numbers in nests). Because there is currently no effective way for surveying *Polistes* individuals using traps in South Africa (Van Zyl 2016), nests of *P. dominula* in its invaded range in North America are most often encountered on man-made structures in urban areas (Gamboa et al. 2002, 2004; MacKenzie et al. 2006; Benadé et al. 2014) and finding nests of paper wasps in natural areas are notoriously difficult (Liebert et al. 2006), we relied on an active search technique to enumerate numbers of foraging wasps.

Materials and methods

Habitat preferences and foraging activity

To determine habitat preferences and seasonal foraging activity periods for both species, the numbers of actively foraging wasps (wasps flying close to the vegetation at ground level that were seemingly searching for prey; i.e. not flying at high altitude and in a straight line) were determined at 40 sites over a period of 12 months (July 2013 to July 2014) in and around the town of Stellenbosch. This area was selected as it contains various habitat types within a relatively short distance from one another, and both *P. dominula* and *P. marginalis* are common in the region (Benadé et al. 2014). Sites comprised four habitat types, each with ten replicates, that were > 1 km apart to minimise pseudo replication. Urban sites included botanical gardens, schools, sport grounds and parks. Agricultural sites (rural) were set up in grassy areas on wine farms surrounding the town. Fringe sites contained transitional vegetation types between urban and natural sites usually with high cover of invasive alien plant species. Natural sites were indigenous fynbos vegetation and were > 1 km from nearest anthropogenic influences.

Visual surveys were undertaken for 20 min at each site during the first week of every month. The number of foraging individuals of *P. dominula* and *P. marginalis* observed was recorded. Active visual surveys consisted of continuous walking at a constant relaxed pace through the site in a randomised fashion by a single observer for ca. 300 meters and counting foraging wasps. Care was taken not to record the same individual more than once by not crossing already surveyed parts of transect. Surveys were conducted only on windless and cloudless days and between 11:00 and 15:00.

Body size, parasitoid load, and colony productivity

Polistes dominula and *P. marginalis* often nest only centimetres from one another on buildings in and around our study area (Benadé 2015). This allows for direct comparisons between the two species in terms of biology and ecology while partially controlling for environmental conditions. To compare body size, parasite loads and colony productivity between these species, nests and individuals were collected for physical measurements and nest-cell counts. Nests of both *P. dominula* and *P. marginalis* were collected at the end of the activity season in May 2014 (i.e. the start of winter), as this is when colonies would likely be mature. Nests were only collected from urban and rural sites, as no nests were observed in fringe and natural habitat types. Collection took place either at night or early morning, as this is when wasp activity was low and the majority of individuals were present on their nests. Nests and accompanying wasps were removed by dislodging nests from the substrate using a honey bee-hive tool and placing these in separate resealable plastic bags. Bags were frozen at − 20 °C to euthanize the wasps and for storage until further processing.

We determined body mass (as individual dry mass) of *P. dominula* and *P. marginalis* wasps collected with their nests after removal of foundress females when present (assumed to be the largest bodied, female individual). Wasps were oven dried at 60 °C for a period of 24 h before determining dry weight of individual wasps using a digital scale (Sartorius Model BP 110 S, Capacity: 0.1 mg–110 g).

Benadé et al. (2014) identified three parasitoids and/or hyper-parasitoids on nests of both the exotic *P. dominula* and the native *P. marginalis*. A fly from the genus *Anacamptomyia* (Tachinidae) was most prominent, allowing comparisons of nest parasitism rates in terms of number of cells affected per nest. Personal observations (FR) indicate that the only other common parasitoid (Eurytomidae) is likely a hyperparasitoid on the *Anacamptomyia* fly as emergence holes are often seen on fly puparia and cells containing these, and never on wasps or cells containing wasps. Unparasitized nest cells can easily be differentiated from those parasitized by *Anacamptomyia* as the latter contain brown fly puparia or their remnants. Parasitoid load for each nest was calculated using the number of cells containing fly puparia as a percentage of the total number of cells per nest.

Colony productivity, as an estimate of the potential number of offspring reared, can be assessed using the number of cells in a nest (Gamboa et al. 2002). To determine the potential colony productivity of *P. dominula* and *P. marginalis*, we therefore determined the total number of cells of each of the collected nests for both *P. dominula* and *P. marginalis*. It has to be noted that *Polistes* species often reuse cells in a nest for successive broods (Karsai et al. 1996). Therefore, actual colony productivity may be an underestimation of true colony productivity, and the degree of this may differ between different species.

Statistical procedures

Data on numbers of foraging wasps, habitat preferences, and monthly counts were statistically compared using generalized linear mixed models (GLMMs) calculated using the *lme4* package in R (Bates et al. 2015). Habitat type (Urban, Rural, Fringe, Natural) and species (*P. dominula*, *P. marginalis*) were used as fixed effects, while observation sites nested within the observation month were used as random effect. GLMMs were calculated using a Laplace approximation, and data fitted to a Poisson distribution (Bolker et al. 2009). Two models were evaluated, the first testing for an additive effect between the fixed effects, and the second, testing for an interaction effect between these. Body size differences between *P. dominula* and *P. marginalis* were also compared using generalized linear models (GLMs) in R. Models tested included dry weight of individuals partitioned by species, the latter variable with the additive effect of wasp sex (male, female), or the interactive effect between these two variables. Similarly, data on total number of nest cells were compared between *P. dominula* and *P. marginalis* using generalized linear models (GLM) in R. Best-fit models were chosen based on the Akaike information criterion (AIC). Models with the lowest AICc scores were considered as best. Percentage data on parasitoid loads for each nest of each wasp species contained numerous zeros, and so we statistically compared parasitoid load data using a Pearson's Chi squared test of independence in R.

Results

Habitat preferences and activity period

During the first 2 months of observations in winter (July and August), no foraging wasps of either species were observed. The first *P. dominula* individual appeared in September in the urban habitat type at the onset of spring as temperatures started to rise. This was more than 2 months before the first foraging *P. marginalis* individual was observed during November. Only one individual of *P. dominula* was observed in September while 12 individuals were observed during October. Abundance of both wasp species was highest in late summer/early autumn (February to April). However, from late autumn (May) onwards into winter (data not shown), their abundance score was zero.

A total of 809 foraging wasp individuals was observed during the entire survey period. This constituted 758 *P. dominula* and only 51 *P. marginalis* individuals respectively. The model that best explained wasp foraging abundance incorporated the interaction of the fixed effects habitat type and species with the random effect of observation site, nested within observation month (AIC = 1231.9; residual deviance/degrees of freedom = 1.177). In the best-fit model, *P. dominula* was significantly more abundant than *P. marginalis* (Table 1, Fig. 1). Habitat type also significantly influenced wasp numbers with greater abundance of foraging wasps of both species within or close to high-density human-settlements (urban and fringe habitats, Table 1, Fig. 1). *P. dominula* was especially abundant in these environments, with far fewer observations in natural and rural areas. In addition to urban and fringe habitats, abundance of *P. marginalis* was higher also in rural areas compared with no wasp individuals encountered in natural habitats (Table 1, Fig. 1).

Body size, parasitoid load, and colony productivity

In total, we collected 132 paper wasp nests. Of these, 101 nests were those of *P. dominula* and 31 nests were *P. marginalis*. Of the nests collected, 46 were still occupied by wasps at the time of collection (27 *P. dominula* and 19 *P. marginalis* nests). From these, a total of 858 *P. dominula* and 265 *P. marginalis* adult wasps were collected, and individual dry mass determined. The best-fit model for evaluating differences in the dry weight of collected individuals included only the difference in species (AIC = − 5875.4). According to this model, there was a significant difference in the dry mass of the two species (estimate = 0.004, standard error = 0.0012, z value = 3.341, $P < 0.0001$). However, the model explained only 1% of the total variation in the data. The median dry mass of the two taxa differed only slightly, and the two taxa had largely overlapping data ranges (Fig. 2). We therefore conclude that this statistical difference is likely due to the large sample size

Table 1 Best-fitting linear mixed-effects model showing the response of abundance of *P. dominula* and *P. marginalis* foraging wasps to the interacting effects of habitat type and species identity

Variable	Estimate	SE	z value
Intercept	− 3.272	1.044	− 3.134**
Habitat type as compared to fringe			
Natural	− 3.311	0.5598	− 5.928***
Rural	− 2.845	0.494	− 5.756***
Urban	1.610	0.335	4.806***
Species (*P. marginalis* vs. *P. dominula*)	− 3.048	0.339	− 8.992***
Interaction as compared to fringe: *P. dominula*			
Natural: *P. marginalis*	− 6.693	58.742	− 0.114
Rural: *P. marginalis*	2.221	0.566	3.921***
Urban: *P. marginalis*	0.396	0.378	1.047

The parameter estimates, standard error (SE), and z values are shown

Significant parameters are indicated as ***$P < 0.0001$; **$P < 0.001$; *$P < 0.05$. Observation site (10 sites) nested within observation month (12) was specified as random effects

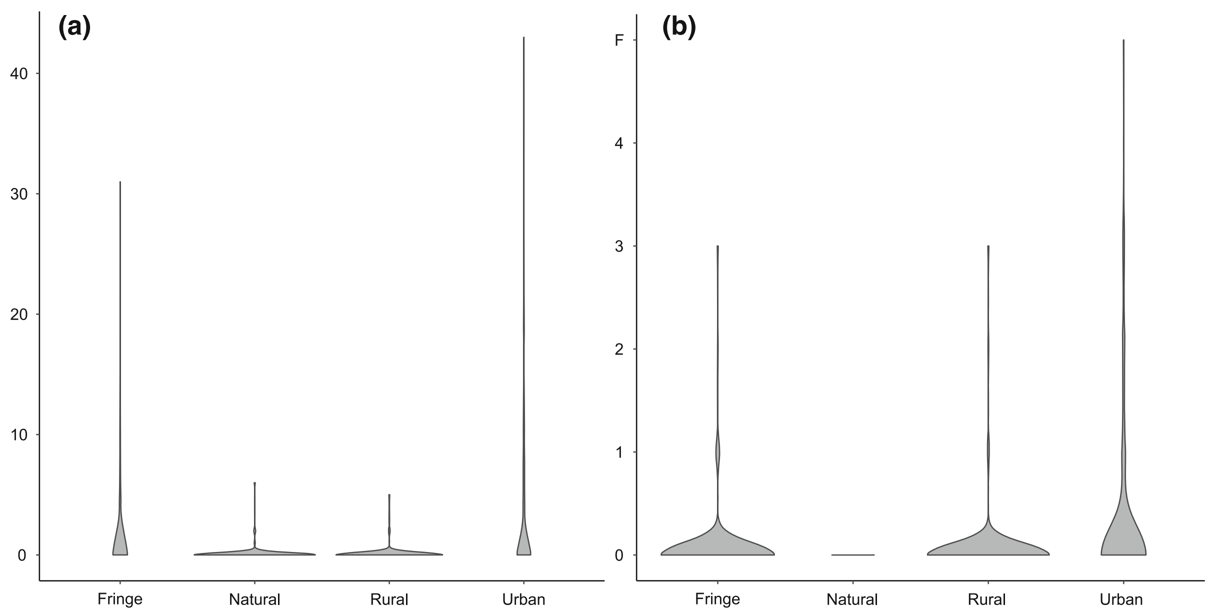

Fig. 1 **a** numbers of individuals of *P. dominula* (n = 758 individuals) and **b** *P. marginalis* (n = 51 individuals) observed at four habitat types (n = 10 sites per habitat) for the entire observational period (n = 12 observational events during 1 year per habitat type). Note the difference in the scale of the y-axes

and that it is not biologically meaningful. We therefore consider the two taxa to be similar in size as measured by individual dry weight.

Overall percentage of cells per *P. dominula* nest parasitized by the *Anacamptomyia* fly was significantly higher than that of *P. marginalis* nests ($x^2 = 124$, degrees of freedom = 96, $P < 0.05$) (Fig. 3). Most *P. marginalis* nests collected did not show any evidence of parasitization by the fly (only 13% of all nests collected showed any evidence of parasitization). In contrast, most nests (85%) of *P. dominula* collected showed some evidence of parasitization by this species. The numbers of cells parasitized in individual nests of *P. dominula* often

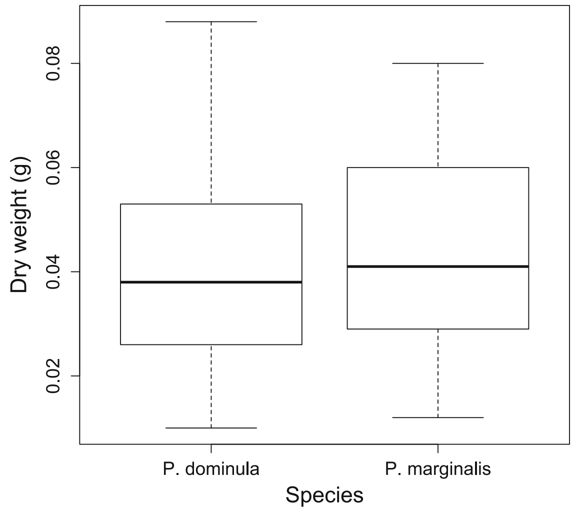

Fig. 2 Median dry weight (g) of *Polistes dominula* and *P. marginalis* individuals collected at the end of the active season

exceeded 15%, and reached > 50%. Even so, *P. dominula* nests generally contained significantly more cells, and therefore had a greater colony productivity potential than those of *P. marginalis* (AIC = 1833.5, % variation explained = 16.7%, residual deviation/degrees of freedom = 1.19, estimate = – 259.36, standard error = 50.80, z value = – 5.105, $P < 0.0001$) (Fig. 3). Nests of *P. marginalis* rarely contained > 100 cells, whereas nests of *P. dominula* in some cases contained 10 × more than that.

Discussion

Polistes dominula was far more abundant in its newly invaded habitat in South Africa than was the native *P. marginalis*, even though they have similar habitat preferences. Foraging workers of *P. marginalis* were most common in association with human activity (i.e. urban, fringe, and rural habitat types). In contrast, *P. dominula* was most abundant in urban habitats, while significantly less at the urban fringe, yet far more abundant than in the natural and rural habitats. This suggests that resources such as prey and nesting sites in urban settings result in high *P. dominula* abundance. Although rural and urban habitat types supported the most nests, the main difference between urban and rural sites was the number of human structures available for constructing nests. For both *P. dominula* and *P. marginalis*, the natural habitat type was least preferred, most probably also due to lack of adequate nesting sites. These results agree with those of Gamboa et al. (2004), who showed that feeding and habitat preferences of the exotic *P. dominula* and native *P. fuscatus* in the USA are similar. As both *P. dominula* and *P. marginalis* probably use similar resources such as food (Cervo et al. 2000) and nesting sites, a high level of indirect competition may exist between these two species as in the USA (Liebert et al. 2006). However, we did not sample sites without *P.*

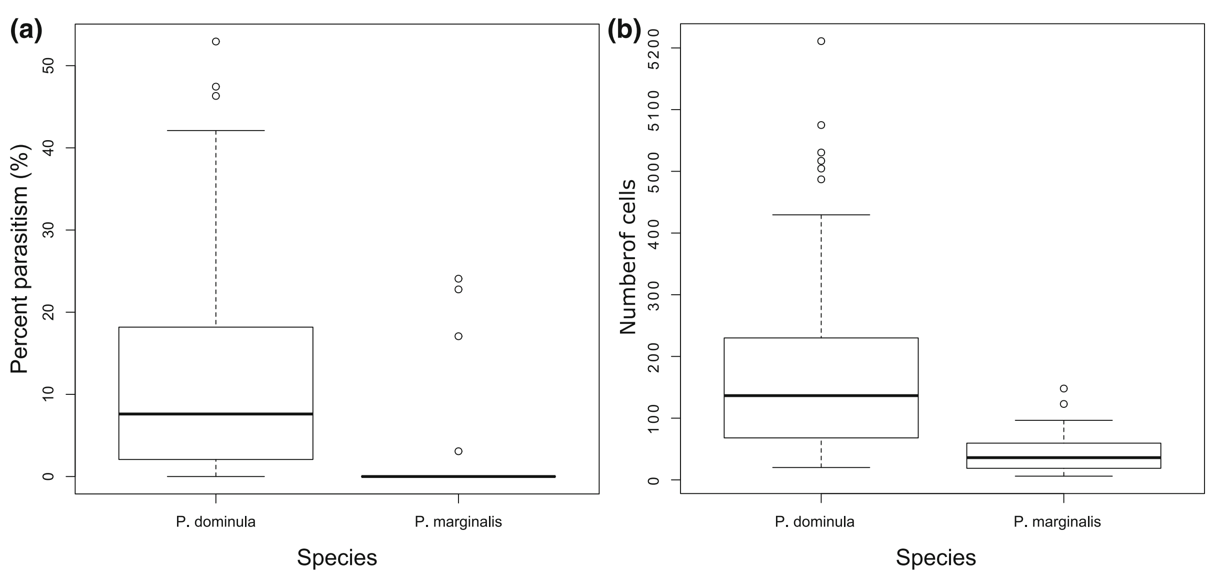

Fig. 3 **a** Percentage of *P. dominula* and *P. marginalis* nest cells parasitized by *Anacamptomyia* sp. **b** Total number of cells in nests of *P. dominula* and *P. marginalis* collected at the end of the activity season

dominula and therefore we cannot enumerate possible competitive effects on the numbers of *P. marginalis* here (Pilowsky and Starks 2018).

When compared with the USA, the great abundance of the exotic *P. dominula* in South Africa may have resulted from a longer seasonal activity period, natural enemy release, smaller body size and/or greater colony productivity (Cervo et al. 2000; Gamboa et al. 2002; Armstrong and Stamp 2003). For example, a smaller body size of an exotic species over a native competitor can lead to a competitive advantage in the exotic species (McGlynn 1999), because a smaller body size can denote a greater number of individuals produced (Bourke and Franks 1995) for the same amount of food resources (energy) available. This leads to a feedback system where greater numbers improves competition for resources (Bourke and Franks 1995). However, we found that *P. marginalis* and *P. dominula* in South Africa are very similar in size and the numerical dominance of the exotic species is therefore not coupled to a smaller body size as may be the case for the interactions between *P. dominula* and *P. fuscatus* in the USA.

Under predictions of the enemy release hypothesis, the exotic wasp would be less affected by parasitoid species than the native wasp species (Colautti et al. 2004). This would therefore give a competitive advantage of the exotic species over the native species in terms of release from top down population regulatory effects. Benadé et al. (2014) found the same taxa of native parasitoids in the nests of *P. dominula* and *P. marginalis* in South Africa. Contrary to expectations, here we show that the nests of *P. dominula* suffer significantly higher parasitism rates (median ca. 7% cells) than the nests of the native species (median 0% cells). Release from natural enemies is therefore unlikely to contribute to the success of *P. dominula* in the region. However, parasitoids, such as *D. cavus* in the USA, may help stabilise the populations of *P. dominula*, especially in the later stages of the invasion process (Miller et al. 2013). It is therefore expected that the parasitoids of *P. dominula* in South Africa may slow the invasion process and prevent populations of the wasp attaining ever greater numbers than at present in the invaded areas. However, Miller et al. (2013) made use of data on the percentage of nests containing signatures of total parasitoids as measure of parasitism levels. They found that ca. 60% of *P. dominula* nests were parasitized, while only ca. 20% of *P. fuscatus* nests showed evidence of parasitoids. When considering parasitism levels at this 'nest' level, and only for the *Anacamptomyia* sp. fly here, 85% of *P. dominula* nests contained signs of parasitism, while only 13% of *P. marginalis* nests were parasitized. Parasitism levels at the nest level for *P. dominula* is therefore close to a maximum in South Africa, but despite this, numbers of *P. dominula* are much higher than *P. marginalis* in the region.

Polistes dominula started actively foraging almost 2 months before the first foraging individuals of *P. marginalis* appeared. This is in sharp contrast to the situation in the USA, where there were no significant difference in the timing of colony initiation between *P. fuscatus* and *P. dominula* (Gamboa et al. 2002, 2004). Despite the similar colony initiation times in that study, workers of *P. dominula* appeared on average a week earlier than *P. fucatus* workers. This faster developmental time was linked to more 'condensed' larval and pupal developmental periods in *P. dominula*, that may be related to its smaller size (Gamboa et al. 2004). However, the early production of *P. dominula* workers in South Africa is probably due to its shorter larval and pupal periods (as nest initiation is earlier for *P. dominula* than *P. marginalis*) bearing in mind that the comparative body size of individuals of the two species are similar. Reasons for the much earlier activity of *P. dominula* in South Africa may therefore relate more to physiological differences between the native and the exotic species, such as greater lower thermal tolerances of the exotic species (Weiner et al. 2010, 2011, 2012). This aspect, together with studies on brood developmental times, should be investigated further. Some anecdotal evidence for the role of physiology in *P. dominula* success is provided by recent range expansion studies in Europe where nest productivity of *P. dominula* is very flexible and closely linked to climatic conditions (Höcherl and Tautz 2015). The much earlier activity of *P. dominula* likely results in a competitive advantage over *P. marginalis* as this allows earlier nest establishment, more advantageous nest placement (in terms of protection from water and predation) and earlier production of workers (Cervo et al. 2000; Gamboa et al. 2002).

At the end of the activity season, nests of *P. dominula* were significantly larger than those of *P. marginalis* and contained 3.8 times more cells (median of 273 cells) than those produced by *P. marginalis* (median of 72 cells). Our results are therefore very similar to those comparing colony size of *P. dominula* to the native *P. fuscatus* in the USA. There, the exotic species exhibited 3–5 times greater colony productivity (as measured by cell counts of nests) than the native congener (Gamboa et al. 2002, 2004). It has to be noted that, although every effort was made not to include nests containing multiple foundress females an re-used nests from previous seasons as was documented for *P. dominula* (Liebert et al. 2008), we cannot be certain that all nests in our study were founded by single females and were constructed in the current season. Therefore, a few of the larger nests may well over-estimate colony productivity. However, superiority in colony productivity by *P. dominula* over native congeners was also detected in its native range in Europe (Cervo et al. 2000), and when compared to *P. metricus* in the USA (Pickett and Wenzel 2000). Evidence is therefore mounting that superior colony productivity, linked to faster brood-developmental times, is one of the most important factors leading to the success of this species as an exotic competitor with native wasp species. As we show here, this can be independent of body size. However, other factors that may also contribute to its invasive success, such as those that contribute to colony productivity (e.g. better foraging rates and resource use) and factors associated with survivorship (e.g. lower usurpasion and predation levels) (Liebert et al. 2006), need further study.

To conclude, the success of *P. dominula* in its newly acquired habitat in South Africa is likely closely linked to its ability to produce large numbers of offspring earlier in season, allowing it to outnumber the native *P. marginalis*, which increases its chances of being a successful invader. Colony productivity of this species is more than three times higher than the native species, even though parasitism levels were significantly higher. The presence of parasitoids on *P. dominula*, although more pronounced than on the native *P. marginalis*, therefore does not reduce their numbers to levels lower than that of the indigenous species. Factors positively affecting colony productivity and survivorship, combined with a preference for human-altered environments, likely significantly contribute to the invasive success of *P. dominula* in the country. As previously indicated (Liebert et al. 2006), when this species successfully establishes itself in a new environment such as in South Africa, *P. dominula* will likely be a permanent member of human-altered environments with possibly a large impact on trophic levels in these environments. It could be either positive when it acts as an effective biological control agent or negative when it removes food sources for organisms at higher trophic levels. Its possible impact on native biodiversity is less clear, as it currently largely avoids these environments. Nevertheless, numbers of the exotic wasp was still much higher than that of the native species in natural environments, and its possible impact on native biodiversity should be monitored closely, especially as this area is a global biodiversity hotspot.

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References

Armstrong T, Stamp NE (2003) Colony productivity and foundress behaviour of a native wasp versus an invasive social wasp. Ecol Entomol 28:635–644

Bates D, Maechler M, Bolker MB, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Benadé PC (2015) Invaded range and competitive ability of the newly invasive *Polistes dominula* compared to that of its native congener species in the Western Cape, South Africa. Dissertation, Stellenbosch University

Benadé PC, Veldtman R, Samways MJ, Roets F (2014) Rapid range expansion of the invasive wasp *Polistes dominula* (Hymenoptera: Vespidae: Polistinae) and first record of parasitoids on this species and the native *Polistes marginalis* in the Western Cape Province of South Africa. Afr Entomol 22:220–225

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bourke AEG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Buck M, Marshall SA, Cheung DKB (2008) Identification atlas of the Vespidae (Hymenoptera, Aculeata) of the northeastern Nearctic region. Can J Arthropod Identif 5:1–492

Cervo R, Zacchi F, Turilazzi S (2000) *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypotheses for its rapid spread. Insectes Soc 47:155–157

Colautti RI, Ricciardi A, Grigorovich IA, Macisaac H (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Eardley C, Koch F, Wood AR (2009) *Polistes dominula* (Christ 1971) (Hymenoptera: Polistinae: Vespidae) newly recorded for South Africa. Afr Entomol 17:226–227

Gamboa GJ, Greig EI, Thom MC (2002) The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insectes Soc 49:45–49

Gamboa GJ, Noble MA, Thom MC, Togal JL, Srinivasan R, Murphy BD (2004) The comparative biology of two sympatric paper wasps in Michigan, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insectes Soc 51:153–157

Höcherl N, Tautz J (2015) Thermoregulation of individual paper wasps (*Polistes dominula*) plays an important role in nest defence and dominance battles. Naturwissenschaften 102:32

Irvin NA, Hoddle MS (2010) Comparative assessments of *Gonatocerus ashmeadi* and the 'new association' parasitoid *Gonatocarus tuberculifermur* (Hymenoptera: Mymaridae) as biological control agents of *Homalodisca vitripennis* (Hemiptera: Cicadellidae). Biol Control 55:186–196

Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. Biol J Linn Soc 23:269–286

Jones CG, Lawton JH (1995) Linking species and ecosystems. Chapman & Hall, New York

Karsai I, Pénzes Z, Wenzel JW (1996) Dynamics of colony development in *Polistes dominulus* a modeling approach. Behav Ecol Sociobiol 39:97–105

Liebert AE, Gamboa GJ, Stamp NE, Curtis TR, Monnet KM, Turillazzi S, Starks PT (2006) Genetics, behaviour and ecology of a paper wasp invasion: *Polistes dominulus* in North America. Ann Zool Fennici 43:595–624

Liebert AE, Hui J, Nonacs P, Starks PT (2008) Extreme polygyny: multi-seasonal "hypergynous" nesting in the introduced paper wasp *Polistes dominulus*. J Insect Behav 21:72–81

MacKenzie JK, Landolt PJ, Zack RS (2006) Attraction to ornamental Peony (*Paeonia lactiflora*, Paeoniaceae) by *Polistes dominulus* Christ (Hymenoptera: Vespidae) demonstrated using olfactometers. J Kans Entomol Soc 79:231–238

Madden AA, Davis MM, Starks PT (2010) First detailed report of brood parasitoidism in the invasive population of the paper wasp *Polistes dominulus* (Hymenoptera, Vespidae) in North America. Insectes Soc 57:257–260

McGlynn TP (1999) Non-native ants are smaller than related native ants. Am Nat 154:690–699

Miller GL, Donnelly CR, Gamboa GJ (2013) A ten-year comparative study of the population dynamics and parasitoidism in the native paper wasp *Polistes fuscatus* and the invasive *P. dominulus*. Insectes Soc 60:49–56

Pickett KM, Wenzel JW (2000) High productivity in haplometrotic colonies of the introduced paper wasp *Polistes dominulus* (Hymenoptera: Vespidae: Polistinae). J N Y Entomol Soc 108:314–325

Pilowsky JA, Starks PT (2018) Displacement and replacement in real time: *Polistes dominula*'s impact on *P. fuscatus* in the northeastern US. Biol Invasions 20:1161–1169

Van Zyl C (2016) Status of the invasive wasp species, *Vespula germanica* and *Polistes dominula* in South Africa, and the feasibility of various management strategies. Dissertation, Stellenbosch University

Veldtman R, Addison P, Tribe GD (2012) Current status and potential future impact of invasive vespid wasps (*Vespula germanica* and *Polistes dominulus*) in South Africa. In: Holland J, Gerowitt B, Alomar O, Bianchi F, Eggenschwiler L, Van Helden M, Moonen C, Poehling H-M, Rossing W (eds) IOBC/wprs Bulletin 75, 245 pp

Weiner SA, Upton CT, Noble K, Woods WA, Starks PT (2010) Thermoregulation in the primitively eusocial paper wasp, *Polistes dominulus*. Insectes Soc 57:157–162

Weiner SA, Noble K, Upton CT, Woods WA, Starks PT (2011) A role for thermoregulation in the *Polistes dominulus* invasion: a comparison of the thermoregulatory abilities of the invasive wasp *P. dominulus* and the native wasp *P. fuscatus*. Insectes Soc 58:185–190

Weiner SA, Noble K, Upton CT, Flynn G, Woods WA, Starks PT (2012) The cost of flight: a role in the *Polistes dominulus* invasion. Insectes Soc 59:81–86