

# **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**

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by

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## Summary

The European paper wasp *Polistes dominula* (Christ)(Hymenoptera: Vespidae: Polistinae) established itself as a prolific invader across the globe and has been recorded and studied on all continents, except those with extremely low temperatures. In the invaded ranges it can displace native wasp species. This invader was first recorded in the Western Cape Province of South Africa in 2008 with little subsequent attention given to it after this initial record. In 2012 it was recorded in Stellenbosch, some 28 kilometres from where it was first seen. It is now fairly common in the region which prompted investigations into its ecology and effect on native biodiversity.

In this study the current invaded range and habitat preferences of *P. dominula* in the Western Cape of South Africa was determined. It was found to have increased its range into numerous towns within the Western Cape Province. However, *P. dominula* seemed for the most part to be confined to the Cape Metropolitan area. The Cape Fold Mountain belt to the east and Atlantic Ocean to the west apparently creating a hinderance to its dispersal. Even so, *P. dominula* was later also found outside of this area with human mediated distribution thought to be the main driving factor. This because, as demonstrated in this study, *P. dominula* prefer human altered environments.

To successfully invade and persist in a new range, *P. dominula* may possess a few advantageous characteristics over native species including release from enemies, greater colony productivity, longer activity season and a smaller body size. Here I investigated these factors by comparing *P. dominula* and the South African native congener species *Polistes marginalis* where these occur in sympatry. Over a period of 12 months (June 2013 to July 2014) foraging wasp activity of both species was recorded and compared. At the onset of winter and when wasp activity ceased, nests from both species were collected in order to determine enemy release, colony productivity and body size. Activity of the invasive *P. dominula* started earlier than the native *P. marginalis* allowing it to have greater abundance than the native species at the onset of *P. marginalis* activity. Nests of *P. dominula* also contained more cells than that of *P. marginalis* denoting greater colony productivity. Body size was not found to be significantly different to that of the native and therefore was not deemed to give *P. dominula* any advantage. Suprisingly, *P. dominula* had a greater parasitisation rate than that *P. marginalis*, refuting predictions under the enemy release hypothesis.



*Polistes dominula* is a prolific invader of newly acquired ranges in South Africa. It has already surpassed the natural barrier that once was the Cape Fold Mountain Range and the possibility exists that it could now invade more inland locations towards the east. It also outperforms the native species on several aspects that may lead to an ability to outcompete native congener species. Its effect on native arthropod taxa that forms part of its diet and on plant pollination has yet to be determined, but all evidence suggests that this species should be controlled as much as possible in order to prevent negative impacts on native biodiversity. These programmes should be focussed in urban areas where these wasps proliferate.

## Opsomming

Die Europese papier perdeby *Polistes dominula* (Christ) (Hymenoptera: Vespidae: Polistinae) is nou gevestig as 'n effektiewe indringer regoor die wêreld en is aangeteken en bestudeer op alle kontinente, behalwe die met baie lae temperature. In nuutgevonde areas kan inheemse perdeby spesies verdring word deur hierdie indringer. *Polistes dominula* was vir die eerste keer in die Wes-Kaap Provinsie van Suid-Afrika in 2008 opgemerk. In 2012 was dit aangeteken in Stellenbosch, sowat 28 kilometer van waar dit vir die eerste keer waargeneem is. Dit is nou volop in die streek, wat die studie van hierdie indringer se ekologie en uitwerking op inheemse biodiversiteit belangrik maak.

In hierdie studie is die huidige omvang en habitat voorkeure van *P. dominula* in die Wes-Kaap van Suid-Afrika bepaal. Daar is gevind dat sy verspreidingsarea toeneem het na verskeie dorpe in die Wes-Kaap. *Polistes dominula* blyk om grootendeels beperk te wees tot die Kaapse Metropolitaanse gebied. Die Kaapse Vou Bergreeks in die ooste en die Atlantiese Oseaan in die weste skep klaarblyklik hindernisse tot sy verspreiding. *Polistes dominula* is wel onlangs buite hierdie area gevind en daar word vermoed dat die verspreiding aangehelp is deur die mens.

Om 'n suksesvolle indringer te wees en te volhard in 'n nuwe habitat, kan *P. dominula* beskik oor 'n paar voordelige eienskappe wat nie by inheemse spesies voorkom nie: vyand ontwyking, uiters produktiewe kolonies, 'n langer aktiewe seisoen en 'n kleiner liggaamsgrootte. Hier ondersoek ek hierdie faktore deur die indringer *P. dominula* en die Suid-Afrikaanse inheemse *Polistes marginalis* te vergelyk in areas waar beide spesies saam voorkom.

Oor 'n tydperk van 12 maande (Junie 2013 tot Julie 2014) was perdeby getalle tydens hul jag aktiviteite aangeteken en vergelyk. Aan die begin van die winter (toe perdeby aktiwiteit gestaak het) was neste van beide spesies versamel om vyand ontwyking, kolonie produktiwiteit en liggaam grootte te bepaal. Aktiwiteit van die indringer *P. dominula* is vroeër aangeteken as die van die inheemse *P. marginalis* wat daartoe gelei het dat daar aansienlik meer aktiewe *P. dominula* was as die inheemse spesies by die aanvang van *P. marginalis* aktiwiteit. Neste van *P. dominula* het ook meer selle as dié van *P. marginalis* bevat wat 'n aanduiding is van meer effektiewe kolonie produktiwiteit van die indringer. Die indringer het egter nie beduidend verskil van die inheemse spesie in terme van liggaamsgrootte nie en dit was daarom nie oorweeg as 'n voordeel nie. *Polistes dominula* was wel meer geparasiteer as

die inheemse *P. marginalis* wat tot gevolg gehad het dat die vyand ontwykings hipotese nie ondersteun word nie.

*Polistes dominula* is 'n produktiewe indringer van nuutverworwe areas in Suid-Afrika. Dit het reeds die natuurlike versperring van die die Kaapse Vou Bergreeks oorgesteek en die moontlikheid bestaan dat dit nou na die binneland in die ooste van Suid Afrika kan versprei. Die indringer is ook meer effektief as die inheemse spesie op verskeie vlakke wat kan lei tot die onderdrukking van die inheemse *P. marginalis*. Die uitwerking van *P. dominula* op inheemse geleedpotige taksa wat deel van sy dieet uitmaak en die moontlikheid van effekte op plant bestuiwing moet nog bepaal word. Die resultate dui daarop dat hierdie spesie bestuur moet word om negatiewe impak op inheemse biodiversiteit te voorkom. Programme om die impak van *P. dominula* in Suid Afrika te bestuur moet gefokus word in stedelike gebiede waar dit meerendeels gevind word.

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**Table of contents**

<b>Chapter 1.....</b>	<b>1</b>
General introduction .....	1
Invasive arthropods: a global perspective .....	1
Invasive arthropods: a South African perspective.....	2
Invasive arthropods and sociality .....	4
The paper wasps (Polistinae).....	5
The European paper wasp ( <i>Polistes dominula</i> ) as an invader .....	6
Objectives of this study .....	8
References .....	9
<b>Chapter 2.....</b>	<b>17</b>
Rapid range expansion of the invasive wasp <i>Polistes dominula</i> (Hymenoptera: Vespidae: Polistinae) and first record of parasitoids on this species and the native <i>Polistes marginalis</i> in the Western Cape Province of South Africa.....	17
References .....	23
<b>Chapter 3.....</b>	<b>27</b>
Invaded range, habitat preferences and activity period of <i>Polistes dominula</i> in the Western Cape Province of South Africa .....	27
Abstract .....	27
Introduction .....	27
Materials and methods.....	29
Invaded range .....	29
Habitat preferences and activity period.....	30
Data Analyses.....	31
Results .....	32
Invaded range .....	32
Habitat preferences and activity period.....	32
Discussion .....	34
References .....	37
<b>Chapter 4.....</b>	<b>41</b>
Greater colony performance of <i>Polistes dominula</i> compared to a native congener explains numerical dominance of this invasive in South Africa .....	41
Abstract .....	41
Introduction .....	41
Materials and methods.....	44
Study sites .....	44
Habitat preferences and activity period.....	44
Enemy release, body size and colony productivity .....	45
Enemy release.....	45
Body size .....	46
Colony productivity.....	47
Results .....	47
Habitat preferences and activity period.....	47

Enemy release, body size and colony productivity .....	49
Enemy release.....	50
Body size .....	50
Colony productivity.....	53
Discussion .....	55
References .....	58
<b>Chapter 5.....</b>	<b>61</b>
General discussion and Conclusions.....	61
Invaded range .....	62
Habitat preferences.....	63
Advantages of the invasive <i>P. dominula</i> over the native <i>P. marginalis</i> .....	64
Future research .....	64
References .....	66

## Chapter 1

### General introduction

Biological invasions by invasive alien species (IAS) often incur high costs, both economically and ecologically, and invasive organisms are now accepted as one of the greatest threats to global biodiversity (Pimentel *et al.* 2005; Carlton & Ruiz 2005; Rands *et al.* 2010). Not surprisingly, considerable efforts have been directed towards the understanding of processes driving human-mediated invasions (Blackburn *et al.* 2012). The extent of IAS today can be attributed to the increased mobility and globalization of humans especially through trading of goods and services, travel and tourism (McNeely *et al.* 2001; Mooney & Cleland 2001; Kolar & Lodge 2001; Mack *et al.* 2000; Sharma *et al.* 2010; Blackburn *et al.* 2012). Also, conversion and fragmentation of natural habitats (Perrings 2001) and a general anthropogenic alteration of natural environments (Vitousek *et al.* 1996) resulted in a clear correlation between the density of IAS and that of people (Shackleton *et al.* 2007; Sharma *et al.* 2010).

IAS can be any animal, plant or microorganism introduced, either deliberately or inadvertently, into a habitat where they do not naturally occur, with the ability to become established and persist through many generations (Vitousek *et al.* 1997; Richardson *et al.* 2000). These often have enormous impacts on ecosystems such as altering species composition, nutrient cycling, primary productivity and hydrology and ultimately results in the extinction of native species (Sackmann *et al.* 2008; Kolar & Lodge 2001; Vitousek 1990). Invasion by IAS also results in a decrease in indigenous biodiversity and an increase in biotic homogenization (Mooney & Cleland 2001). Loss of biodiversity, in turn, impacts on many ecological aspects, including loss of ecosystem services (Balvanera *et al.* 2006; Snyder & Evans 2006) and the ability of environments to buffer the effects of environmental change (Loreau *et al.* 2001). There are also numerous unknown consequences for human welfare that may result from biodiversity loss (Perrings 2001). All of these consequences have also been identified for invasive arthropods (Snyder & Evans 2006).

### *Invasive arthropods: a global perspective*

An estimated 480 000 non-native species have been introduced around the world, with 20-30% of these having successfully established and causing ecological problems in the newly acquired habitats (Pimentel *et al.* 2001). They also result in a loss of 5% of the world economy (Pimentel *et al.* 2001). In America alone, more than 50 000 non-native species have

been introduced, resulting in an annual expenditure of \$134 billion to combat them (Pimentel *et al.* 2001). About 4500 of these non-native species are arthropods that lead to a decline of biodiversity, and have incurred expenditures of >\$20 billion annually for control and restoration (Pimentel *et al.* 2005). Europe has been invaded by an about 11 000 non-native species, costing an estimated €20 billion annually (Kettunen *et al.* 2008), with this problem set to increase as about 10 new invasive species become established in Europe each year. Thirty percent of these are arthropods (Hulme *et al.* 2010).

Examples of invasive arthropods causing considerable damage world-wide include: 1) the Asian citrus psyllid (*Diaphorina citri*), originally from China is now widely distributed (Batool *et al.* 2007). On its own it is not much of a threat as an invasive species, but as a carrier of the pathogenic Citrus Greening Disease (Huanglongbing) it has caused devastating consequences for the citrus industry (Halbert & Manjunath 2004) to the extent that it is known as the worst citrus pest in the world (Stokstad 2006); 2). The Gypsy moth (*Lymantria dispar*) originally from Europe and Asia (Sharov *et al.* 2002) has contributed to the defoliation of more than 81 million ha of forest in the United States, resulting in large scale mortalities and decreased tree growth (USDA 1995), 3). The Asian tiger mosquito (*Aedes albopictus*), originally from Asia, as a vector for more than 30 arboviruses (Gratz 2004) including Denque and Chikungunya (Enserink 2008), has been described as one of the fastest spreading animal species in the world. It is now known from 28 countries outside of its native range, including South Africa (Benedict *et al.* 2007).

Invasion efficacy can be attributed to multiple factors including generalist diets, shorter brood development and the absence of natural predators and parasites also known as the enemy release hypothesis (Cervo *et al.* 2000; Colautti *et al.* 2004). Hence the effort and drive behind biological control - a low-cost, chemical free means (Roderick 2012), to reconnect invasives in newly acquired ranges with predators and parasites from their original habitat (Irvin & Hoddle 2010). The management of the cottony-cushion scale (*Icerya purchasi*) by the vedalia beetle (*Rodolia cardinalis*) in California and South Africa is an excellent example of the effectiveness and long lasting effect of introducing a well-studied controlling agent from an invasives original habitat (Caltagirone & Douth 1989).

#### *Invasive arthropods: a South African perspective*

South Africa has long been plagued by the presence of non-native species (Richardson & van Wilgen 2004). The study of alien invasives in South Africa, however, seems to be limited to the more attractive and conspicuous plants and arthropods, as little is known regarding most



non-native invertebrates in South Africa (Picker & Griffiths 2011). The total number of invasive species that have been recorded in South Africa is estimated at around 9 300, of which 388 are arthropods. These cost the country an estimated R100 billion annually (Picker & Griffiths 2011). Giliomee (2011) showed that, in the case of insects, 13 non-native species have established within South Africa in only the previous 12 years, and that phytosanitary control at national entry points should be considerably improved. The recently published and updated list of alien and invasive species in the National Environmental Management Biodiversity Act (NEMBA Act No. 10 of 2004) includes, among others, the following arthropods as current and potential threats to biodiversity in South Africa: 1) the Asian fruit-fly (*Bactrocera dorsalis*), originating from Sri Lanka (Picker & Griffiths 2011), is regarded as one of the greatest dangers to the fruit export industry worldwide (Ekesi *et al.* 2006). Its hosts include both cultivated and wild hosts ranging from mango, tomato to avocado, and marula fruit (Ekesi *et al.* 2006) to guava (Picker & Griffiths 2011), 2) the Large grain borer (*Prostephanus truncates*), originally from Central America (Boxall 2002, Picker & Griffiths 2011), has spread to several countries in Africa and was first reported in South Africa in 1999 (Picker & Griffiths 2011). It is recognized as the greatest threat to stored maize products (Boxall 2002) directly impacting multiple African countries with resource scarcities (Picker & Griffiths 2011), 3) the Argentine ant (*Linepithema humile*), a native to northern Argentina, Brazil, Paraguay and Uruguay, is now established in New Zealand, South Africa, Japan, Australia, Europe and the USA (Defeo *et al.* 2009). It is ranked as one of the world's 100 worst invasive species (Lowe *et al.* 2000). In South Africa, it is known to interfere with in-ground, natural storage of proteaceous Fynbos seeds and pollination systems (Lach & Thomas 2008), leading to disruption of plant communities. In addition, its sociality contributes to its efficacy in disrupting native ant mutualisms (Picker & Griffiths 2011).

In South Africa, biological control has been implemented for more than 100 years with varying degrees of effectiveness (Giliomee 2011; Moran *et al.* 2013). The vine mealy bug (*Planococcus ficus*) is regarded as major pest insect in the South African table grape and wine industry (le Vieux & Malan 2013) and has been shown to be controlled to some extent by coccinellid beetles among other arthropods (Walton & Pringle 2004; le Vieux & Malan 2013). The ineffectiveness of these parasitoids is attributed to the fact that they can only attack the mealybug if exposed (Holm 2008) and when free from interference by the Argentine ant (*Linepithema humile*) which is also an invasive in South Africa (Mgocheki & Addison 2009).

*Invasive arthropods and sociality*

Only 2% of all arthropods are considered to be eusocial (Roy *et al.* 2011), whereas 24% of all truly invasive arthropods are eusocial (Beggs *et al.* 2011). Eusociality is an evolutionary advanced level of existence almost exclusively limited to insects (Wilson & Hölldobler 2005; Jarvis 1981), more specifically the Hymenoptera (Ants, Bees and Wasps), Isoptera (Termites), and some Homoptera (Aphids and Thrips) (Krebs & Davies 1993). Eusociality is characterized by a generational overlap of individuals (meaning that there are multiple viable individuals available to continue the nest if a queen should be removed or killed), all of which are able to contribute to the co-operative care through establishing a caste system (Krebs & Davies 1993; Wilson & Hölldobler 2005). This allows a species to rapidly reach high abundance and directly compete with other species in terms of numbers (Beggs *et al.* 2011).

Two degrees of eusociality or ‘true’ sociality exist. Highly eusocial insects create complex nest structures containing numerous workers and a few queens (Wilson 1971). Primitive eusocial insects create simpler nest structures containing only a few workers and pronounced interaction from the queen(s) (Wilson 1971). One of the major advantages of eusociality is that only one egg laying queen (foundress) is needed to establish a new population (West-Eberhard 1969; Beggs *et al.* 2011). Also, only a single queen can maintain the population of hundreds of nurturers that can devote all their time to brood care and not spend time on reproduction (Krebs & Davies 1993). Eusociality therefore is a divergence from the norm in that adults invest considerable time and energy towards brood care (Cervo 2006). The loss of ‘care costs’ allows the breeding female to stay at the nest and concentrate only on egg laying (Krebs & Davies, 1993) and therefore directly increases her own fecundity (Cervo 2006). This strategy is employed and perfected by wasps (West-Eberhard 1969) and is thought to add considerably to the ability of these insects to invade new habitats.

The vespoid wasps cover all degrees of sociality, from the solitary Eumenidae to the primitively social Polistinae to the highly social Vespinae (West-Eberhard 1969). A correlation can be drawn between the degree of sociality and invasion success of wasps. To date, all truly invasive alien vespoid species are eusocial (Beggs *et al.* 2011) even though only 20% of all species employ eusociality (Pickett & Carpenter 2010). This sociality allows for plasticity among the wasps that increases their ability to respond to environmental changes and to adapt to newly acquired ecosystems (Moller 1996). Evidence of invasive success by wasps are clear, considering the ability of the German wasp (*Vespula germanica*) to successfully invade several areas across the globe, including Australia, New Zealand, South

America (Reeson *et al.* 2003) and South Africa (Whitehead & Prins 1975). Even though social wasps are more conspicuous than their solitary counterparts (Beggs *et al.* 2011) there is still a major lack of research on these in South Africa. For example, even though very conspicuous, limited information exists on the ecology (and even species numbers) of native South African paper wasps (Polistinae).

### *The paper wasps (Polistinae)*

Polistinae wasps build aerial paper-like nests (Beggs *et al.* 2011) commonly attached to man-made structures (West-Eberhard 1969; Evans & West-Eberhard 1970; Cervo *et al.* 2000) or on vegetation (Rusina 2008). Vespinae nests, although also paper-like, are mostly below ground (Beggs *et al.* 2011). Polistinae nests are attached to the chosen surface with one or more petioles that support the comb consisting of closely grouped cells. Nests are constructed from a variety of organic and inorganic components, but predominantly from dry woody substances that are in close proximity to the nesting site (Bagriacik 2012). These fibres are held together by oral secretion added in the process of mastication (West-Eberhard 1969). Nesting components can also be collected from a variety of man-made decaying woody sources such as fence posts, garden furniture, telephone poles etc. (Pers. obs.). Nest size might be determined by chosen nesting site (Bagriacik 2011) and number of foundresses present on the nest (West-Eberhard 1969).

Fecund female wasps leave the nest at the end of the season (late summer/autumn) in order to undergo diapause in aggregation (Rau 1930; West-Eberhard 1969; Beggs *et al.* 2011). Diapause occurs within any kind of hibernacula deemed safe by the wasp, ranging from crevices in walls and rocks, to roof tiles and loose tree bark (Rau 1930; West-Eberhard 1969). Wasps often return to the same hibernacula year after year (Rau 1930). Nest initiation/founding follows in spring (Dapporto *et al.* 2004; Dapporto *et al.* 2006) and is usually done in close proximity to, or even on, parental nests from the previous season (West-Eberhard 1969), but usually not close to hibernacula (Rau 1930). Nests can be established by one (monogynic foundation) or more foundresses (polygynic foundation) (Pardi 1948; West-Eberhard 1969; Dapporto *et al.* 2004; Dapporto *et al.* 2006) and nest-establishment by the foundress ends with eclosion of the first workers. As workers eclose, the non-dominant females inherit the role of worker (Pardi 1948). Social hierarchy is first established between foundresses and later the workers of a colony. This results in a correlation between dominance order and degree of ovarian development (Pardi 1948; West-Eberhard 1969).

In general, foundress presence at a nest depends on food prey quantity consisting of soft bodied insects (Pers. Obs). In the study done by Armstrong & Stamp (2003), foundresses remained at, and maintained, the nest when food was ample and foraged more when food was less abundant. With the arrival of the first worker, freedom of parental duties is achieved by the queen thereby permitting her to direct all efforts towards increasing her own fecundity (Cervo 2006). Her fecundity is also increased if an auxiliary female oviposits in the nest as she feeds on this egg and lays her own (West-Eberhard 1969). The queen will continue to produce workers (predominantly female) to fulfil all social functions (except laying eggs) that include building and maintaining the nest, foraging and feeding larvae and nest defence (Pardi 1948). As the season nears its end food sources dwindle, newly eclosing adults are either non-workers or males, neither of which actively contribute to colony tasks and proceed to mob returning workers of food. This leaves few resources for the remaining larvae still present (West-Eberhard 1969). After cessation of oviposition by the queen, West-Eberhard (1969) observed females removing larvae and pupae from cells and either feeding these to other nestmates or dropping them from the nest. At the end of the season the newly eclosing females are usually larger, have more fat reserves than normal and spend most of their time on the nest. These copulate with males, undergo diapause and establish new nests in the following season (Pardi 1948).

*The European paper wasp (Polistes dominula) as an invader*

*Polistes dominula* (Christ) is a primitive eusocial paper wasp (Wilson 1971; Reeve 1991). It is often incorrectly referred to as *P. dominulus* or *P. gallicus* (Pardi 1948). *Polistes dominula* is aposematically coloured (black & yellow) (Eardley *et al.* 2009), unlike other South African *Polistes* species (Cervo *et al.* 2000), and looks very similar to the infamous aggressive *Vespula germanica*. The original extent of *P. dominula* is the Old World (Cervo *et al.* 2000; Gamboa *et al.* 2004), and includes Europe, Asia and Africa (Cervo *et al.* 2000), where it is predominantly associated with Mediterranean climates. However, it is a notorious invader and has now established on all continents except Antarctica (Carpenter 1996; Miller *et al.* 2013). *Polistes dominula* was first recorded in North America during the late 1970s from where it rapidly spread southwards (Hathaway 1981). It is thought to have reached the USA by establishing nests in shipping crates transported from Europe (Hathaway 1981). It reached South America, Australia and New Zealand during in the late 1970s (Cervo *et al.* 2000; Buck *et al.* 2008). The first record of *P. dominula* in South Africa was in 2008 in Kuilsriver in the Western Cape Province (Eardley *et al.* 2009). This area also exhibits a Mediterranean climate with long dry summers and short wet winters. Subsequent range expansion by *P. dominula* to

other areas in the Western Cape was recorded by Veldtman *et al.* (2012). This rapid range expansion can likely be attributed to human-mediated invasion, higher productivity rates and a release from natural predators and parasitoids (Cervo *et al.* 2000; Armstrong & Stamp 2003; Ward *et al.* 2005; Liebert *et al.* 2006).

In its invaded range, *P. dominula* may be in competition with congener species for food and nesting sites due to niche overlap (Benadé *et al.* 2014). It is known to consume a diverse array of insect genera (Richter 1990). Therefore this species may not only have a negative effect on native wasp diversity, but also on the diversity of other arthropods in its invaded range. This effect on prey will be exacerbated if the density of invasive wasps is much higher than that of native wasps pre-invasion. For example, Armstrong & Stamp (2003) showed that the native *P. fuscatus* and invasive *P. dominula* consumed similar amounts of food per individual in natural conditions, but the former has a body size 1.5 times larger than that of *P. dominula*. This meant that *P. dominula* could produce 2.5 times more offspring than *P. fuscatus* and may be one of the reasons why the density of the invasive wasp was much higher than that of the native wasp in that system (Armstrong & Stamp 2003). In its invaded range in South Africa, *P. dominula* often co-occurs with the native *P. marginalis* (Pers. Obs.). This provides the opportunity to investigate whether wasp size differences could indeed play a role in the ability of the invasive wasp to compete with native wasps.

A further advantage that could contribute to the invasion success of *P. dominula* and its ability to compete with native wasps are shorter brood development times than its counterparts, allowing for higher nest productivity (Cervo *et al.* 2000; Armstrong & Stamp 2003), and therefore greater competitive fitness compared to slower maturing species (Gamboa *et al.* 2002). Higher nest productivity will result in nests with a larger number of cells than those of less productive species, which allows for indirect comparison of overall productivity (Gamboa *et al.* 2002; Gamboa *et al.* 2004). Gamboa *et al.* (2002) found that the invasive *P. dominula* was able to out-compete its native counterpart (*Polistes fuscatus*) due to its ability to be twice as productive. At season's end, nests of *P. dominula*, on average, consisted of three times more cells than that of the native *P. fuscatus* (Gamboa *et al.* 2002). Even though *Polistes* wasp nests house far fewer individuals than their Vespinae counterparts (West-Eberhard 1969), nest abundances of 210 nests per ha can easily have 6000 wasps present at any given time (Clapperton 1999).

A lesser degree of predation due to its aposematic colouration and the release from parasites from its original habitat is thought to increase the invasive success of *P. dominula* (Cervo *et*

*al.* 2000; Gamboa *et al.* 2002; Gamboa *et al.* 2004). In the study by Gamboa *et al.* (2002), no parasitoids were recorded for the invasive *P. dominula*, but parasitoids were recorded for the native *P. fuscatus*. This could be ascribed to the fact that parasitoids did not recognize *P. dominula* as a viable host (Cervo *et al.* 2000). In recent times, however, multiple parasitoids were identified on both native *P. fuscatus* and invasive *P. dominula* in North America (Miller *et al.* 2013). Biological control aimed at social wasps however, has not been implemented to a great extent (Beggs *et al.* 2011) and evidence suggests that the effect is not long-lasting (Beggs *et al.* 2008)

#### *Objectives of this study*

This project is aimed at addressing the following questions regarding the newly invasive European paper wasp (*Polistes dominula*) in South Africa:

1. What is the extent of the invaded range (distribution) of *P. dominula* in the Western Cape of South Africa? (Chapter 2)(Chapter 3). Is the wasp confined to the Cape Metropolitan area or has its distribution gone beyond the Cape Fold Mountains (which ostensibly could act as a natural barrier to its spread).
2. What are the habitat preferences and activity period of *P. dominula* in its invaded range? (Chapter 3). Determining habitat preference activity period allows for accurate predictions of future spread and also indicates where and when eradication efforts should be focussed.
3. Investigating the advantages, if any, that the invasive *P. dominula* has over its native congener *P. marginalis* (Chapter 4). Hypothesized advantages could include greater reproductive ability, enemy release, a smaller body size and longer activity periods.

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## Chapter 2

### **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.**

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Invasive organisms are one of the greatest threats to global biodiversity (Pimentel *et al.* 2000; Rands *et al.* 2010). Considerable efforts have been put towards the understanding of the processes driving invasion success which is essential when devising management strategies to limit the spread and impacts of invasive alien species (IAS) (Kolar & Lodge 2001). The success of IAS (animal species in particular) in novel regions is often attributed to the absence of natural enemies and a subsequent decrease in population regulation (Liebert *et al.* 2006), a phenomenon referred to as the enemy release hypothesis (Jeffries & Lawton 1984). As a result, biological control initiatives are largely geared to reconnect IAS with their natural predators and parasites (Irvin & Hoddle 2010). Unfortunately this necessitates the release of yet another alien organism (Veldtman *et al.* 2011).

The European paper wasp *Polistes dominula* (Christ), often incorrectly cited as *Polistes dominulus* (Buck *et al.* 2008) or *Polistes gallicus* (e.g. Pardi 1948) is a recently recorded alien species in South Africa. Its native range comprises predominantly Mediterranean climates, including Europe, Asia and northern Africa (Cervo *et al.* 2000). It was first recorded in North America during the late 1970s from where it rapidly spread southwards (Cervo *et al.* 2000; Buck *et al.* 2008) replacing native paper wasp species within a few years (Gamboa *et al.* 2002; Gamboa *et al.* 2004). A highly invasive species, it has now been recorded from all continents except Antarctica (Miller *et al.* 2013). To date, three published records documenting the presence of *P. dominula* in South Africa have appeared. The first published observation of its presence was made in the Western Cape Province in 2008 by Eardley *et al.* (2009) in the suburb of Kuilsriver. At that time it was also noted that this species has the potential to spread and become invasive over much of South Africa as it is not confined only to Mediterranean climatic zones (Eardley *et al.* 2009). Giliomee (2011) also noted its presence, citing Eardley *et al.* (2009). The most recent published record described a range expansion to Stellenbosch (13 km east of Kuilsriver) (Veldtman *et al.* 2012).



We studied student entomological collections housed at the Stellenbosch University Entomological Collection during June 2013 (SUEC, Stellenbosch, South Africa). Numerous specimens have been collected in the vicinity of Stellenbosch between 2010 and 2013 and it is clear that this species has now become well established in Stellenbosch. Data labels now also confirmed the presence of *P. dominula* in Jonkershoek to the east, Paarl to the north and Somerset West/Strand to the south of Stellenbosch (first specimens from all areas recorded during 2012) (Fig.1). It therefore seemed that the Hottentots-Holland mountain range (mountain range running from Betty's bay northwards, Fig. 1) curbed the spread of this species. However, during 2013 we collected four *P. dominula* individuals from Grabouw and another specimen was collected from Knysna, *ca.* 380 km east of Stellenbosch (Fig.1). This type of 'jump dispersal' is usually associated with anthropogenic mediated spread of invasive species (Suarez & Tsutsui 2008; Wilson *et al.* 2009) and we now consider this species not only as established in South Africa, but also as an invasive organism (following definition of Richardson *et al.* 2000). It seems to prefer moister areas (areas with forests or fynbos vegetation) as no specimens have yet been collected from drier sites (e.g. sites with Succulent Karoo vegetation, Fig. 1).

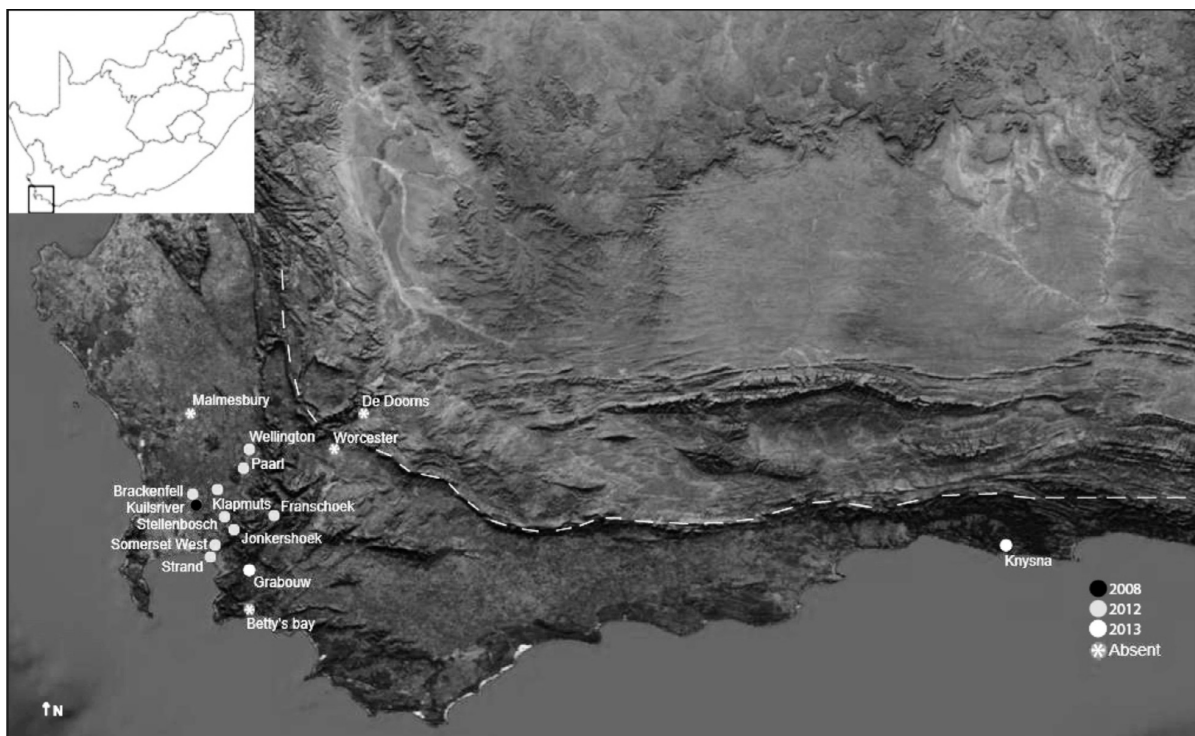


Figure. 1. Confirmed locations and dates of collection of *Polistes dominula* within the Western Cape Province, South Africa. The dashed line roughly indicates a possible natural barrier (biome related) to the dispersal of *P. dominula* (Fynbos vegetation and forests to the south and Succulent Karoo vegetation to the north).



The impact of *P. dominula* on natural and anthropogenically altered areas in the south-western Cape is currently unknown. Nests are often made on buildings and other man-made structures where these fairly aggressive wasps come in close proximity to humans. The most noteworthy current anthropogenic impact is their emergence as problematic organisms in some Stellenbosch vineyards. Large numbers of nests are made on vines and supporting structures in vineyards which cause financial losses in terms of man hours lost to eradicate nests and expenditures on insecticides. Due to the presence of the wasp in certain areas, grapes are not harvested, resulting in reduced production (Stellenbosch wine farmers, pers. comm.). Numerous other potential impacts on humans may become more evident if wasp numbers continue to increase. For example, in Colorado, U.S.A., *P. dominula* has been observed cutting into and feeding on fruit crops including, among other, grapes (*Vitis vinifera*) and sweet cherries (*Prunus avium*), resulting in a 25% loss of fruit crop yield (Cranshaw *et al.* 2011).

The ecological impact of *P. dominula* may also be substantial. In common with other higher Hymenoptera the characteristic threaded waist (petiole) restricts their diet intake to mainly liquid forms, be it carbohydrates or protein sources. The adults feed their larvae a diverse array of soft-bodied insects whilst adults also collect nectar (Harris 1991; Kasper *et al.* 2004; Liebert *et al.* 2006). This feature, in conjunction with the internal anatomy allows for rapid feeding and the regurgitation of the ingested liquids to nest mates and contributes to the characteristic nutritional interdependence found in most Social Hymenoptera societies (Trophallaxis) (Hunt 1991). The feeding biology of this species is therefore very similar to that of the European wasp, *Vespula germanica*, another invasive wasp to the Western Cape Province (Kasper *et al.* 2004) and to the three South African indigenous genera of (Polistine) paper wasps; *Polistes*, *Ropalidia* and *Belonogaster* (Scholtz & Holm 1985; [www.waspweb.co.za](http://www.waspweb.co.za)). The distinct possibility exists that these taxa are in direct competition for resources due to niche overlap (Miller *et al.* 2013) and preliminary field observations indicate that *P. dominula* has now become one of the dominant wasp species in the Stellenbosch area, displacing the native *P. marginalis*. Here, *P. marginalis* will not only have to compete for food resources with the two invasive wasp species, but also for nesting sites in the case of *P. dominula*, as nesting preferences are likely to be similar (Armstrong & Stamp 2003; Gamboa *et al.* 2004). Other aspects that may add to the success of *P. dominula* over native species may include its general (elastic) diet, multi-foundress nests, re-use of old nests, short brood development time, aposematic coloration, release from natural predators and parasites (Cervo *et al.* 2000; Gamboa *et al.* 2004) and human-mediated range expansion of

inseminated queens (Ward *et al.* 2005).

When present in their introduced range, parasitoids have been shown to reduce exotic paper wasp numbers by up to 25% (Toft *et al.* 1999) and reduce their competitive exclusion success over native congener species (Miller *et al.* 2013). In order to slow the spread of *P. dominula* in South Africa we would ideally like to identify native candidates for biological control. However, the natural enemies of native congeners of IAS are poorly studied, also for social insects (Schmid-Hempel 1995). This hampers initial control efforts and limits the use of responsible classical biological control (Seymour & Veldtman 2010; Veldtman *et al.* 2011). Also, natural enemies shared between IAS and native species may have negative biodiversity consequences (Carvalho *et al.* 2008) as IAS can potentially act as reservoir for parasitoids (Roy & Lawson Handley 2012) facilitating a ‘spill over’ of native parasitoids from IAS to native organisms (Kelly *et al.* 2009). The most common parasites on *P. dominula* in its original habitat include *Endurus argiolus* Rossi (Hymenoptera: Ichneumonidae) and *Xenos vesparum* Rossi (Strepsiptera: Stylopidae) (Beani *et al.* 2011; Miller *et al.* 2013) as well as the obligate social parasite *Polistes sulcifer* Zimmermann (Dapporto *et al.* 2004). Until 2004, no parasites were recorded in association with *P. dominula* in its invaded North American range (Cervo *et al.* 2000; Pickett & Wenzel 2000; Gamboa *et al.* 2004), possibly because they were not recognised as a host by indigenous parasitoids. This absence of natural enemies was considered to have significantly contributed to its invasive success (Cervo *et al.* 2000; Gamboa *et al.* 2004). More recently however, three different parasitoid taxa were identified from both the native *Polistes fuscatus* and the invasive *P. dominula* in North America (Miller *et al.* 2013). These included *Dibrachys cavus* Walker (Hymenoptera: Pteromalidae), *Chalcoela iphitalis* Walker (Lepidoptera: Pyralidae) and *Sacophaga* sp. (Diptera: Sarcophagidae) which questions the hypothesised effect of parasitoids on its invasion success. No parasitoids have been recorded for either *P. dominula* or the native *P. marginalis* in South Africa.

Preliminary observations revealed the presence of minute holes in some nest cells of *P. dominula* in Stellenbosch, indicating the possible presence of parasitoids. To verify this, nests of *P. dominula* (n=7) and *P. marginalis* (n=2) were collected from building eaves where these were found sympatrically during 2012/2013 and kept in heavy duty sealable clear plastic bags at room temperature for five days.



Figure. 2. A parasitoid wasp from the family Eurytomidae collected from the nests of *Polistes marginalis* and *Polistes dominula*.

Three parasitoid taxa emerged from the collected nests, including two species from the families Eurytomidae (Fig. 2) and Eupelmidae (Fig. 3) and one species of parasitic fly from the genus *Anacamptomyia* (Tachinidae) (Fig.4). The eurytomids emerged from nests of both *P. marginalis* (n=1) and *P. dominula* (n=2) (156 and 55.5 individuals on average respectively). The *Anacamptomyia* sp. was also present in the nests of both *P. marginalis* (n=2) and *P. dominula* (n=5) (21.5 and 16.6 individuals on average respectively). A single specimen from the family Eupelmidae (*Eupelmus* sp.) was also recorded. It is not certain whether it came from a *P. marginalis* or *P. dominula* nest. The origin of the parasitoids on *P. dominula* is unknown, but it is probably from the congener native species as these parasitoid taxa have not been recorded from *P. dominula* in its native range and demonstrates a possible ‘spillback’ phenomenon of native parasites onto the invasive species (Kelly *et al.* 2009).



Figure. 3. A parasitoid wasp from the family Eupelmidae (*Eupelmus* sp.) that emerged from the nest of *Polistes* sp.

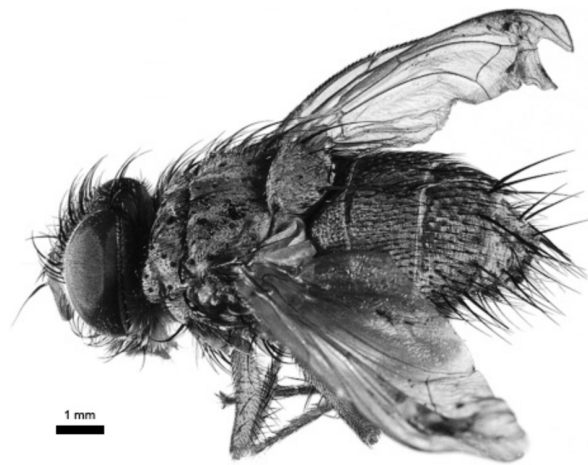


Figure. 4. A parasitic fly (*Anacamptomyia* sp., Tachinidae) collected from nests of *Polistes marginalis* and *Polistes dominula*.

We have shown that *P. dominula* is now well established in the Western Cape Province of South Africa and that it is rapidly expanding its range. Indications that this species may have significant future economic impacts are also emerging. Eradication or control of *P. dominula* will be extremely difficult as *Polistes* wasps, unlike their *Vespula* counterparts, are not attracted by dead forms of protein, rendering toxic baiting inadequate (Harris & Etheridge 2001; Toft & Harris 2004). The use of carbohydrate-based toxic bait traps is not desirable since this could result in killing of non-target species (Spurr 1996). Future studies should therefore focus on understanding the ecological and anthropogenic impact of this species as well as the use of the identified biocontrol agents in order to develop future management strategies.

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## Chapter 3

### Invaded range, habitat preferences and activity period of *Polistes dominula* in the Western Cape Province of South Africa.

#### Abstract

The invasive European paper wasp *Polistes dominula* was first recorded in South Africa in 2008. Subsequently range expansion was recorded in 2012 and 2014, but it was still confined within the barrier of the Cape Fold Mountain Belt (CFMB), except for one instance thought to be human mediated. As yet no focussed research has been conducted on habitat preferences, activity period and the current invaded range of *P. dominula*. To determine habitat preferences and activity period, 40 sites of four habitat types (n=10 for each of urban, rural, fringe and natural) were monitored for foraging wasp activity for a period of 12 months (June 2013 – June 2014) in and around the town of Stellenbosch. *P. dominula* was found to prefer urban and fringe habitat types and was nearly absent from natural habitats. Its invaded range was determined by visiting towns one after the other from Kuilsriver (the first recorded locality of the species in South Africa) radiating outwards and searching for foraging wasps within the urban habitat type. Of the 27 towns visited *P. dominula* was found to be active in 13, one of which was outside the CFMB. Activity period was between September and May with a peak during March/April corresponding with seasonal temperature fluctuations. *P. dominula* preferred habitats in close proximity to human settlements where numerous sturdy nesting structures in the form of buildings are available. Future range expansion is therefore likely to manifest in cities and towns to the north and east of the current distribution range of this species.

#### Introduction

An estimated 480 000 non-native species have been introduced across the globe (Pimentel *et al.* 2001). Approximately 8818 of these have been introduced within the borders of South Africa (Pimentel *et al.* 2001). Estimating the environmental impact brought on by a non-native species entering a new habitat can be difficult (Pimentel *et al.* 2001). In the Fynbos biome of the Western Cape Province alone, 80% of endangered species are at risk due to invasion by non-native species (Armstrong 1995). However, the bulk of the research on the effects of invasive species is aimed at more conspicuous organisms like flora and larger fauna, while more inconspicuous organisms such as insects are relatively understudied (McGeoch *et al.* 2011).

The European paper wasp *Polistes dominula* is a highly invasive species (Eardley *et al.* 2009) recently recorded in the Western Cape Province, of South Africa (Eardley *et al.* 2009; Benadé *et al.* 2014, Chapter 2). Its original extent included Europe, Asia and northern Africa (Cervo *et al.* 2000). Its first documented occurrence outside of its original habitat was documented in the 1970s in North America (Buck *et al.* 2008). These major dispersal jumps can be attributed to human mediated introductions (Buck *et al.* 2008; Ward *et al.* 2005) and today it has been recorded on every continent except Antarctica (Miller *et al.* 2013). Its invasive success and expansion of its invaded range is thought to be aided by its plasticity (or ability to adapt to new environments), its ability to undergo diapause (when environmental conditions are unsuitable), its generalist diet and short brood development time (Cervo *et al.* 2000).

In South Africa, the presence of *P. dominula* was first recorded in 2008 by Eardley *et al.* (2009) in the suburb of Kuilsriver in the Western Cape Province. Subsequently Veldtman *et al.* (2012) reported a range expansion of 13 km to the town of Stellenbosch in the Cape Winelands. Benadé *et al.* (2014, Chapter 2) showed that this species rapidly spread to many neighbouring towns within the Cape Metropolitan area, confined within the Cape Fold Mountain belt. However, the results of that study were based solely on museum records and field surveys are needed to determine whether this species does occur outside this range.

Nests of *P. dominula* seem to be predominantly established in urban areas on man-made structures in close proximity to humans (MacKenzie *et al.* 2006; Benadé *et al.* 2014). This apparent close association with anthropogenically altered habitats could indicate that its ecological impact in pristine areas may not be very extensive. It may also be attributed to the difficulty in locating nests in natural habitats (Liebert 2004). However, this problem may be solved by actively searching for foraging wasps instead of trying to locate nests in natural habitats. At present nothing is known regarding the habitat preferences or distribution of this wasp in its newly acquired invasive range of the Western Cape. Determining habitat preferences will allow for accurate predictions of possible future spread and will also benefit possible eradication efforts.

Efforts to determine the invaded range of *P. dominula* might, however, be complicated by its seasonal traits, like that of diapause (West-Eberhard 1969). Diapause occurs at the end of the season, presumably during late summer and beginning of autumn, when fecund females leave the nest to spend the colder period of the year in aggregation within hibernacula (Rau 1930; West-Eberhard 1969). During diapause efforts to find even foraging wasps will be very cumbersome as nest and wasp activity ceases (West-Eberhard 1969). Diapause is a trait that

could contribute to the invasive abilities of *P. dominula*. Insects have been shown to enter a state of diapause based on both environmental cues and availability of food (Pieloor & Seymour 2001).

The aims of this study are three-fold: 1) to determine the invaded range of *P. dominula* using an active search method, 2) to determine its habitat preferences within and around the town of Stellenbosch 3) and finally to determine its activity period. This information is seen as central to facilitate understanding of the current extent of the invaded range of *P. dominula* in South Africa and possible future range expansions and feasibility of eradication.

## **Materials and methods**

### **Invaded range**

Using the BGIS online mapping program ([bgis.sanbi.org](http://bgis.sanbi.org)) numerous towns were selected within the Western Cape Province (Appendix 1). Towns surrounding the known invaded range were chosen by means of an elimination process: If *P. dominula* was found in one particular town (after sampling) the next town was also included, further from the known invaded range (Benadé *et al.* 2014). If it was not found in the next town, subsequent towns were not visited. In each town three sampling sites were selected in urban areas (e.g. Fig. 1) as wasps are usually easily detected in these habitats. To avoid recoding the same foraging wasp twice, study sites within a town had a minimum distance of 1 kilometre between them – more than double the recorded foraging distance of *Vespula germanica* in Argentina (Masciocchi & Corley 2013). Sampling was conducted during summer (February to March 2014).

At each of the three sampling sites within a town 20 minutes was spent conducting active visual searches for foraging *P. dominula*. Active visual surveys consisted of continuous movement at a constant relaxed pace and counting foraging wasps. Sites were visited only once. Surveys were only conducted on windless and cloudless days and between 11:00 and 15:00.



Figure 1: Example of survey sites selected (in red shading) to determine the invaded range of *Polistes dominula* in the town of Malmesbury, South Africa (Urban habitat type).

#### Habitat preferences and activity period

Structured sampling/observation was conducted at 40 sites (Fig. 2) over a period of 12 months (July 2013 to July 2014) in and around the town of Stellenbosch. Sites comprised four preselected habitat types (Table 1) each with ten replicates that were at least one kilometre apart. Stellenbosch is an ideal study area as it contains multiple habitat types within a relatively short distance from one another for comparative purposes. Benadé *et al.* (2014, Chapter 2) also indicated that *P. dominula* is common and active in the region after it was first recorded by Eardley *et al.* (2009) in Kuilsriver about 20 km to the West. At each site 20 minute active visual surveys of the area were conducted and the number of foraging individuals of *Polistes dominula* was recorded as outlined above. Surveys were repeated monthly for 12 months during the first week of every new month.

Table 1: Characteristics of habitat types used to determine habitat preferences of *Polistes dominula* in and around the town of Stellenbosch, South Africa.

Habitat Type	Description
Urban	Urban setting including botanical gardens, schools, sport grounds and parks
Natural	Natural areas ca. 500 m from nearest anthropogenic influences
Fringe	Transitional vegetation types separating urban and natural areas that usually contain a large number of invasive plant species.
Rural	Areas used for agricultural purposes (e.g. wine farms)



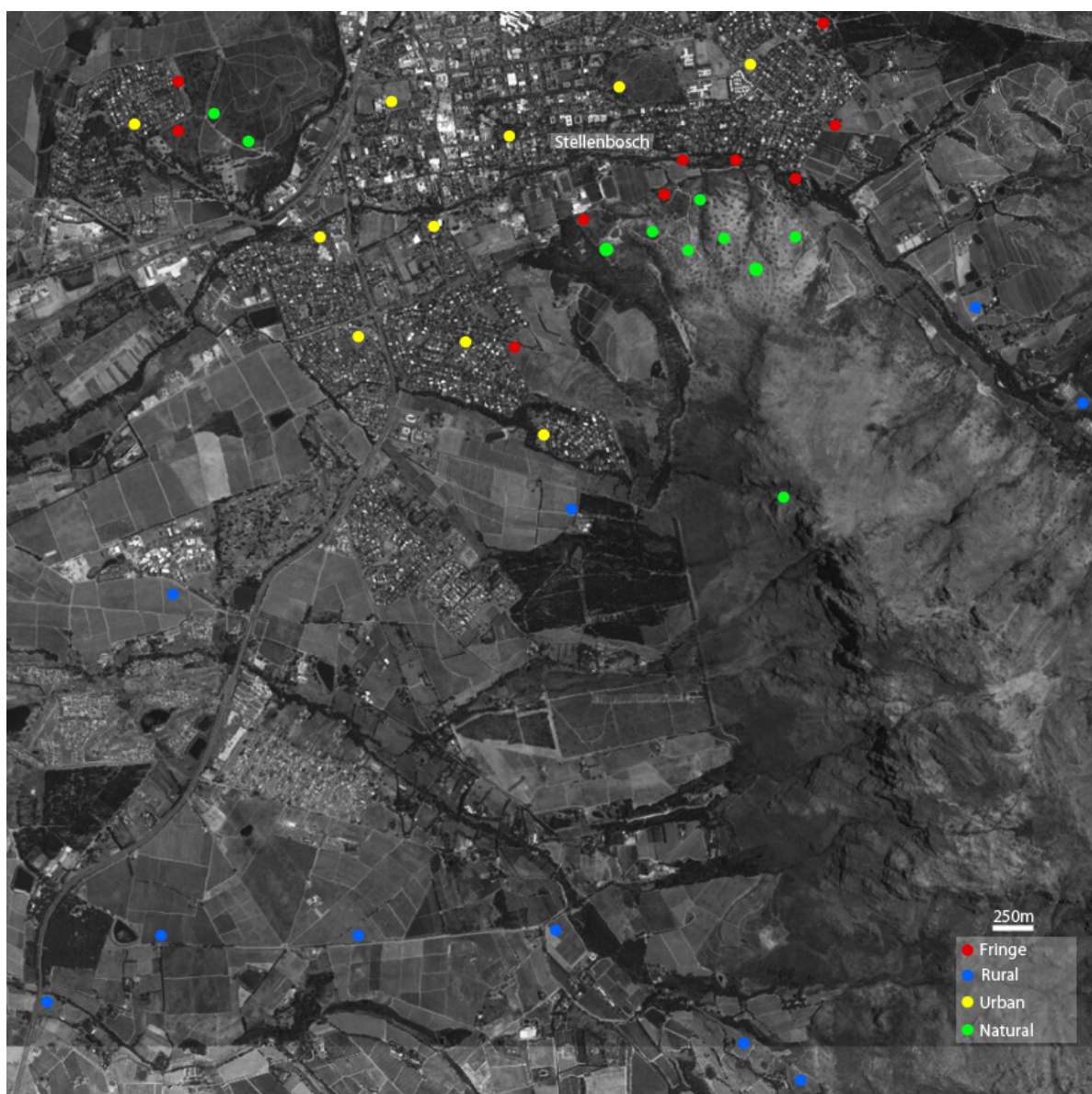


Figure 2: Locality of 40 study sites in and around the town of Stellenbosch to determine habitat preferences and activity periods of *Polistes dominula* in the Western Cape of South Africa.

### Data Analyses

Data for habitat preferences were analysed using STATISTICA 12 (StaSoft Corporation, Dell, USA) and a repeated measures ANOVA (as I repeatedly sampled the same 40 sites over a period of 12 months) with a Bonferroni post-hoc test within the software to compare number of *P. dominula* wasp individuals observed.

## Results

### Invaded range

In total, 27 towns were visited (Fig. 3, Appendix 1) and *P. dominula* was found to be present in 13 of these – including Kuilsriver where it was first recorded by Eardley *et al.* (2009). The current distribution of *P. dominula* was found to be confined to the Cape Metropolitan area, bordered by the Cape Folds Mountain Belt (CFMB) to the east and the Atlantic Ocean to the west, except for one instance (Fig. 3). Outside of the CFMB, *P. dominula* was also recorded in Grabouw.

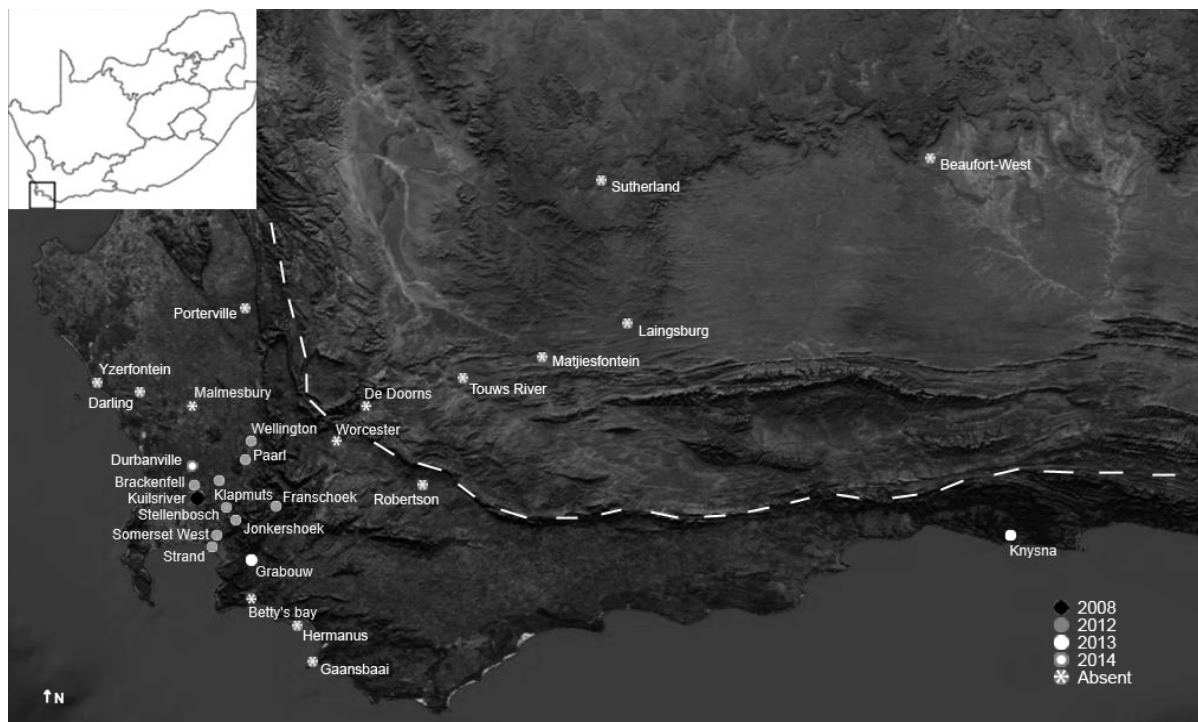


Figure 3: Confirmed locations for *Polistes dominula* presence or absence in the Western Cape Province, South Africa.

### Habitat preferences and activity period

A total of 758 *P. dominula* individuals were observed by implementing an active search method over a period of 12 months in and around the town of Stellenbosch in all the habitat types combined (Table 2). *P. dominula* was most abundant in urban and fringe habitat types and less numerous in rural and natural habitat types ( $F_{(33, 472)} = 4.77$ ,  $p < 0.05$ ) (Fig. 4.).

Table 2: Total number of *Polistes dominula* individuals observed within each habitat type in and around the town of Stellenbosch over the 12 month study period.

Habitat Type	Number of <i>P. dominula</i> observations
Urban	539
Natural	11
Fringe	192
Rural	16

During winter (June to August) no foraging wasps were observed in any of the four habitat types. The first foraging *P. dominula* was observed within the urban habitat type in September (4 wasps) at the start of spring (September to November). During the month of October *P. dominula* was observed in both the urban (7 wasps) and fringe habitat (2 wasps) types. In November wasps were recorded from the urban (24 wasps), fringe (3 wasps) and natural habitat types (1 wasp). During summer (December to February) an increase in wasp activity was observed for both the urban (71 wasps) and fringe habitat types (26 wasps). In January, *P. dominula* was recorded in the rural habitat type (11 wasps) for the first time. All habitat types exhibited *P. dominula* activity in February as summer came to an end. Numbers seemed to peak during March at the start of autumn. From April onwards numbers started to decrease. By June no more individuals of *P. dominula* were observed (Fig. 4).

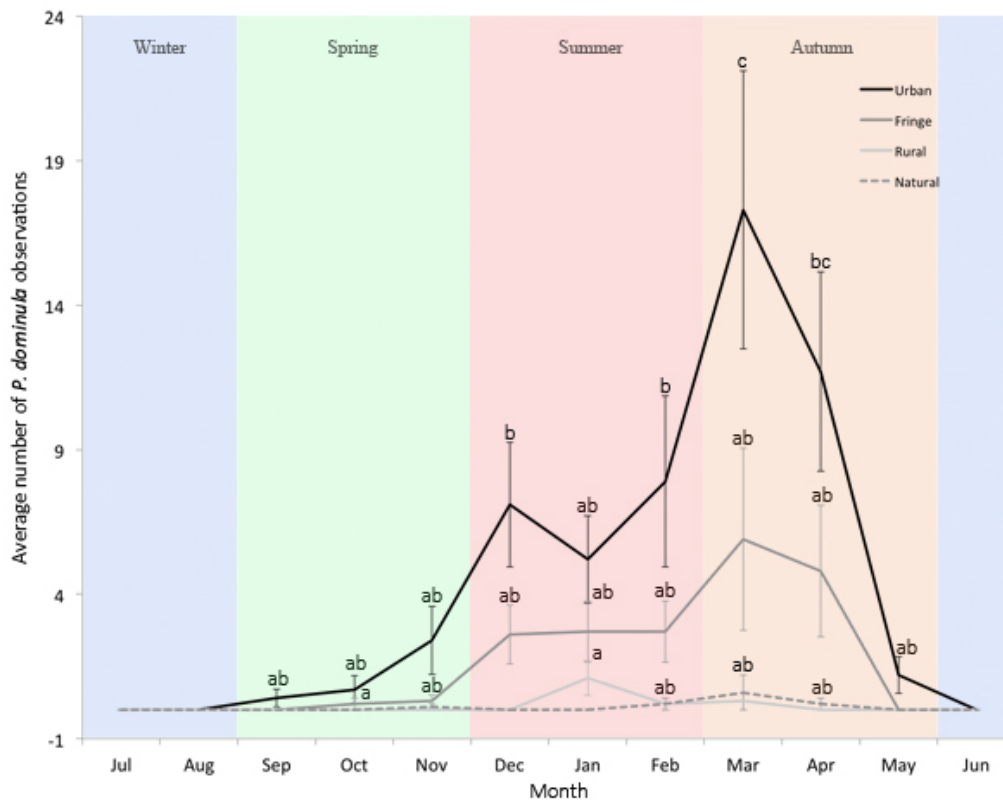


Figure 4: Habitat preferences and activity period of *Polistes dominula* over a period of 12 months using an active searching method at 40 sites (10 per habitat type) in and around Stellenbosch (different letters indicate significant difference; vertical bars denote 95% confidence intervals).

## Discussion

All available data suggest that *P. dominula* is rapidly expanding its geographical range in the Western Cape Province of South Africa. Since it was first recorded in Kuilsriver in 2008 (Eardley *et al.* 2009) it has expanded its range to include 13 towns within a period of five years. A single extreme expansion point indicating *ca.* 400 km dispersal by *P. dominula* could have either been facilitated by human mediated dispersal (Benadé *et al.* 2014, Chapter 2) or could be as a result of erroneous student insect collection data. Other than this outlier, most collection and observational data still suggest that *P. dominula* is largely confined to the west of the CFMB as postulated by Benadé *et al.* (2014, Chapter 2). However, there is a possibility that *P. dominula* will continue to self disperse northwards along the west coast. Rapid expansion in this direction may be hampered by generally drier conditions and the relatively low human population density in the region. Also, *P. dominula* is now established in the Grabouw region. There is, therefore, a strong possibility that *P. dominula* can easily establish eastwards without much assistance as very little other natural barriers to its dispersal are found eastwards into the rest of South Africa (with the possible exception of the drier Karoo and succulent Karoo regions).



*P. dominula* was found to be both most active and abundant in urban areas. This is likely attributed to the preference of *P. dominula* to building nests on sturdy man-made structures (MacKenzie *et al.* 2006; Benadé *et al.* 2014) with decaying nest materials in close proximity (e.g. fence posts, telephone poles etc.). Nesting in natural habitat types can occur (Rusina 2008), but was not observed during this study. Also, in a previous study in the USA *P. dominula* was found to prefer to forage in open grass areas (as one would find maintained near urban areas) rather than nearby natural woody areas (Gamboa *et al.* 2004). A similar situation exists in the study area where green belts in urban areas are dominated by exotic grasses and natural habitats are dominated by woody shrubs. The activity of *P. dominula* in fringe areas in this study may also be explained by its preference to forage in fire prevention belts that are often associated with these areas and along nearby rivers dominated by alien trees and grassy vegetation. Fire prevention belts contain many low growing grasses (Forsyth & Bridgett 2004), that are maintained (much like sport and other fields in urban areas) to keep fires from natural areas spreading into urban areas.

Urbanization leads to biotic homogenization (McKinney 2006) that often aid establishment of invasive species by decreasing competition with native taxa (McKinney & Lockwood 1999). The abundance of *P. dominula* in urban and fringe habitats as opposed to their low numbers in other habitat types may therefore also be due to decreased competition with native species in these habitats versus more natural systems. In the Western Cape Province a native congener species, *P. marginalis*, is fairly common. The possibility exists that the two species may be in direct competition for resources such as food and nesting sites as was found to be the case for *P. dominula* and *P. fuscatus*, a congener species native to the USA where *P. dominula* also invaded (Gamboa *et al.* 2004). Further research in South Africa is, however, needed.

*Polistes* species are known to prefer soft-bodied insects consisting predominantly of lepidopteran larvae and Diptera (Ward & Ramon-Laca 2013). However, the impact of *P. dominula* predation on native biodiversity is largely undetermined, as food preferences in South Africa have not yet been investigated. Given its affinity for highly disturbed habitat types within its invaded range, it is unlikely to have a large direct impact on native biodiversity. These altered habitats are known to be low in biodiversity and are dominated by exotic taxa (McIntyre & Hostetler 2001; Kowarik 2008). Many of these are considered pests, and it is possible that these wasps may be partially beneficial in gardens where they feed on

exotic lepidopteran larvae. Prey availability and abundance may thus be another explanation for observed habitat preference.

Data collected in this study provide the first details of activity periods and seasonal abundance for *P. dominula* in South Africa. It does, however, not indicate diapause as this study determined activity periods and not the environmental cues that are thought to initiate diapause. It's known that fecundated queens undergo diapause, also regarded as a stress tolerance mechanism, as ambient temperatures decrease and winter draws near. (West-Eberhard 1969). Queens undergoing the process of diapause could explain why no wasp activity was recorded between June and August. Wasp activity increased as an increasing numbers of foraging wasps were observed from spring when nests are expected to expand greatly and wasp numbers increase (West-Eberhard 1969). Wasp numbers continuously build up through summer and reach a peak in early autumn. Autumn would therefore be the best time for programmes that are intended to monitor wasp numbers and areas for potential establishment of new colonies. When temperatures decrease (and presumably when potential prey numbers also decrease) wasp activity decreases at the onset of winter. Generally during this time period wasp activity decreases and queens search for areas to overwinter (West-Eberhard 1969). Sites chosen to overwinter could include crevices in walls and rocks, roof tiles and under tree bark (Rau 1930; West-Eberhard 1969). It is also during this time that queens may hide in areas that would aid their dispersal via human transport systems such as shipping containers and wood products (Hathaway 1981).

I have found the invaded range of *P. dominula* to be limited to the Cape Metropolitan Area (in close proximity to humans) in predominantly urban areas within the confounds of the CFMB, except for one confirmed instance. The current extent allows for the potential control and management of this invasive species in South Africa, although complete eradication is unlikely. Management and control of *P. dominula* should be directed toward towns (where people could also report sightings) on the outer perimeter of the current invaded range (within the confounds of the CFMB) as to prevent further spread. The time of year that management and control is implemented is critical. If control strategies are implemented in late season when nests are big and multiple wasps are present the potential exists that fecund wasps may escape and start nests anew. If control is exercised as new nests are initiated at the onset of spring however, eliminating the fecundated nest-building queen could potentially eliminate a colony and prevent an increase in the invaded range.

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## Appendix

Towns visited within the Western Cape, South Africa in order to determine the invasion range of *Polistes dominula* using active searching.

Town	GPS Coordinates		
Porterville	-33.017143, 18.998236	-33.020727, 18.989265	-33.008989, 19.002601
Yzerfontein	-33.337802, 18.163188	-33.340770, 18.162290	-33.349137, 18.150421
Darling	-33.382724, 18.383862	-33.377560, 18.378543	-33.378322, 18.388162
Malmesbury	-33.468597, 18.716695	-33.462436, 18.725820	-33.461220, 18.735891
Wellington	-33.637872, 18.997572	-33.643183, 19.011291	-33.632506, 19.023156

Paarl	-33.737843, 18.973617	-33.738964, 18.961357	-33.727326, 18.961032
Durbanville	-33.831932, 18.631721	-33.829439, 18.643582	-33.833523, 18.660912
Town	GPS Coordinates		
Brackenfell	-33.879334, 18.704715	-33.869203, 18.706902	-33.850008, 18.728319
Kuilsriver	-33.936962, 18.701651	-33.934007, 18.696197	-33.938989, 18.692390
Klapmuts	-33.802040, 18.861168	-33.808528, 18.867175	-33.812289, 18.860418
Stellenbosch	-33.936056, 18.865579	-33.933709, 18.873314	-33.933862, 18.855408
Somerset West	-34.059364, 18.837913	-34.060920, 18.845321	-34.052523, 18.819888
Strand	-34.112804, 18.839551	-34.115319, 18.825976	-34.097375, 18.817629
Jonkershoek	-33.968146, 18.934266	-33.964142, 18.925908	-33.954185, 18.910502
Betty's Bay	-34.363844, 18.898833	-34.369367, 18.892744	-34.356661, 18.899642
Grabouw	-34.154830, 19.014377	-34.155108, 19.004778	-34.148952, 19.011409
Hermanus	-34.415710, 19.244398	-34.420951, 19.233413	-34.402913, 19.268202
Gaansbaai	-34.572850, 19.349954	-34.579394, 19.348800	-34.587491, 19.349474
Franschhoek	-33.905274, 19.112791	-33.906918, 19.119447	-33.914237, 19.122793
Robertson	-33.805514, 19.878641	-33.798179, 19.877309	-33.800093, 19.889069
Worcester	-33.644541, 19.443284	-33.637310, 19.431625	-33.640186, 19.451833
De Doorns	-33.481922, 19.662204	-33.481922, 19.665148	-33.481564, 19.655715
Touws River	-33.342552, 20.032862	-33.336843, 20.030309	-33.347925, 20.022453
Matjiesfontein	-33.230916, 20.580500	-33.2318289, 20.582842	-33.229888, 20.581293
Laingsburg	-33.193213, 20.846183	-33.195549, 20.849249	-33.194347, 20.859118
Sutherland	-32.400266, 20.660810	-32.395691, 20.657978	-32.392340, 20.663837
Beaufort-West	-32.364085, 22.589256	-32.351064, 22.600232	-32.346136, 22.583521

## Chapter 4

### **Greater colony performance of *Polistes dominula* compared to a native congener explains numerical dominance of this invasive in South Africa**

#### **Abstract**

In its newly invaded range in the Western Cape of South Africa, *Polistes dominula* intrudes into the habitat of the native *P. marginalis*. Here it seems to be a better potential competitor as their numbers have increased substantially in recent years, outnumbering that of the native species. Reasons for the perceived superior competitiveness of *P. dominula* across the globe are numerous, including the longer activity periods, enemy release, greater colony productivity and smaller body size. Whether these same factors lead to its success in South Africa is not known. Here I investigate which factors could aid in the ability of *P. dominula* to successfully invade this niche. I monitored the activity period and abundance of both species at 40 sites of four habitat types (n=10 for each urban, rural, fringe and natural) for a period of 12 months in and around the town of Stellenbosch to determine activity periods and habitat preferences. The effect of seasonal activity period, enemy release, colony productivity and body size as potential competitive advantages were assessed by, respectively, comparing activity period, parasitism rate, nest size and body length and dry weight between *P. dominula* and *P. marginalis*. Both species preferred anthropogenically altered habitats, but *P. dominula* was significantly more abundant than *P. marginalis*. The invasive species had a substantially shorter period of inactivity over the colder months. Interestingly, *P. dominula* suffered significantly higher parasitism than the native species. However, *P. dominula* had greater colony productivity. Body size was not found to be a significant factor in explaining *P. dominula*'s success. These results indicate that, *P. dominula* is able to reach much greater population size than *P. marginalis* due to a longer activity period and greater nest productivity, explaining observed numerical dominance of the invasive.

#### **Introduction**

When there is substantial niche overlap between two congener species of which one is a recently introduced invasive, there are usually negative consequences for populations of the native species due to competition for resources (e.g. similar food and habitat resource requirements) (Benadé *et al.* 2014), whereas niche overlap between two naturally occurring species leads to a natural balance (Zavaleta *et al.* 2001). The ability of many invasive eusocial arthropod species to establish in newly invaded ranges can be attributed to multiple factors including: generalist diets, shorter brood development times and greater reproductive abilities



than congener taxa (Cervo *et al.* 2000; Colautti *et al.* 2004; Gamboa *et al.* 2004). Furthermore, the success of an invasive species in a newly acquired habitat can also be attributed to the lack of population regulation by native predators because of its novelty, also referred to as the enemy release hypothesis (Jefferies & Lawton 1984; Liebert *et al.* 2006). Benadé *et al.* (2014, Chapter 2) identified multiple parasitoids and/or hyper-parasitoids on both the invasive *P. dominula* and the native *P. marginalis* nests. Determining the traits that make an invasive species successful over ecologically and taxonomically similar species in a newly acquired habitat may provide information needed for its control and prevention of further invasions (Jones & Lawton 1995).

*Polistes dominula* (Christ) (Hymenoptera: Vespidae) originally from the northern hemisphere, including parts of Europe, Asia, Russia and northern Africa has now successfully spread to every continent except Antarctica (Miller *et al.* 2013) including South Africa (Eardley *et al.* 2009; Veldtman *et al.* 2012). On many of these continents it has now invaded, and appears to be intruding into the niche of native congener species (Gamboa *et al.* 2002; Gamboa *et al.* 2004). This leads to direct competition with native species for food, foraging habitat and nesting sites (Gamboa *et al.* 2002; Gamboa *et al.* 2004; Benadé *et al.* 2014). In South Africa, potential competition with the native *P. marginalis* (Fabricius) for these resources has also been noted (Benadé *et al.* 2014) where they are often observed nesting only centimetres apart (Pers. Obs). This provides opportunities to investigate the reasons for the invasive success and potential superior competitive abilities of *P. dominula* over *P. marginalis* and to compare these results to other studies around the globe.

The success of invasion of newly inhabited ranges by non-native species is often attributed to the lack of regulation by natural enemies (Jefferies & Lawton 1984; Liebert *et al.* 2006). Hence the drive behind biological control efforts is usually to reconnect invasive species with their natural predators and parasites (Irvin & Hoddle 2010). Until recently, no evidence existed of *P. dominula* being negatively influenced by any parasitic or predatory species outside of its native range which was thought to aid its invasive potential. However, in 2013 and 2014, Miller *et al.* (2013) and Benadé *et al.* (2014) reported parasitism of *P. dominula* outside its native range in North America and South Africa, respectively. In its invaded range in North America Miller *et al.* (2013) found *P. dominula* to be parasitized by *Dibrachys cavus* Walker (Hymenoptera: Pteromalidae), *Chalcoela iphitalis* Walker (Lepidoptera: Pyralidae) and *Sarcophaga* sp. (Diptera: Sarcophagidae) and in South Africa, nests often contain larvae of the parasitic fly *Anacamptomyia* sp. (Tachinidae) (Benadé *et al.* 2014, Chapter 2). This fly



is thought to have moved onto *P. dominula* from the native *P. marginalis* (Benadé *et al.* 2014), providing opportunity to assess parasitisation rate on both taxa and to evaluate the biotic release hypothesis as a reason for successful invasion (i.e. parasitisation rate is expected to be much lower on the invasive species than the native species).

In addition to enemy release, a smaller body size has also been shown to contribute to the invasive potential of *P. dominula* in a study by Armstrong & Stamp (2003) in the United States of America as a smaller body size requires less energy to be consumed. McGlynn (1999) found for ants, smaller body sizes denote a greater number of individuals produced (e.g. workers in ant colonies) when compared to larger counterparts (Bourke & Franks 1995) resulting in superiority through numbers and a greater degree of colony productivity. The advantages of greater numbers include greater foraging efficacy, brood care and interference with other species through competition (Bourke & Franks 1995). Investigating the invasive success of *P. dominula* where its newly invaded range is shared with a native congener species *P. fuscatus* (Saussure), Armstrong & Stamp (2003) found that *P. dominula* possessed multiple advantages that could aid its ability to invade successfully. These advantages included smaller body sizes, greater foraging efficacy and a reproduction rate 2.5 times greater than that of the native *P. fuscatus*. Similar findings were made by Gamboa *et al.* (2002; Gamboa *et al.* 2004) also looking at the invasive *P. dominula* and *P. fuscatus*. Here, shorter brood development times allow for greater colony productivity and as a result, greater competitive fitness (Cervo *et al.* 2000; Gamboa *et al.* 2002; Armstrong & Stamp 2003). The greater colony productivity of *P. dominula* over that of *P. fuscatus* manifests as a greater number of cells constructed (Gamboa *et al.* 2002). At season's end, *P. dominula* was twice as productive as its native counterpart and that nests consisted of three times as many cells as that of the native *P. fuscatus* (Gamboa *et al.* 2002). This link between smaller body size, greater number of nest cells constructed, greater nest productivity and consequently increased competitive fitness of *P. dominula* over *P. fuscatus* (Gamboa *et al.* 2002), may also explain the competitive advantage of *P. dominula* over *P. marginalis* in South Africa.

Here I aim to determine if the invasive *P. dominula* have characteristics that result in a performance advantage over its native congener *P. marginalis*. I specifically compare these two species in terms of i) habitat preferences (overlap), ii) differences in activity periods iii) possible role of enemy release (i.e. parasitism rates), iv) differences in body sizes and v) differences colony productivity (in terms of cell numbers). If there are differences in these

characteristics this could explain the success of the invasive species relative to a native congener in the invaded region.

## Materials and methods

### Study sites

A study of habitat preferences of *P. dominula* in North America (Gamboa *et al.* 2002; Gamboa *et al.* 2004) showed that nest productivity was greater in more disturbed, anthropogenically altered habitats (urban habitats) than in natural habitats. Similarly, this species seems to prefer urban habitats in its invaded range in South Africa (Benadé *et al.* 2014, Chapters 2 and 3). Therefore, study sites to investigate competitive interactions between *P. dominula* and the native *P. marginalis* here were similar to those identified in Chapter 3 (Chapter 3, Table 1) and included 10 sites in each of urban landscapes, rural landscapes, fringe landscapes and natural landscapes in and around the town of Stellenbosch.

### Habitat preferences and activity period

To determine preferred habitat types and activity periods for both *P. dominula* and *P. marginalis* a structured sampling/observation method was implemented at the same 10 sites within the urban, rural, fringe and natural habitat types (Chapter 3, Table 1) used in Chapter 3 (also following methods outlined in Chapter 3). This consisted of active visual surveys of 20 minutes at each of the 40 sites from the urban, fringe, rural and natural habitat types (Chapter 3, Figure 2), done once a month for a period of 12 months (July 2013 to July 2014). Active searches entailed continuously moving throughout the habitat type, observing and recording foraging wasps of both species. Observations were done within the first week of each month on consecutive days between 09h00 and 16h00 on sunny and windless days. I also determined the average temperature for each month during the observation period by using temperature data obtained from the Stellenbosch University weather web page (<http://weather.sun.ac.za>).

Seasonal activity periods and habitat preferences of both *P. dominula* and *P. marginalis* were investigated using a repeated measures ANOVA - also referred to as a correlated ANOVA as I repeatedly sampled the same 10 sites within the specified habitat types - with a Bonferonni post-hoc test (using STATISTICA 12, StaSoft Corporation, Dell, USA) to compare number of individuals observed at 40 habitat types sampled monthly during the first week of every month over a period of 12 months.

### Enemy release, body size and colony productivity

To determine enemy release, body size and colony productivity I collected nests and wasps for physical measurements and cell counts. Nests of both *P. dominula* and *P. marginalis* were collected when wasp activity and temperatures decreased in May of 2014 (i.e. the start of winter). Nests were collected from 17 different study sites within Stellenbosch only from the urban and rural habitat types because no nests were observed in fringe and natural habitat types. All reachable nests (also those reachable by ladder) were collected. Collection was done either at night or early morning as wasp activity was lowest at these times and most individuals were still present on the nests. All nests were removed by hand, using a bee hive tool (as used by beekeepers). The bee hive tool was used to break off the petiole that secures the nest to its supporting structure (predominantly buildings). Collected nests and accompanying individuals were separately placed into re-sealable plastic bags, which were then placed in a freezer at -20°C to euthanize the wasps and subsequently stored for later investigations.

### Enemy release

Inspecting collected wasp nests I found the parasitic fly from the genus *Anacamptomyia* (Tachinidae) was most prominent and allowed me to determine nest parasitism rates in terms of cells affected per nest for both *P. dominula* and *P. marginalis*. It was easy to differentiate unparasitized nest cells from those parasitized by *Anacamptomyia* as the latter contain brown parasitic fly puparia (Figure 1) or remnants thereof. Percentage parasitism for each nest was calculated as the number of parasitized cells as a percentage of the total number of cells per nest. These data were normally distributed and therefore an ANOVA in Statistica (STATISTICA 12, StaSoft Corporation, Dell, USA) was used to compare mean parasitism rate between the two wasp species (using combined data from the urban and rural sites, and between the site-types for *P. dominula* and *P. marginalis* separately. A Tukey honest significant difference (HSD) post-hoc test was used to determine differences between means.



Figure 1: A brown puparium from the parasitic fly *Anacamptomyia* in the nest of the invasive paper wasp *Polistes dominula* used to determine parasitisation rates.

### Body size

As an indicator of body size for both *P. dominula* and *P. marginalis* I determined both dry weight, and measured the length of the left hind tibia (LHT) of wasps collected with their nests. Wasps were oven dried at 60 °C for a period of 24 hr before determining dry weight of individual wasps using a digital scale (Sartorius Model BP 110 S, Capacity: 0.1mg -110g), and LHT using digital callipers (150 mm Digital Callipers). Body size data were not normally distributed. A Kruskal-Wallis ANOVA and median test within the Statistica software was used (STATISTICA 12, StaSoft Corporation, Dell, USA), due to the nonparametric distribution of the data, to compare median LHT and dry weight between the two species, and within a species between the rural and urban habitat types. In both instances LHT and dry weight were the dependant variables and habitat type and species the independent variable, respectively. In addition, I determined the strength of correlation between dry weight and

LHT for both species separately (urban and rural habitat types combined for each species, respectively) using Spearman rank order correlation analyses in Statistica.

#### Colony productivity

Colony productivity, an estimate of the potential number of offspring reared, can be based on the number of cells in a comb (Gamboa *et al.* 2002). To determine the potential colony productivity of *P. dominula* and *P. marginalis* I counted the number of cells of each of the collected nests for both *P. dominula* and *P. marginalis*. An ANOVA was used, because of the normal distribution of data, with a Tukey honest significant difference (HSD) post-hoc test to determine nest size difference averages between the two wasp species (for both species the data was combined for both habitat types for each species respectively) and between sites for the two species separately.

### Results

#### Habitat preferences and activity period

In total this study recorded 809 foraging wasps (758 *P. dominula* & 51 *P. marginalis* respectively) (Fig. 2). *P. dominula* generally was more abundant than *P. marginalis* in all habitat types (Wilks lambda = 0.84716,  $F_{(6, 1030)} = 14.844$ ,  $p < 0.05$ ) (Fig. 2). For both *P. dominula* (KW- $H_{(3, 520)} = 78.653$ ,  $p < 0.05$ ) and *P. marginalis* (KW- $H_{(3, 520)} = 32.254$ ,  $p < 0.05$ ) the wasp abundance in the urban habitat type was found to be significantly greater than any of the other habitat types (Fig. 2).

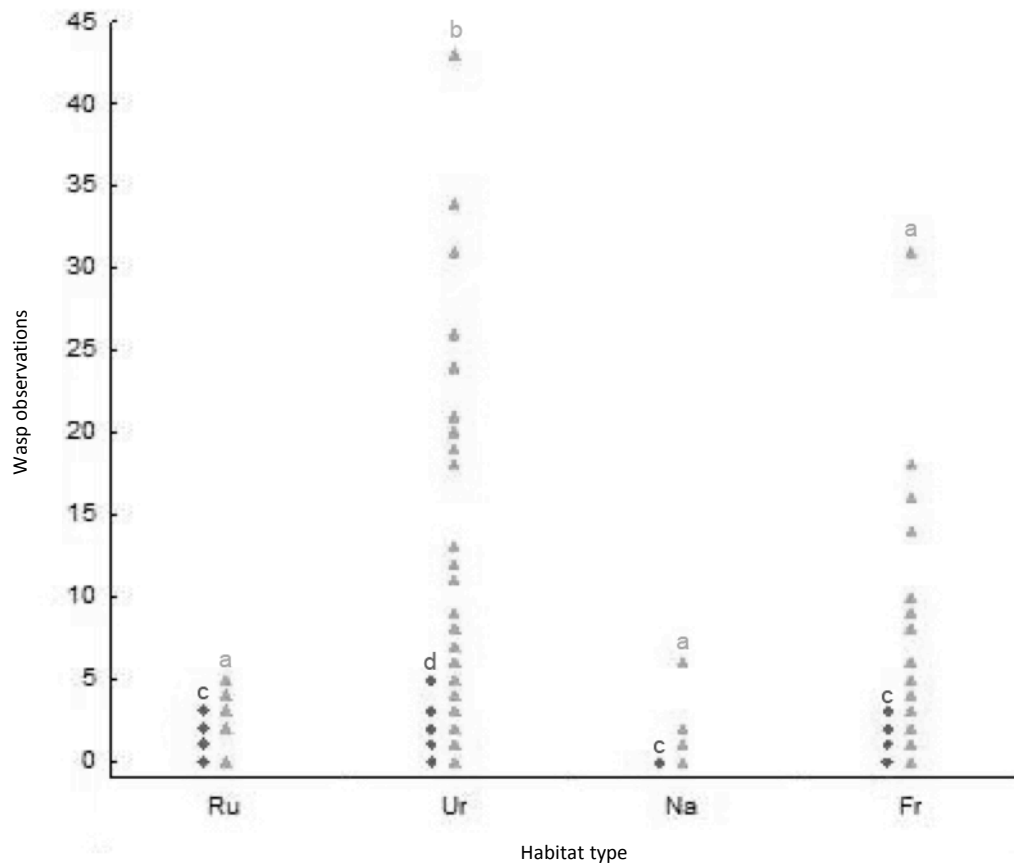


Figure 2. Number of *P. marginalis* (dark grey) and *P. dominula* (light grey) observed using an active search method in Rural (Ru), Urban (Ur), Natural (Na) and Fringe (Fr) habitat types. Each symbol (triangle or diamond) represents one observation instance and the number of wasps counted for that instance in the given habitat type on the Y axis. (different letters indicate significant difference between habitat types within a species – dark grey for *P. marginalis* and light grey for *P. dominula*).

Over the 12 month observation period, *P. dominula* presented a significantly greater number of foraging wasps compared to *P. marginalis* over the same time period (Wilks lambda = 0.79168,  $F_{(24, 1012)} = 5.2242$ ,  $p < 0.05$ )(Fig. 3).



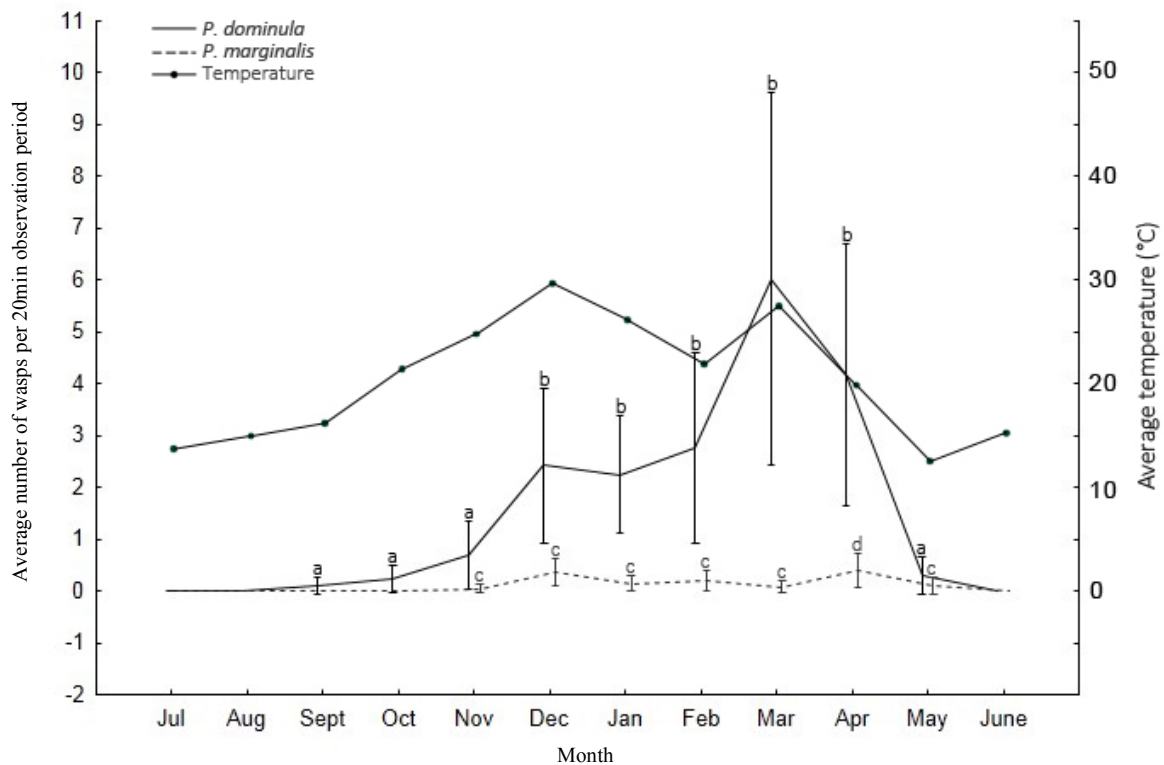


Figure 3: Activity patterns of *Polistes dominula* and *P. marginalis* for four habitat types combined within each month for a period of 12 months. The temperature indicated is the average for each month. (different letters indicate a significant difference between months; vertical bars denote 95% confidence intervals).

During the first two months of observations in winter (July and August) no foraging wasps of either species was observed. The first *P. dominula* appeared in September in the urban habitat type, more than two months before the first foraging *P. marginalis* was observed during November. *P. dominula* observations increased continuously from September until the peak in March and *P. marginalis* also became more abundant during the later stages of its activity period in February, March and April. For both wasp species, activity decreased as temperatures lowered and winter neared and completely ceased to appear in May (Fig. 3).

#### Enemy release, body size and colony productivity

In total, 132 paper wasp nests (101 *P. dominula* & 31 *P. marginalis* respectively) were collected from 17 different study sites within the urban and rural habitat types. Of the nests collected, 46 still had wasps present at the time of collection (27 *P. dominula* & 19 *P. marginalis*, respectively).

### Enemy release

Overall parasitism rate (data for urban and rural habitat sites combined for each species respectively) of *P. dominula* was found to be significantly higher than that for *P. marginalis* ( $F_{(1, 130)} = 17.2145$ ,  $p < 0.05$ ) (Fig. 4). Parasitism rates for the two species did not vary significantly between urban and rural habitat types ( $F_{(1, 29)} = 2.4551$ ,  $p > 0.05$ ;  $F_{(1, 99)} = 0.0135$ ,  $p > 0.05$  for the two species respectively).

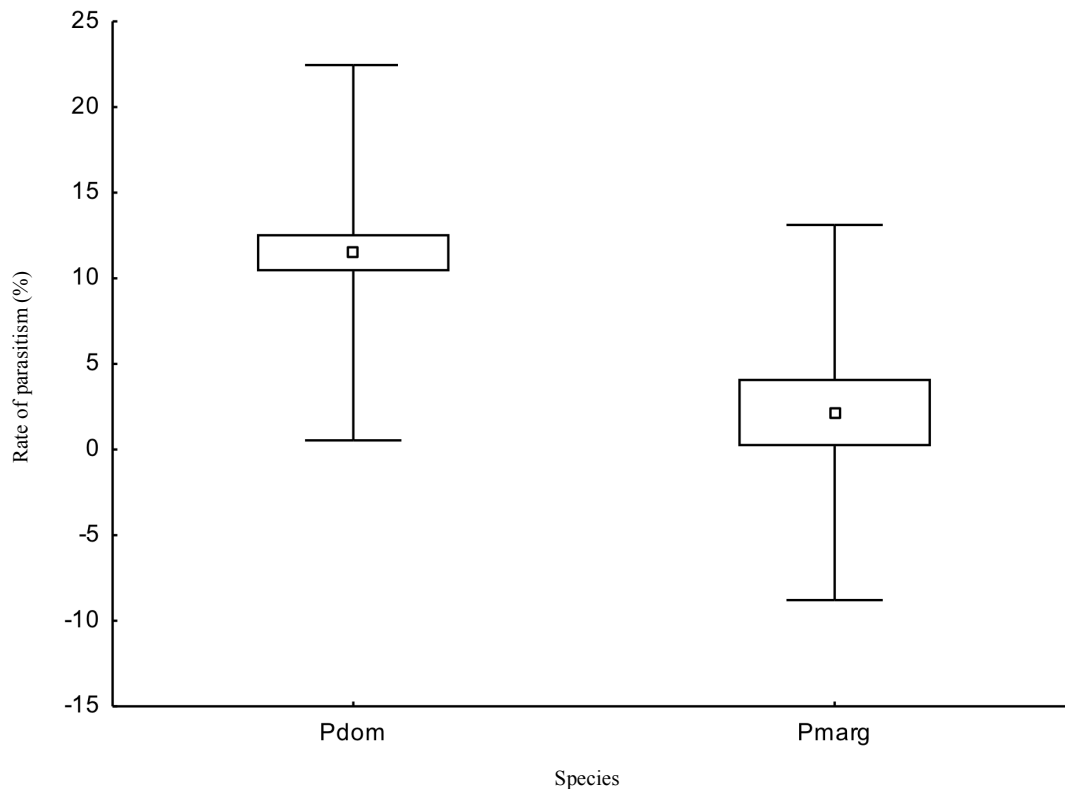


Figure 4: Overall parasitism rates (urban and rural habitat type combined for each species respectively) of nests of *Polistes dominula* and *P. marginalis* by an *Anacamptomyia* sp. collected in and around Stellenbosch. (Mean is indicated by the middle point, standard error indicated by the box and standard deviation by the whiskers).

### Body size

A total of 858 *P. dominula* and 265 *P. marginalis* adult wasps were collected on nests in May 2014 (Table 2).



Table 2. Mean phenotypic values of male and female *P. dominula* and *P. marginalis* wasps in Urban and Rural habitat types. DW = Dry weight (in mg), LHT = Left hind tibia (mm). F = female, M = male.

	Species	Sex	Mean		Range		n	
			Urban	Rural	Urban	Rural	Urban	Rural
DW	<i>P. dominula</i>	F	0.039	0.040	0.010 - 0.081	0.010 - 0.078	241	413
		M	0.036	0.038	0.010 - 0.070	0.010 - 0.070	85	119
	<i>P. marginalis</i>	F	0.046	0.045	0.012 - 0.080	0.012 - 0.079	157	81
		M	0.046	0.051	0.021 - 0.080	0.020 - 0.079	19	8
LHT	<i>P. dominula</i>	F	3.18	3.28	2.21 - 4.47	2.23 - 4.29	241	413
		M	3.10	3.20	2.28 - 4.08	2.21 - 4.10	85	119
	<i>P. marginalis</i>	F	3.95	3.87	2.54 - 4.64	2.27 - 4.69	157	81
		M	3.87	3.76	3.15 - 4.42	3.34 - 4.64	19	8

Overall dry weight (urban and rural habitat sites combined for each species respectively) of *P. dominula* did not differ significantly from that of *P. marginalis* ( $KW-H_{(1, 1123)} = 9.5222$ ,  $p > 0.05$ ). Dry weight also did not differ significantly for either *P. dominula* or *P. marginalis* between the urban and rural habitat types (*P. marginalis*:  $KW-H_{(1, 265)} = 2.4085$ ,  $p > 0.05$ ; *P. dominula*:  $KW-H_{(1, 858)} = 1.6284$ ,  $p > 0.05$ ).

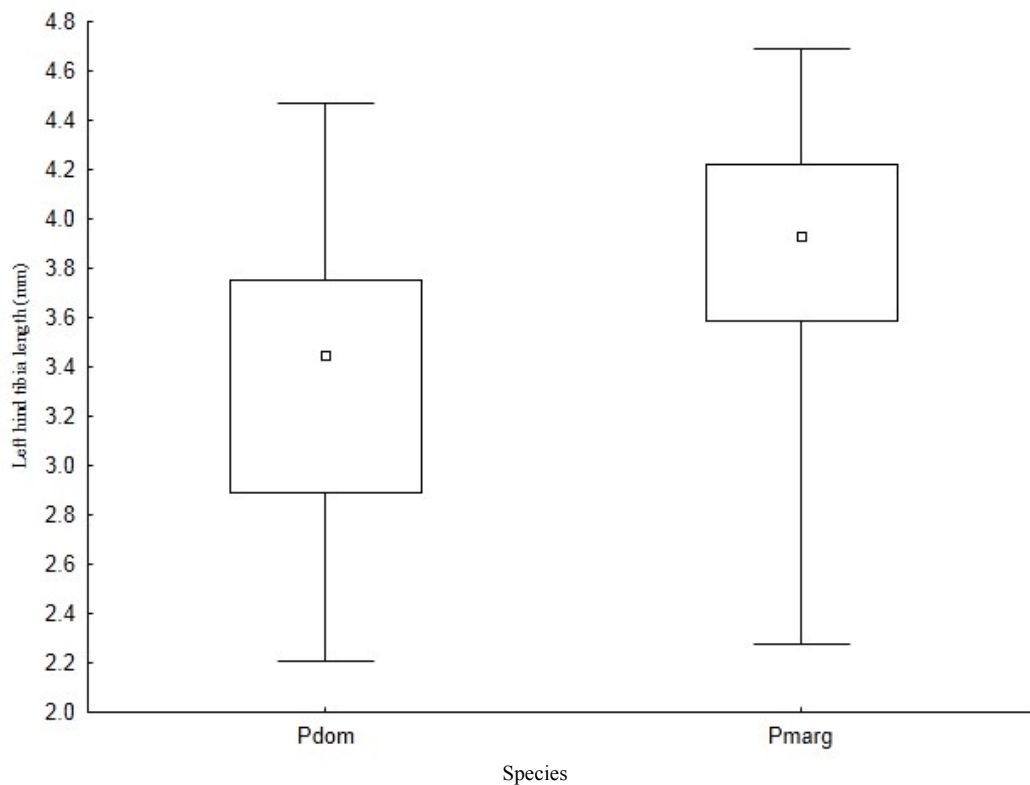


Figure 5: Left hind tibia length for *Polistes dominula* and *P. marginalis* individuals. (Median is indicated by the middle point, 25%-75% percentile is indicated by the box and range indicated by the whiskers).

Left hind tibia length (urban and rural habitat sites combined for each species, respectively) differed significantly between *P. dominula* and *P. marginalis* (KW- $H_{(1, 1123)} = 212.0689$ ,  $p < 0.05$ )(Fig. 5). Differences in LHT length between habitat types were detected for both *P. dominula* and *P. marginalis*. Both species had longer LHT lengths in the urban habitat type (*P. marginalis*: KW- $H_{(1, 265)} = 4.6640$ ,  $p < 0.05$ ; *P. dominula*: KW- $H_{(1, 858)} = 10.9543$ ,  $p < 0.05$ )(Fig. 6).

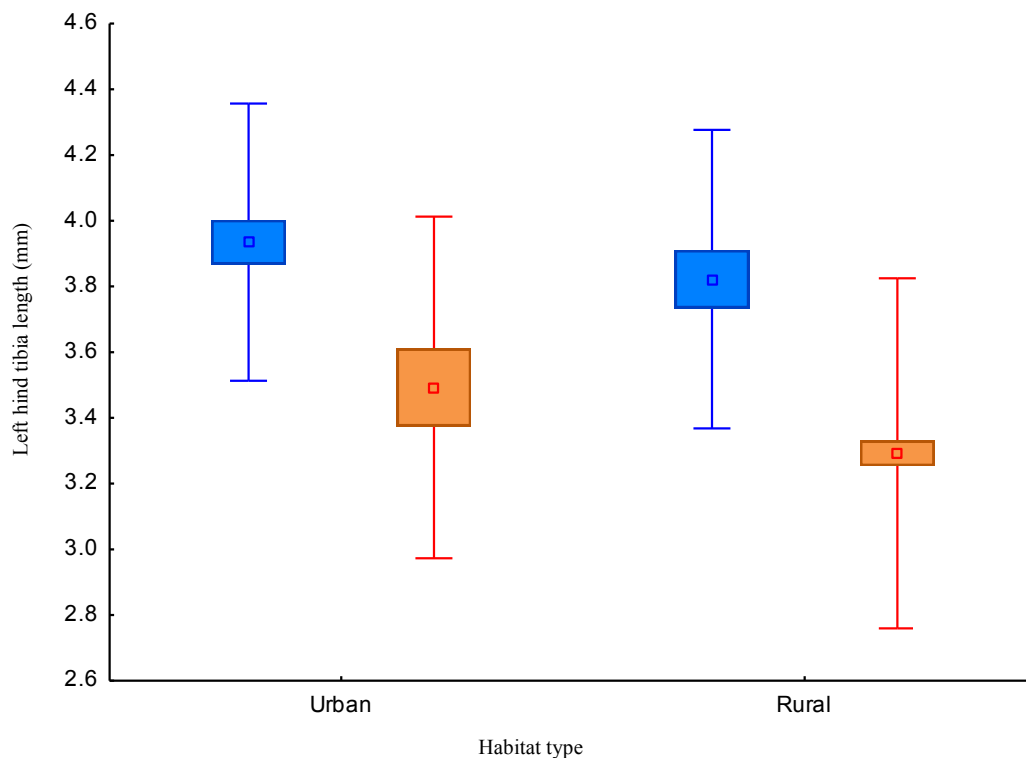


Figure 6: Left hind tibia length for *Polistes dominula* (on the right within each habitat type) and *P. marginalis* (on the left within each habitat type) individuals collected from urban and rural habitat types in and around Stellenbosch. (Median is indicated by the middle point, 25%-75% percentile is indicated by the box and range indicated by the whiskers).

Left hind tibia length and dry weight was significantly correlated for both *P. dominula* ( $r = 0.0787$ ,  $p < 0.05$ ) and *P. marginalis* ( $r = 0.2154$ ,  $p < 0.05$ )(Fig. 7).

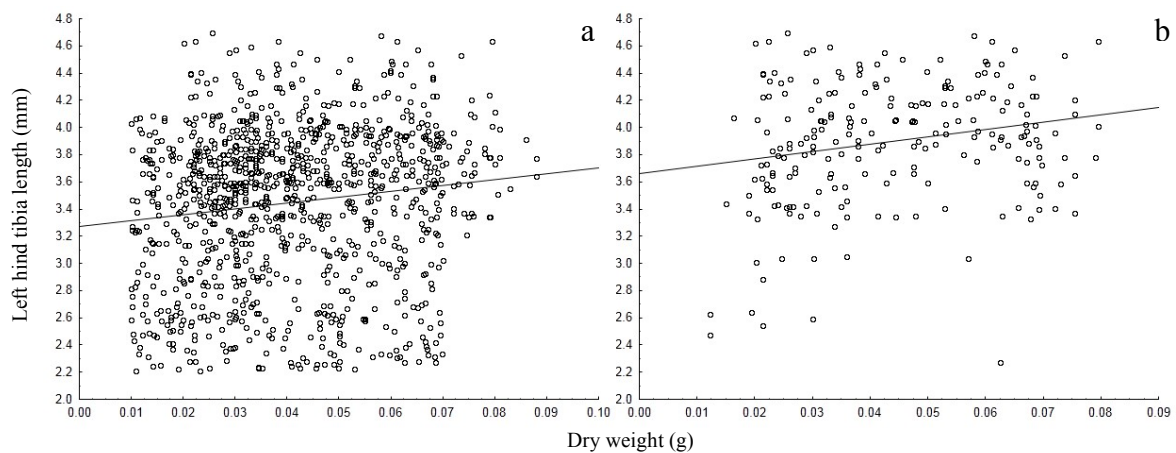


Figure 7: Correlation of left hind tibia length to dry weight of *Polistes dominula* (a) and *P. marginalis* (b) individuals.

### Colony productivity

To determine colony productivity (a measure of the potential reproduction) the number of cells for 132 paper wasp nests were counted (101 *P. dominula* and 31 *P. marginalis*). Overall (urban and rural habitat sites combined, for each species, respectively). *P. dominula* nests contained significantly more cells and therefore had a greater colony productivity potential than that of *P. marginalis* ( $F_{(1, 130)} = 26.1601$ ,  $p < 0.05$ ) (Fig. 8). Considering the two habitat types separately, *P. dominula* had significantly more cells per nest in rural areas when compared to urban areas whereas *P. marginalis* did not differ significantly in terms of cell numbers between the two habitat types (*P. marginalis*:  $F_{(1, 29)} = 0.003$ ,  $p > 0.05$  *P. dominula*:  $F_{(1, 99)} = 5.1707$ ,  $p < 0.05$ ). (Fig. 9).

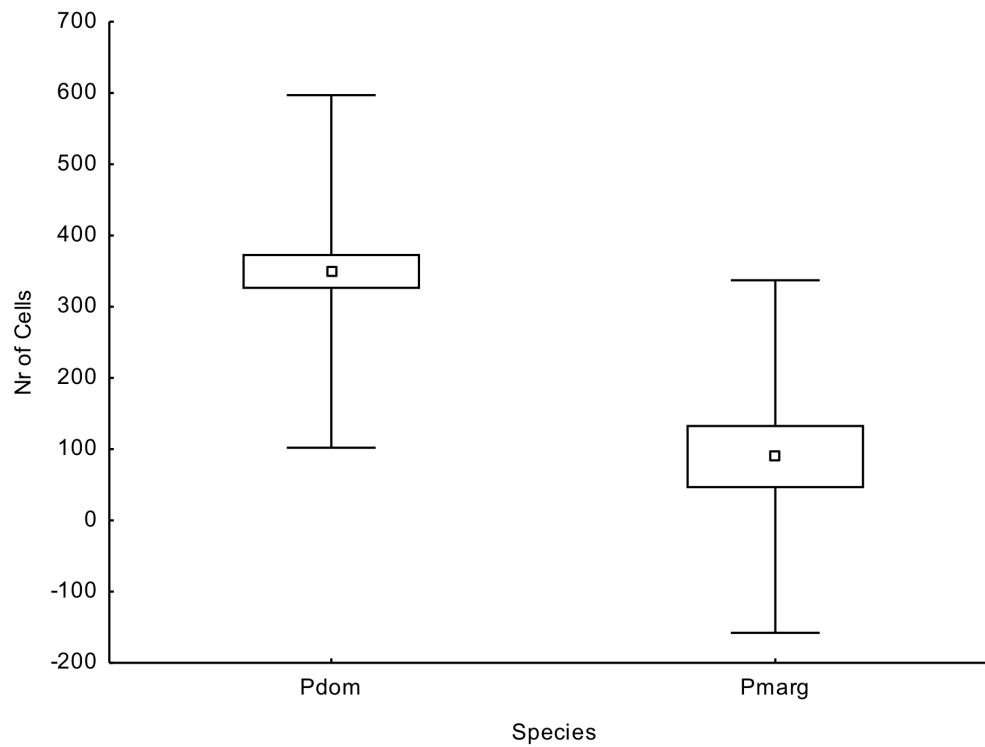


Figure 8: Overall number of cells for nests of *Polistes dominula* and *P. marginalis*. (Mean is indicated by the middle point, Standard error indicated by the box and Standard deviation by the whiskers).

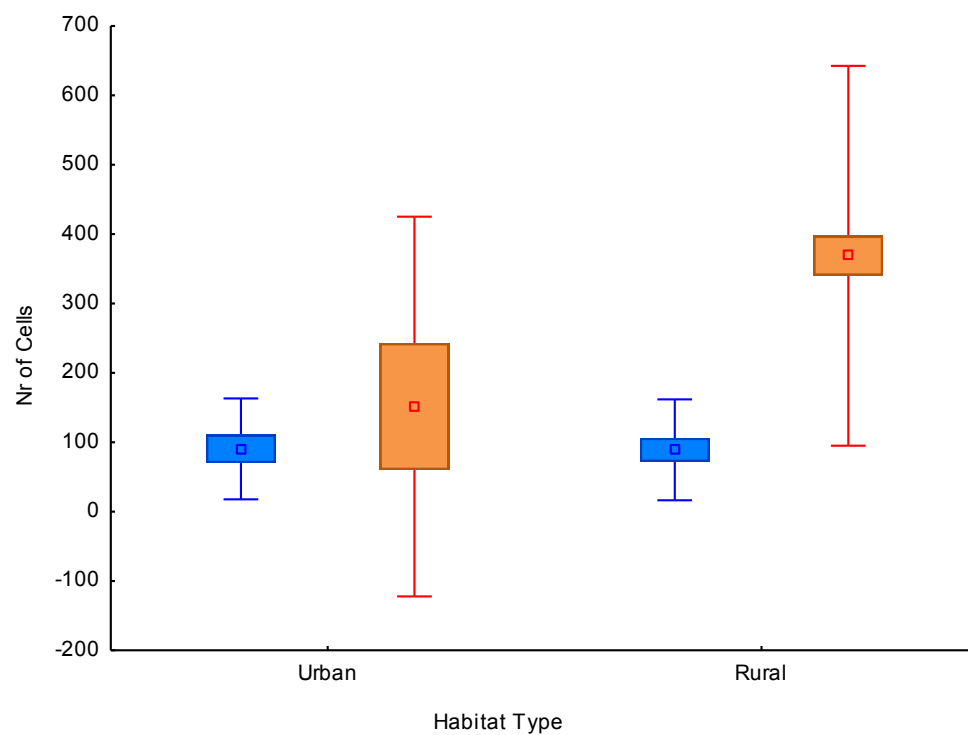


Figure 9: Number of cells for *Polistes dominula* (on the right within each habitat type) and *P. marginalis* (on the left within each habitat type) nests collected from urban and rural habitat types. (Mean is indicated by the middle point, Standard error indicated by the box and Standard deviation by the whiskers).

## Discussion

Results indicate that *P. dominula* is more abundant in its newly invaded habitat in South Africa than the native *P. marginalis* in spite of their similar habitat preferences. Activity for both species was most pronounced in the anthropogenically altered habitats such as urban, fringe and rural habitat types. Rural and urban habitat types also hosted the most nests. For both *P. dominula* and *P. marginalis*, the natural habitat type was least preferred, most probably due to lack of adequate nesting sites (Gamboa *et al.* 2004). These results agree with those of Gamboa *et al.* (2004) who showed that feeding and habitat preferences of the invasive *P. dominula* and native *P. fuscatus*, in America, are similar. As both species are likely to use similar resources such as food (Cervo *et al.* 2000) and nesting sites, a high level of potential competition may exist between these two species.

The superiority in numbers of the invasive species could have been the result of its shorter period of inactivity (allowing it to start nest construction earlier), greater degree of enemy release, its and greater colony productivity (Cervo *et al.* 2000; Gamboa *et al.* 2002; Armstrong & Stamp 2003). For example, under predictions of the enemy release hypothesis it could be expected that the invasive wasp would be less affected by parasitoid species than the native wasp species (Collautti *et al.* 2004). This would therefore lead to a competitive advantage of the invasive over the native species in terms of release from top down population regulatory effects. However, Benadé *et al.* (2014) found the same parasitoids in the nests of *P. dominula* and *P. marginalis* in South Africa. Contrary to expectations, this study has shown that the nests of *P. dominula* suffer significantly higher parasitism rates (average of 13%) than the nests of the native species (average of 3%). Release from natural enemies is therefore unlikely to contribute significantly to the success of *P. dominula* in the region due to the possible spill over of parasites from the less abundant native to the more abundant invasive (in terms of wasps and nests) (Roy & Lawson Handley 2012).

With regards to activity period, *P. dominula* started actively foraging almost two months before the first individuals of *P. marginalis* appeared. *P. dominula* also exhibited a prolonged activity period that was almost a month longer than that of *P. marginalis*. The shortened period of inactivity of *P. dominula* in South Africa likely results in a competitive advantage over *P. marginalis* as this allows earlier nest establishment, more advantageous nest

placement (in terms of protection) earlier production of workers and potential predator avoidance (Cervo *et al.* 2000; Gamboa *et al.* 2002). Body size, however, was not found to be a defining factor in the success of *P. dominula* in its newly invaded range.

The potential number of offspring that can be reared based on the number of cells in a comb or nest gives an indication of colony productivity (Gamboa *et al.* 2002). Studies comparing the native *P. fuscatus* and the invasive *P. dominula* in the USA, found that the latter exhibited 2.5 times greater colony productivity than *P. fuscatus* (Gamboa *et al.* 2002; Gamboa *et al.* 2004). Similarly, I found that *P. dominula* had significantly larger nests than *P. marginalis*, containing on average almost three times more cells, indicating significantly greater potential colony productivity.

*P. dominula* constructed significantly larger nests in the rural habitat types than in the urban settings, whereas nest sizes for *P. marginalis* did not differ significantly between these two habitat types. The larger nests constructed in the rural areas is probably linked to increased energy availability in the form of prey as parasitoidism rates were unaffected by habitat type. Biotic homogenization (a decrease in diversity) brought on by the process of urbanization could also play a role in rural habitat types exhibiting larger nests (McKinney 2006). This indicates that the invasive success of this species is most likely directly linked to food availability. The abundance of *P. dominula* - in terms of foraging wasps – in urban areas can be linked to its preference to forage in disturbed (managed grassy areas) areas such as sport fields and fire belts.

The success of *P. dominula* in its newly acquired habitat likely relies on its ability to produce large numbers of offspring earlier in season, allowing it to outnumber the native *P. marginalis* and increase its chances of being a successful invader. Colony productivity of this species is almost three times higher than the native species while parasitism was only 12% higher. *P. dominula* can thus easily achieve a much greater population size than that of the native congener. At this time the presence of parasitoids on *P. dominula*, although more pronounced than on the native *P. marginalis*, does not seem to influence its colony productivity.

Due to the high reproductive capacity of *P. dominula* using natural insect biological control agents to reduce population size and thus spread, is unlikely and may therefore not be a viable option. Instead, other control options such as chemical control, toxic baiting and the use of pathogens should be investigated in South Africa. To date chemical control and toxic baiting has been shown to be effective against the Vespidae, but more so *Vespula* and *Vespa* species

than *Polistes* species (Beggs *et al.* 2011). Chemical control management by means of targeted pesticide use to eliminate nests at the start of the reproductive phase (in spring) would prevent *P. dominula* from realising its colony growth potential. The use of pathogens has also shown to be affective against eusocial wasps such as *P. dominula* and *Vespula vulgaris* (Harris *et al.* 2000), but its effectiveness has not yet been determined on *P. dominula*. It would be important to determine what percentage of nests destroyed would result in marked population reduction, and how many follow up control efforts would be required to eradicate this species from an area (Toft & Harris 2004).

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## Chapter 5

### General discussion and Conclusions

The pressure on global biodiversity because of increased globalization of humans through trading, travel and tourism is gaining momentum (Mack *et al.* 2000; Sharma *et al.* 2010; Blackburn *et al.* 2012). A huge detrimental drawback to increase in human mobility is the rise of biological invasions aided by the anthropogenically-mediated spread of invasive alien species resulting in cumulative economic and ecological costs (Pimentel *et al.* 2005; Carlton & Ruiz 2005; Rands *et al.* 2010). One of these organisms includes the primitive eusocial paper wasp *Polistes dominula* (Christ). It has shown itself to be a robust invasive species as it has been recorded on all continents except Antarctica (Carpenter 1996; Miller *et al.* 2013) and has now also established itself in the Western Cape Province of South Africa (Benadé *et al.* 2014), therefore contributing to the invasion problem. The economic impact of invasion by this species includes damage of grapes *Vitis vinifera*, sweet cherries *Prunus avium* and other thin-skinned stone fruits (Cranshaw *et al.* 2011). Its effects on biodiversity is far less understood but may include costs relating to consumption of large quantities of native prey items (Gamboa *et al.* 2002; Gamboa *et al.* 2004) that will have cascading effects on higher trophic levels. When this species co-occurs with wasps within similar habitats, food requirements and habitats (i.e. similar niches), competition can cause displacement of the native species (Gamboa *et al.* 2004; Miller *et al.* 2013). This is especially expected when the native species is congeneric to the invasive species, as these two taxa will likely have very similar niches due to recent evolutionary history. This is exemplified by competitive interactions identified between *P. dominula* and *P. fuscatus* in the USA where numerous potential reasons for the superior competitiveness of the invasive over the native species has been suggested (Cervo *et al.* 2000). These include release from predators and parasitoids (Cervo *et al.* 2000) and various factors related to colony productivity (e.g. shorter diapause times and smaller body size).

Prior to this study virtually nothing was known about the invaded range and possible interactions between *P. dominula* and native organisms in South Africa. Therefore this project aimed at addressing the following main questions:

1. What is the current extent of the invaded range (distribution) of *P. dominula* in the Western Cape Province of South Africa? (Chapters 2 and 3). Will it be able to establish in other parts of the country in the future?
2. What are the habitat preferences of *P. dominula* in its invaded range? (Chapter 3).
3. To what extent may the release from natural enemies aid in the invasive success of *P. dominula* (Chapters 2 and 4).
4. Is this exotic species potentially in direct competition with the native *P. marginalis*? (Chapter 4)
5. What competitive advantage, if any, does the invasive *P. dominula* have over its native congener? (Chapter 4).

### **Invaded range and habitat preferences of *P. dominula***

#### *Invaded range*

The invaded range of a species in a newly acquired habitat serves as an indication of its area of influence and rate of spread of a period of time, assuming that historical data for this exists. In the case of recently recorded invasive like *P. dominula* no historical invaded range data exists, except for a single record by Eardley *et al.* (2009) and mention of it's presence in Stellenbosch by Veldtman *et al.* (2012). My aim was therefore to expand on the knowledge regarding the invaded range of *P. dominula* in South Africa. In this study, I have recorded a considerable range expansion by *P. dominula* as it was only recorded in the town of Kuilsriver. Only five years later (over a period of three years – 2012 to 2014) and visiting 27 towns, I have shown that the range of this invasive species has now expanded to include 12 towns within the Western Cape Province of South Africa. At the moment the invaded range of *P. dominula* seems to be largely confined to the west of the Cape fold mountains. However, this species has managed to pass this barrier recently to the east via Grabouw.

In addition to this, a single record from Knysna to the far east of the distribution has been recorded (although requiring confirmation). These events are deemed to have been human mediated instances of abnormal range expansion of *P. dominula*, especially in the case of the Knysna record which is 400 km to the east (in the Southern Cape) from where it was first recorded in Kuilsriver. We have not recorded any instances of *P. dominula* expanding its range into the direction of the Karoo. This area may therefore not be suitable for habitation by this species due to the much drier climate. However, many of the coastal regions to the east of the invaded range have a similar climate to the areas invaded by this insect and may well be easily invaded. This was also foreseen by Eardley *et al.* (2009). We therefore expect this

species to substantially increase its range to the east in the near future, as natural barriers to its further dispersal are limited in these areas.

Successful management and control of any further range expansion of *P. dominula* is possible. This will however be a very labor-intensive process. Working from the outer limits of its spread inwards, the removal of any female nest initiating wasps at the start of the new season (around August) will not allow time for new fecundated wasps to appear. Similarly, control at the end of the season may also be a viable option to control the further rapid spread of this species. Fecund queens only appear and are impregnated late in the season when males are specially nest reared for this. If a successful removal effort were to be undertaken at this stage of the wasp cycle, future generations will also most likely be prevented. It has to be mentioned however that eradication of this species is probably no longer a viable option as many of these nests are difficult to locate. This will also not guarantee slower spread of this species as hibernating queens can easily be transported via cars etc. to new localities at the end of the activity season. Complete eradication of social insects will be extremely difficult, due to the generational overlap of individuals allowing for the replacement of poisoned or parasitized individuals. Beggs *et al.* (1998) set out to poison nests of *Vespula vulgaris* in New Zealand, and although effect on site at the nest, foraging workers reinhabited the nests ultimately reducing the effectiveness of the attempt. Attempts at managing social wasps should be carefully considered as the expense in terms of man hours and money can be tremendous.

#### *Habitat preferences*

Determining the habitat preferences of an invasive species in a new habitat will allow for the opportunity to identify possible management strategies as this will focus control efforts. To determine the habitat preferences of *P. dominula* in the Western Cape Province I conducted a 12 month survey of 40 sites in four habitat types (Urban, Fringe, Rural and Natural). I often found *P. dominula* nesting sites close to human habitation (MacKenzie *et al.* 2006). This could be due to the ample sturdy structures to establish nests that some of these buildings allow (Armstrong & Stamp 2003). This habitat preference could also be associated with increased food resources in these areas in the form of exotic pests and diminished resistance from competition and predation in arguably more sensitive natural areas.

I have shown that the presence of *P. dominula* (if present at all) can be easily determined by visiting an open grassy habitat like that of a sports field in summer. This is important, as an effective bait to attract this species in South Africa does not yet exist. Therefore, the only

way to currently track the invasion of this species, and to monitor their numbers are these visual surveys in preferred habitats. Additionally entomological collections can be continuously screened for the presence of this insect to identify newly acquired habitats.

Using this active survey technique I was able to show that *P. dominula* and the native *P. marginalis* have similar habitat requirements and that there is likely direct competition between these two species. I was also able to determine that activity period differed between the *P. dominula* and *P. marginalis* similar to the results obtained by Gamboa *et al.* (2002; 2004).

#### *Advantages of the invasive P. dominula over the native P. marginalis*

The success of an invasive species in a new habitat can be determined by numerous factors including: enemy release, plasticity (or ability to adapt to new environments), the ability to undergo diapause (used as a stress tolerance mechanism when environmental conditions become adverse), a generalist diet and efficient colony productivity (Cervo *et al.* 2000; McGlynn 1999; Armstrong & Stamp 2003). Potential competition with a native species, however, may result in decreased invasion success, depending on how well the native species can compete for resources etc.

Contrary to expectations, I found the native *P. marginalis* was far less parasitized than the invasive *P. dominula*. There was therefore no support for the enemy release hypothesis in aiding its invasive success in South Africa. This agrees with the findings of other workers on *P. dominula* in other parts of the world (Miller *et al.* 2013). However, *P. dominula* has numerous competitive advantages over the native *P. marginalis*. Colony productivity of *P. dominula* compared to *P. marginalis* was found to be far greater than that of the native wasp. Similar findings were made by Gamboa *et al.* (2002) and proposed by Cervo *et al.* (2000). The greater potential colony productivity could potentially be the factor that allows *P. dominula* to thrive even though it is parasitized to a greater degree than the native, and also directly translates to more nest cells and therefore more offspring that could compete with the native *P. marginalis* for nesting sites, food etc.

#### **Future research**

As yet, only the invaded range, habitat preferences and advantages of the invasive *P. dominula* over that of the native *P. marginalis* have been researched in South Africa. I recommend that the effect of *P. dominula* on indigenous prey be considered in future studies, as the amount of prey consumed by invasive wasp species in newly acquired habitats can be

staggering (Gamboa *et al.* 2002; Gamboa *et al.* 2004). In conjunction with establishing the amounts of prey consumed, one could also determine the types (species) of prey consumed, as this would give an indication of the potential effect on native biodiversity. Comparing food intake and diversity of food items between the invasive wasp and native competitors could also show to what extent these are in competition for the same resources. Furthermore, it would also aid future management and control plans if the micro habitat of *P. dominula* could be determined in terms of nesting site preference, as this would guide the search for viable nesting sites and removal of nests.

It would also be beneficial to study the aforementioned management techniques. Removing a nest-initiating queen at the beginning of a season will not allow for the establishment of new colonies and a subsequent increase of fecundated females in the following season. However, if practices such as these would be able to slow the spread (or lead to lower numbers of the wasps) is unknown. Experiments should therefore be conducted to test the feasibility of these practices.

To conclude, the results of this study in terms of the invaded range of *P. dominula* in the Western Cape Province not only serve as an indicator of the spread of this invasive, but also underline the usefulness of data mining entomological collections to determine invaded range of a given species. In the study by Benadé *et al.* (2014, Chapter 2) student entomological collections were used to determine the invaded range of *P. dominula* up until June 2013. In the present study, focused observational surveys were conducted and indicated that there was not much difference between the two data sets, as most localities were confirmed and only few extra distribution records were obtained. These types of collections can therefore be an invaluable research tool because it allows for a way of gathering data (data mining) that could take considerable time and finances to collate using direct surveying techniques. Not only did these collections save time, but they also served as a historical record to map the invasion rate. To provide institutions such as universities, colleges and even schools the permission to collect, establish and add to museum collections for research purposes should therefore be encouraged. This would be particularly important in areas beyond the known range of the species, to ascertain any new distributional spread, but care should be taken to confirm reports and have people with the proper knowledge identify the species as to prevent unnecessary expenses.



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