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Research

Population Ecology

Nesting Ecology and Colony Survival of Two Invasive *Polistes* Wasps (Hymenoptera: Vespidae) in New Zealand

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Abstract

We examined the abundance, nesting ecology, and colony survival of two invasive species of paper wasp, *Polistes dominula* Christ (Hymenoptera: Vespidae) and *Polistes chinensis* Pérez (Hymenoptera: Vespidae), within their invaded range in New Zealand. The more recent invader, *P. dominula*, exhibited a strong habitat preference, reaching the highest abundances within suburban areas with an average of 87.4 wasps per 1,000 m^2. Coastal habitats were also found to be suitable environments for *P. dominula*, although wasp abundance in these areas was comparatively lower than suburban sites at 26.5 wasps per 1,000 m^2. Although *P. chinensis* were observed to build more nests in coastal habitats, this was not reflected in the abundance of adult wasps in these areas. Nests of *P. dominula* were larger and more productive, likely a result of the multiple founding and earlier emergence of workers compared to *P. chinensis.* Both species exhibited significant differences in nest survival, with *P. dominula* observed to have a higher colony survival rate, particularly in suburban habitats where this species utilized man-made substrates as nesting sites. Neither species nested within forest sites and translocated nests of *P. dominula* failed to thrive within forest habitats. Findings of this research suggest that *P. dominula* will not pose a threat to species inhabiting forested areas. Instead, biodiversity managers should focus their efforts on suburban and coastal environments as native species in these areas will require the greatest protection.

Key words: invasive species, paper wasp, *Polistes dominula*, *Polistes chinensis*, nesting ecology

Invasive species have adverse consequences for biodiversity and ecosystem processes (Pysek and Richardson 2010, Spatz et al. 2017, Pysek et al. 2020). Invasive social insects count among the most wide-ranging and destructive species (Pilowsky and Starks 2018, Lester and Beggs 2019). These social insects constitute a large portion of invasive invertebrate research due to their ability to reach high densities, often having a wide host range and feeding across trophic levels (Snyder and Evans 2006, Roy et al. 2011, Ward and Morgan 2014). Social wasps can cause considerable ecological and economic damage in the ecosystems that they invade (Beggs et al. 2011, Lester and Beggs 2019). Numerous factors contribute to the success of social wasps and colony productivity is arguably the most important (Perez-Bote et al. 2020). Productivity depends on both ecological and environmental factors.

The European paper wasp, *Polistes dominula* Christ (Hymenoptera: Vespidae), and Asian paper wasp, *Polistes chinensis* Pérez (subspecies: *antennalis*) (Hymenoptera: Vespidae), are two predatory social wasps that have established in New Zealand. The most recent invader of the two species is *P. dominula*, whose presence in New Zealand was first realized in 2016, although it has been estimated that this wasp could have arrived as early as 2011 (MPI 2016). The more widespread and established *P. chinensis* has been in New Zealand since the 1970s (Clapperton et al. 1996). Native wasps in New Zealand are predominantly solitary, so there are concerns about the impact these social wasp species could have on native communities. Research into the abundance and impact of *P. chinensis* has already been conducted in some parts of New Zealand, with nest densities reaching 210 nests per hectare and wasps consuming as much as 957 g of invertebrate biomass per hectare per season (Clapperton et al. 1996, Clapperton 1999, Clapperton and Lo 2000). Lepidoptera have been identified as the predominant prey in the *P. chinensis* diet (Ward and Ramón-Laca 2013). As *P. dominula* is such a recent invader, little research has been conducted on this species in their newly invaded range. To help biodiversity managers, more information is needed on its habitat preference, colony growth, abundance, and survival.

The native range of *P. dominula* is predominantly the Mediterranean region. With the assistance of human activity, this wasp has spread to other temperate areas across several continents (Cervo et al. 2000, Liebert et al. 2006, Benade et al. 2014). The success of *P. dominula* as an invader has largely been attributed to its generalist diet, comparatively short development time, and cofounding behavior. Multiple studies investigating the success of *P. dominula* compared with native paper wasp species within its invaded range have found *P. dominula* to be the more successful species (Gamboa et al. 2004, Liebert et al. 2006, Pilowsky and Starks 2018, Roets et al. 2019). This success was often attributed to *P. dominula* being less parasitized, with higher nest survival rates and the utilization of human structures. Research within both the native and invaded range of this wasp found it to be a predominantly urban species; however, it has been observed in other habitats (Gamboa et al. 2005, Roets et al. 2019).

Here, we compare nesting characteristics in New Zealand of the recent invader *P. dominula* to the more established *P. chinensis*. We specifically compare these two species in terms of 1) habitat effects on productivity, 2) differences in seasonal activity phases, 3) differences in colony productivity (cell numbers in nests and wasp abundance), and 4) nest survival. An understanding of the nesting locations and abundance of *P. dominula* will allow biodiversity managers to predict the likely effects of this newly invaded wasp.

Materials and Methods

Study Site

This study was conducted in the Nelson-Tasman region of New Zealand (41.299° S, 173.244° E; Supp Fig. 1 [online only]) over two reproductive cycles of the wasps, from late spring to early autumn: 19 November 2018 to 18 March 2019 and 11 November 2019 to 16 March 2020. Nelson is the site where *P. dominula* was first observed in New Zealand and is believed to be the area where this wasp has been at the longest, although it has established in other areas of the upper part of the South Island. More recently, there have been reports of *P. dominula* reaching more southern regions of the island (Howse et al. 2020). The only sightings of *P. dominula* in the North Island have been in Auckland. Temperature and precipitation in these areas appear to be favorable for *P. dominula* (Howse et al. 2020).

To determine whether habitat influenced the success and productivity of *P. dominula* and *P. chinensis*, habitat was categorized into three types: suburban, coastal, and forest (Supp Fig. 2 [online only]). Suburban sites were residential areas, each containing a house with a garden area. A news story on the intended paper wasp research was publicized, asking for volunteer Nelson residents that would be comfortable with us identifying and monitoring paper wasps at their homes over a season. In total, 16 suburban sites were used over the two summers (Supp Fig. 1b [online only]). Coastal sites had at least one boundary within 100 m of the high tide line. In total, seven coastal sites were used over the two summers (Supp Fig. 1b [online only]), which were comprised of a mix of shrubs, herbaceous plants, sedges, and grasses. No permanent anthropogenic structures were present; however, some sites contained plant protectors as part of a tree restoration program (Supp Fig. 2a [online only]). These protectors were made of plastic, standing 40 cm tall, designed to protect plants from rabbits (*Oryctolagus cuniculus* Linnaeus (Lagomorpha: Leporidae)) and herbivorous birds, Pukekos (*Porphyrio melanotus* Temminck (Gruiformes: Rallidae)). Plant protectors were found to be frequently used as nesting sites by both *Polistes* species (Supp Fig. 3c [online only]). Forest sites had boundaries at least 50 m in from the forest edge and a minimum canopy cover of 50%. There were six forest sites, which were classified as industrial pine, native beech, native podocarp, or a mix of regenerating native and exotic forest.

Abundance and Productivity

The abundance and productivity of *P. dominula* in Nelson were compared with the longer-established exotic congener *P. chinensis*. It should be noted that there is a third exotic congener, *Polistes humilis* Fabricius (Hymenoptera: Vespidae), in New Zealand, but this species is not present in Nelson. To compare nest productivity of *P. dominula* and *P. chinensis*, changes in nest size (number of cells) were recorded each week from late spring (mid-November, calendar week [CW] 47) until the end of the season in autumn (mid-March, CW 12), for both years. In a few instances, *P. dominula* foundresses had reused a nest from the previous season, although only cells being utilized in the current season were included in the counts. Additionally, the number of adult wasps on each nest was recorded over the summer of 2019–2020 to compare changes in the abundance of both *Polistes* species over a season. Wasp densities were monitored every fortnight at five sites within each habitat type. These counts were conducted in the early hours of the day, typically between 6.30 and 9.00 a.m. when all wasps were likely to be present. An additional five suburban sites, one coastal, and one forest were also monitored on a monthly basis to supplement fortnightly counts and provide a more robust estimate of wasp abundance. As not all sites were of the same size (ranging from roughly 350 to 1,700 m^2), the counts of adult *Polistes* wasps were adjusted to give an estimate of abundance per 1,000 m^2. For analysis, abundance was broken down into three main phases of the nesting cycle: founding phase, worker phase, and reproductive phase (Pilowsky and Starks 2018). The founding phase is when the foundress(es) or reproductively active individuals begin constructing the nest, laying eggs, and feeding the subsequent larvae. The founding phase ends when the first adults emerge from the nest (Höcherl and Tautz 2015), transitioning into the worker phase. During the worker phase, the nest grows in size at a greater rate and wasp densities increase as more workers emerge. The reproductive phase follows the worker phase, which is evident by the emergence of gynes (reproductive females) and males. There is also a slowing or complete stop to nest growth during this time. The reproductive phase is when wasp densities on each nest reach their peak.

Nest Survival Rates

Survival time in weeks was analyzed from late spring, 11 November 2019 (CW 46) until the end of the season in autumn, 16 March 2020 (CW 12). To determine whether there was a preferable habitat for *P. dominula* or *P. chinensis*, the abundance, growth, and survival of nests were monitored each week. The substrate on which a foundress chose to nest was recorded as being either natural or man-made, to determine whether this choice affected the chance of a nest successfully surviving until the end of the season. Natural substrates were often the stems of small shrubs (<1 m in height), herbaceous plants, sedges, and rocks. Man-made substrates included metal, treated timber, concrete, or plastic. The number of foundresses on each nest was also recorded and verified in the fortnightly wasp count before the first workers emerged. Nests were classified as abandoned when there were no wasps present and when at least one of two further conditions was satisfied: (a) there were no eggs, larvae or pupae, (b) the nests were substantially damaged. Damaged nests that were truly abandoned were usually attacked by predators and any remaining eggs or larvae removed by the next count, most likely by ants. These nests were checked in subsequent weeks to ensure the nest had been abandoned and that no workers had successfully emerged.

Translocation of *P. dominula* Nests

After completing the first summer of data collection, it became apparent that neither *P. dominula* nor *P. chinensis* nested in forest habitats within the study area, except in areas that had been disturbed by human modification. These forested sites were often surrounded by infestations of *Polistes* spp. wasps. Given the close proximity of *Polistes* spp. to these sites, it appears that dispersal ability was not the limiting factor preventing these wasps from establishing in forest habitats.

To determine whether *P. dominula* were not found in forests because they were unable to survive in these environments, a nest translocation experiment was conducted. This experiment was done in Nelson, from 24 January to 20 February 2020. That period was selected as nests were in the worker phase when nest survival rates and wasp densities are higher than in the founding phase, and therefore less likely to be abandoned due to bad weather, ant invasion, or foundress death. Nests of *P. dominula* were attached to the inside of plastic containers (n = 24; Supp Fig. 4 [online only]). Eight nests were translocated into two forest habitats (four nests in each), and changes in nest growth, wasp densities, and nest survival were monitored. One forest site was an industrial pine forest, the other regenerating native forest. The remaining nests were evenly divided and translocated into two suburban and two coastal habitats as controls. The number of cells per nest and number of adult wasps were recorded before and after the experiment. Research has found temperature to have an important effect on *P. dominula* nest growth (Höcherl and Tautz 2015) and foraging (Weiner et al. 2011), with wasps failing to forage for food at temperatures below 20°C (Kovac et al. 2019). To compare temperatures between habitats, HOBO Pendant UA-001-08 temperature data loggers were placed within each site on the nest boxes, logging the temperature every 10 min. A comparison was made between habitat types, of the proportion of hours over the 28-day trial that exceeded 20°C.

Statistical Analysis

Statistical analyses were conducted in R 3.6.0 (R Development Core Team 2020). To compare the abundance of wasps for *P. dominula* and *P. chinensis*, a 2 × 2 factorial analysis of variance (ANOVA) was conducted with habitat type (coastal, suburban) and species (*P. dominula* and *P. chinensis*) as factors at each of the three phases of the nesting season. The main effects of each treatment on the abundance of wasps per 1,000 m^2, and interactions between factors were tested using a permutational ANOVA, as the data were non-normal. The analyses were conducted using 'perm.anova' from the package 'RVAideMemoire' (Hervé 2018).

Polistes nest survival was investigated using the packages 'survival' (Lin and Zelterman 2002) and 'survminer' (In and Lee 2019) to generate Kaplan–Meier plots to visualize survival curves (Jager et al. 2008). Differences between survival curves were then analyzed using log-rank tests. A logistic regression with data fitted to a binomial distribution was conducted on nest survival for each *Polistes* spp. using the 'lme4' package (Bates et al. 2014), with nest substrate and number of foundresses as factors and site as a random effect. As data failed to meet the assumption of normality, a permutational multivariate ANCOVA was conducted on changes in nest size and wasp densities of translocated nests using the 'vegan' package (Dixon 2003). The factor in the model was habitat type, with initial nest size and initial wasp abundance included as covariates. Differences in the proportion of hours that were equal to or over temperatures of 20°C within each habitat were tested using a chi-squared test.

Results

Abundance and Productivity

Nests of *P. dominula* and *P. chinensis* were monitored once a week to record changes in nest size (number of cells) during the summer seasons of 2018–2019 and 2019–2020. During the summer of 2018–2019, 117 *P. dominula* and 60 *P. chinensis* nests were monitored across 18 locations. In the following year, we monitored 129 *P. dominula* and 220 *P. chinensis* nests across 10 locations. All monitored nests were within coastal or suburban areas (Supp Fig. 3 [online only]), as no nests of either *Polistes* species were found within forest habitats. Nests were discovered in the final stages of the founding phase in late spring/early summer (calendar week [CW] 46–50). Over the nesting season, *P. dominula* nests typically had more cells than the nests of *P. chinensis* (Fig. 1). Higher numbers of cells in a nest increases the probability of a greater reproductive output (Pickett and Wenzel 2000). *Polistes dominula* workers began emerging around CW 48, with 80% of nests in 2018–2019 and 84% of nests in 2019–2020 having workers by CW 2. By comparison, workers of *P. chinensis* emerged slightly later, with workers beginning to emerge in CW 49 and only 70 and 53% of nests having workers by CW 2 for the summers of 2018–2019 and 2019–2020, respectively. Nests at CW 2 were larger for *P. dominula* (mean: 58.9 cells, SE: 4.16) than for *P. chinensis* (mean: 46.7 cells, SE: 2.49). Once the workers had emerged, the number of cells added to the nest each week increased substantially for both species.

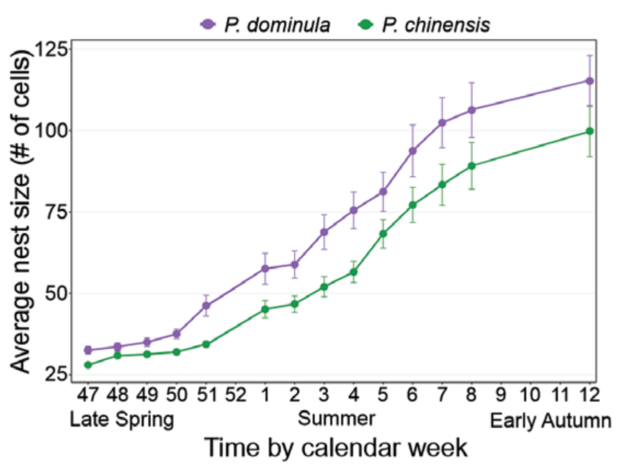

Fig. 1. The average nest size (number of cells) ± 1 SE of *Polistes dominula* and *Polistes chinensis* over 18 wk of the nesting season for 2 yr (2018–2019 and 2019–2020) in Nelson, New Zealand. Gaps in the data are for weeks where no nests were monitored. In total, 246 *P. dominula* nests and 280 *P. chinensis* nests contributed to this analysis.

During the founding phase, species had a significant main effect on wasp abundance (permutational ANOVA: $F_{1,28} = 4.87$, $P = 0.033$) with *P. dominula* reaching higher densities (mean: 12.1 wasps per 1,000 m^2, SE: 2.58) than *P. chinensis* (mean: 5.08 wasps per 1,000 m^2, SE: 2.23, Fig. 2). Habitat had no main effect on wasp abundance at the founding phase of the nesting season (permutational ANOVA: $F_{1,28} = 2.73$, $P = 0.115$). During the worker phase, species was again found to have a main effect on wasp abundance (permutational ANOVA: $F_{1,28} = 11.21$, $P = 0.002$; Fig. 2). There was an average abundance of 21.3 (SE: 4.57) *P. dominula* wasps per 1,000 m^2 across habitats compared to the 5.1 (SE: 2.11) *P. chinensis* wasps per 1,000 m^2. This difference in abundance is likely due to the higher failure rates of *P. chinensis* nests and the comparatively earlier emergence time and population growth of *P. dominula*. By the reproductive phase (CW 8), species and habitat had strong interacting effects on wasp abundance (permutational ANOVA: $F_{1,28} = 4.47$, $P = 0.037$; Fig. 2).

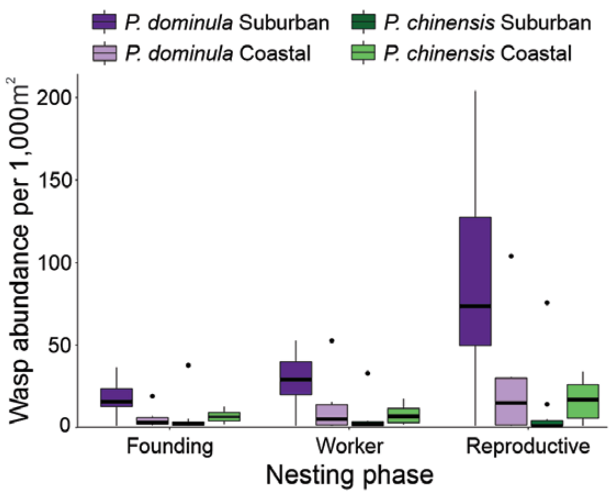

Fig. 2. Boxplots showing the abundance of *Polistes dominula* and *Polistes chinensis* per 1,000 m^2 based on habitat type spanning 18 wk of the nesting season for the summer of 2019–2020 in Nelson, New Zealand. Habitat types were suburban (n = 10) and coastal (n = 6). Nests were surveyed at three points in time: the founding phase in November (calendar week [CW] 48), after worker emergence in January (CW 2), and during the reproductive phase in February (CW 8). Within nesting phases, *P. dominula* boxplots are on the left, *P. chinensis* on the right.

Suburban habitats had the highest abundance of paper wasps, which were predominantly *P. dominula*. In suburban habitats, the average abundance of *P. dominula* and *P. chinensis* was 87.4 (SE: 21.0) and 9.1 (SE: 7.30) wasps per 1,000 m^2, respectively. In coastal habitats, the abundance of *P. dominula* was 26.5 (SE: 16.10) wasps per 1,000 m^2 and for *P. chinensis*, 15.4 (SE: 5.50) wasps per 1,000 m^2. In summary, these results indicate that *P. dominula* thrives in suburban habitats and was typically over ninefold more abundant in these areas than *P. chinensis* at the peak of the nesting season. The more recently arrived *P. dominula* was also more abundant than *P. chinensis* in coastal areas.

Nest Survival

Nests of *P. dominula* had a higher survival rate over a season compared to *P. chinensis* (log-rank test, $\chi^2 = 20.8$; $P < 0.001$), with 46% of *P. dominula* nests surviving until the end of the season, compared with only 21% survival of *P. chinensis* nests. Nest survival for *P. dominula* was greater for nests built in suburban habitats, with 72% of *P. dominula* nests surviving until the end of the season, whereas only 31% of coastal nests survived (log-rank test, $\chi^2 = 17.5$; $P < 0.001$; Fig. 3a). The odds of nest success were 5.4 times higher for *P. dominula* nests built on man-made substrates compared to nests built on natural substrates (coefficient = 1.677, $Z = 2.413$, $P = 0.016$, Fig. 4). It should be noted that of the surviving nests within coastal sites, 90% of those that we discovered were built within man-made plant protectors (Supp Fig. 2a [online only]). Nests were either built on the plant within the protector, on the supporting bamboo stick keeping the protector in place, or on the plastic of the protector itself. These protectors probably provided wind and rain protection, plus the benefit of a warmer temperature. There was no significant difference in *P. chinensis* nest survival between habitats (log-rank test, $\chi^2 = 0$; $P = 1$; Fig. 3b). Of the 220 *P. chinensis* nests that were monitored for survival, 76% were built in coastal sites, suggesting there was a preference for these areas, despite the fact they conferred no survival advantage. Nest substrate for *P. chinensis* also did not significantly affect nest survival ($P = 0.821$; Fig. 4). Further information on the nest substrates utilized by each species can be viewed in the supplementary information (Supp Tables S1 and S2 [online only]).

In the summer of 2019–2020, 30% of *P. dominula* nests had two or more foundresses (mean: 3.4 foundresses). The number of foundresses had a significant, positive effect on nest survival (coefficient = 0.481, Z = 2.426, $P = 0.015$), with the odds of nest success

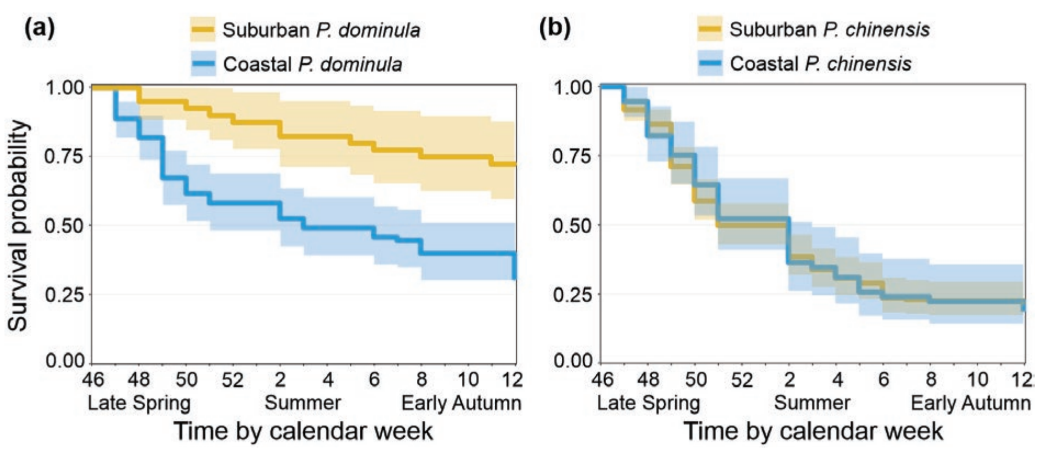

Fig. 3. Kaplan–Meier survival estimates (± 95% confidence interval) on the nest survival of (a) *Polistes dominula* (n = 129) and (b) *Polistes chinensis* (n = 220) based on habitat type (suburban and coastal) over 18 wk of the nesting season in Nelson, New Zealand. Survival curves are the results of the summer 2019–2020. A log-rank test was used to compare survival of nests for *P. dominula* and *P. chinensis* in each type of habitat.

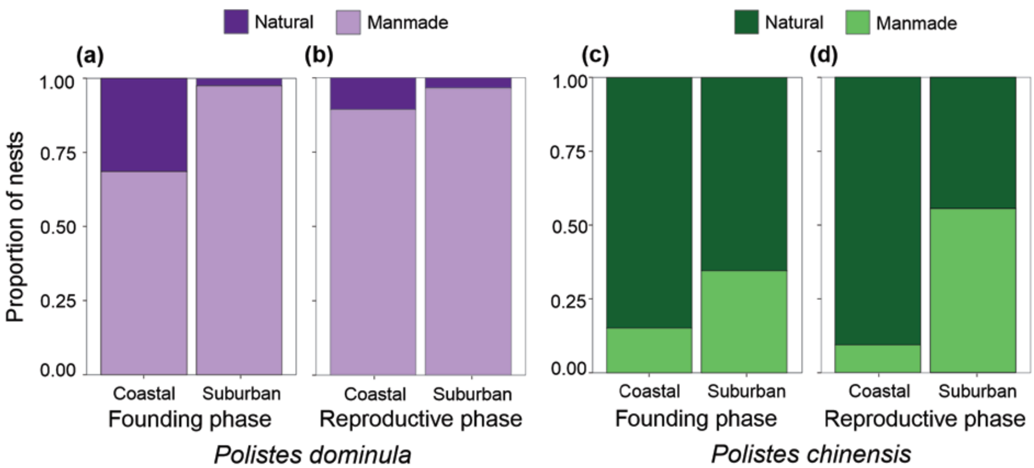

Fig. 4. The proportion of active nests built on natural/man-made substrates for (a) *Polistes dominula* at the founding phase at the start of the season (n = 129) and (b) *P. dominula* nests that survived until the reproductive phase near the end of the season (n = 57). The proportion of active *Polistes chinensis* nests built on natural/man-made substrates at (c) the founding phase (n = 220) and (d) reproductive phase (n = 41). Nests are split into two habitat types (coastal and suburban). Data presented are for the summer of 2019–2020 in Nelson, New Zealand.

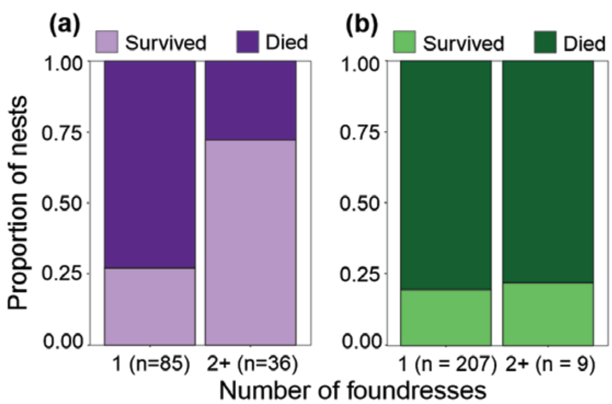

Fig. 5. The proportion of (a) *Polistes dominula* and (b) *Polistes chinensis* nests that survived based on foundress number over 18 wk of the nesting season of 2019–2020 in Nelson, New Zealand. For *P. dominula*, as many as 10 gynes cofounded the nest, whereas for *P. chinensis*, the maximum number of foundresses observed was two.

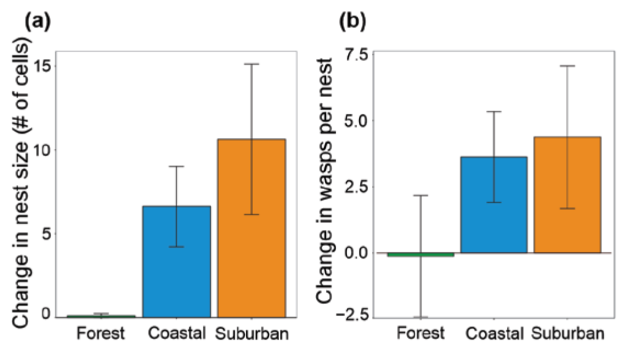

Fig. 6. Average changes in (a) nest size (number of cells) ± 1 SE and (b) number of *P. dominula* adult wasps per nest ± 1 SE. Nests were translocated into three habitat types: forest, coastal, and suburban (n = 8 nests per habitat type). Translocated nests were placed within each site for one month and changes to the number of cells and wasps per nest were compared across habitats.

1.6 times greater for each additional foundress present on the nest. Of the nests with two or more foundresses, 72% survived, whereas single-foundress nests had a survival rate of only 27% (Fig. 5a). The maximum number of *P. dominula* foundresses observed on a nest was ten. Only 4% of *P. chinensis* nests had more than one foundress, and the maximum number of foundresses observed on a nest was two. Nests of *P. chinensis* did not appear to have an increased chance of survival compared with nests with a single foundress, with survival rates of 22 and 20%, respectively (Fig. 5b). The rarity of cofounding observed for *P. chinensis* in this experiment was in accordance with findings from previous research (Miyano 1980, Clapperton and Dymock 1997).

Translocated Nests

Previous research on *P. chinensis* in New Zealand has demonstrated that this species is not commonly found in forest habitats (Clapperton et al. 1996, Ward and Morgan 2014). As a new invader to New Zealand, no similar research had been conducted on *P. dominula*; therefore, nests were translocated into forest habitats to monitor their success. Habitat was found to have a significant effect on *P. dominula* nest growth and wasp abundance in the translocation experiment (permutational multivariate ANCOVA: $F_{2,19}$ = 4.01, P = 0.028; Fig. 6). Nests placed within forest habitats only increased by an average of 0.1 cells (SE: 0.12) in a month, whereas nests placed in coastal and suburban sites increased by an average of 6.62 cells (SE: 2.39) and 10.6 cells (SE: 4.50), respectively (Supp Table 3 [online only]). Wasp abundance in forest habitats decreased (mean: −0.1 wasps, SE: 2.30) with only 50% of nests translocated into this habitat surviving the 28-d trial. In suburban habitats, wasp abundance increased by an average of 4.4 wasps (SE: 2.70), with 75% of nests surviving. In coastal habitats, translocated wasp abundance increased by 3.6 wasps (SE: 1.71) and 100% of nests survived. The proportion of hours where the temperature of the nest boxes exceeded 20°C for the 28 d of the experiment differed significantly between habitat types (χ^2 = 80.3, P < 0.001). Forest habitats had the lowest number of hours meeting or exceeding 20°C, with only 36% of the hours monitored reaching these temperatures. This differed significantly to the proportion of hours reaching ≥20°C in suburban (48%) and coastal (61%) habitats. Nest boxes in forest sites only reached a maximum of 30.1°C, whereas nests in suburban sites reached temperatures as high as 41.3°C and coastal sites reached 43.1°C (Supp Table 4 [online only]). Despite the high temperatures in suburban and coastal sites, the wasps seemed to survive and thrive.

Discussion

Our research on the abundance, nest growth, and survival of *P. dominula* and *P. chinensis* found that *P. dominula* exhibited a strong habitat preference. Although habitat did not have a main effect on wasp abundance during the founding or worker phase, the interaction between habitat and species by the reproductive phase found *P. dominula* to be the most abundant species, reaching the greatest densities in suburban habitats. Across all phases of the nesting season, and in both habitats examined, *P. dominula* was found in greater abundance relative to *P. chinensis*. The difference in abundance is likely explained, in part, by cofounding which is frequently exhibited by *P. dominula*, with one third of nests in this study having more than one foundress. Cofounding involves multiple foundresses working together to build the nest, feed larvae, and defend the nest, increasing the number of wasps per nest at this phase of the nesting season. This advantage early in the season likely contributed to the earlier emergence of workers and higher abundance of *P. dominula* at the start of the worker phase. Cofounding is rarely exhibited by *P. chinensis*, so only a single foundress is expanding the nest and feeding larvae at this time (Miyano 1980, Clapperton and Dymock 1997). The habitat in which *P. chinensis* was most abundant was coastal areas, although the abundance of wasps for this species did not differ significantly between habitat types. An unusually high abundance of *P. chinensis* nests (46 nests within an area of 1,300 m^2) at a particular suburban site could provide a possible explanation for our insignificant results. This site contained many small shrubs and grasses, which *P. chinensis* appears to nest on preferentially. Previous research conducted in New Zealand has found *P. chinensis* to be most abundant in shrubland and flax salt meadow sites (Clapperton et al. 1996), which accords with observations from this study.

Nests of *P. dominula* were larger than *P. chinensis* over the nesting season. Workers of *P. dominula* emerged earlier than *P. chinensis*, which could have given *P. dominula* a competitive advantage, as the number of wasps per nest have been found to be a significant predictor of nest growth (Grinsted and Field 2018). Studies comparing the productivity of *P. dominula* and another congener, *Polistes fuscatus* Fabricius (Hymenoptera: Vespidae), also found *P. dominula* workers emerged earlier, relatively (Gamboa et al. 2005, Pilowsky and Starks 2018).

The higher nest survival rates of *P. dominula* compared with *P. chinensis* agreed with previous research that found *P. dominula* to be a successful invader and have advantages over congeners such as *P. fuscatus* and *Polistes marginalis* Fabricius (Hymenoptera: Vespidae) (Armstrong and Stamp 2003, Gamboa et al. 2004, Pilowsky and Starks 2018). Survival of *P. dominula* nests was highest in suburban habitats. It has been suggested that urban areas can provide warmer habitats for invasive wasps that originate from warmer climates (Sorvari 2018). *Polistes chinensis* had a similar survival rate across both habitat types, suggesting there was no survival advantage for this species to nest in either coastal or suburban sites. Nest survival rates for *P. chinensis* were similar to those observed previously in New Zealand, where overall colony survival was 22–25% (Clapperton and Dymock 1997). Although no *Polistes* nests were found under the canopy of forest habitats, nests could be found in open areas created by human disturbances (walking tracks, camp sites, etc.), predominantly on anthropogenic structures. Research has found *P. dominula* does nest within forest habitats, but in that particular study the forest sites were in close proximity to the forest edge (<50 m; Gamboa et al. 2005). A previous citizen science project conducted in New Zealand found some paper wasps in forest habitats, however they were individual wasps, not nests, and it was unclear how far into the forest habitat those individuals were found (Clapperton et al. 1996). A significant, negative correlation has also been observed between canopy cover and both *Polistes* and *Vespula* spp. wasp densities elsewhere in New Zealand (Schmack et al. 2020).

Nest substrate was found to significantly affect nest survival for *P. dominula*, with the majority of nests that survived the nesting season built on man-made substrates. This behavior of nesting on man-made substrates has been observed for numerous social wasp species in urban areas and may be an advantageous strategy, as it can provide shelter from harsh weather conditions and protect against many natural predators (Detoni et al. 2018). However, it has also been found in urban environments that human activity was the main cause of nest failure (Reed and Vinson 1979, Perez-Bote et al. 2020). *Polistes chinensis* evidently does not utilize man-made structures to the same extent as *P. dominula*, as only half of all *P. chinensis* nests that survived until the reproductive phase in suburban areas were built on man-made substrates. Similar results on the use of man-made structures as nesting sites were observed in an earlier study of *P. chinensis* in New Zealand, prior to the establishment of *P. dominula* (Clapperton and Lo 2000).

Having more than one foundress per nest provided a survival advantage for *P. dominula* nests, which has been observed in other areas of this species' range (Tibbetts and Reeve 2003, Höcherl and Tautz 2015). Cofounding acts as a safeguard in the event that if a foundress dies before the worker phase, the other foundress(es) keep the colony alive. It also has the potential to increase the amount of food that can be gathered to feed larvae, which could explain why workers hatched earlier in the season relative to *P. chinensis*. Cofounding was seldom used as a strategy by *P. chinensis*, as so few nests had more than one foundress. Multiple founding by this species is also uncommon within its native range of East Asia (Miyano 1980). Co-operative nesting in *Polistes* wasps is likely driven by climate, with multiple founding observed in paper wasps such as *P. dominula*, from warmer and wetter climates (Sheehan et al. 2015).

The findings from this study on the abundance and survival of both *Polistes* spp. are based on the nests that were found within our study sites, but it is likely that not all nests within these areas were discovered. The nests of *P. dominula* and *P. chinensis* are frequently hidden from view and reach an average size of only 100–120 cells by the end of the season. Our results are therefore quite conservative, as the abundance of wasps within each site was likely higher than we observed, particularly in suburban areas, as anthropogenic structures were more difficult to search thoroughly in comparison to a sedge or shrub.

Nests of *P. dominula* failed to thrive in forest habitats in our translocation experiment. The nests did not grow in size and half of the nests were abandoned by their foundresses and workers. *Polistes* nests have been found to grow larger with faster larval development and more offspring in sun-warmed sites than in cooler sites (Inagawa et al. 2001). It has also been suggested that *P. dominula* do not forage for food at temperatures below 20°C (Weiner et al. 2011, Kovac et al. 2019). In our experiment, forest sites had the lowest proportion of hours that reached or exceeded 20°C. These cooler temperatures may have prevented wasps from reaching the body temperature necessary for flight as frequently as was required for nest survival. Reduced foraging time could lead to starvation of both the adults and larvae, driving the adults to abandon the nest.

Understanding the nesting ecology and habitat preference of invasive wasps can help inform conservation and biodiversity managers of the potential risks that each species can pose within its new invaded range. *Polistes dominula* has proven itself to be a suburban species, not only in New Zealand, but also in other areas of its native and invaded range (Gamboa et al. 2005, Roets et al. 2019). By reaching such high abundances in suburban areas, this species is likely to have a greater impact on human health than *P. chinensis*, as there is the potential for a greater frequency of wasp stings. As predators, these species will also impact New Zealand's ecosystems. The diets of the two species differ to some extent, with *P. chinensis* predominantly predating upon Lepidopteran larvae (Ward and Ramón-Laca 2013), whereas *P. dominula* has a broader and more generalist diet (Howse et al. 2021). Although *P. dominula* was less abundant in coastal habitats, this species can thrive in these areas. As *P. chinensis* is also prominent in these habitats, coastal communities are likely experiencing extra pressure from the presence of these two predators. Research on *P. chinensis* has found this species capable of consuming large quantities of prey (Clapperton 1999). The impact of *P. dominula* on communities in New Zealand has also proven to be significant, with declines in Lepidopteran species since this predator arrived (McGruddy et al. 2020). This is of concern for New Zealand's local invertebrate communities, as an increase in the abundance of invasive species tends to cause a decline in native populations and communities (Bradley et al. 2019). The discovery in the current study that neither *Polistes* species nest within forest habitats suggests that these wasps are unlikely to have a significant impact on invertebrate species in these areas.

The findings of this research have management implications, as conservation and biodiversity managers can be guided to where protection is most needed, specifically urban and coastal habitats, but not forest environments. We have identified that *P. dominula* prefer nesting on man-made structures and are found at the highest densities in urban habitats. These wasps also invade coastal habitats, which, in this study, did not contain permanent anthropogenic structures. However, housing or resort development beside coastal areas would likely increase *P. dominula* abundance in these ecosystems. The use of plant protectors as nesting sites by *P. dominula* suggests that although this conservation method may promote the growth of native plants, it can also support populations of invasive wasps. Although wasps nesting in these protectors could be problematic for local conservationists tending to these restoration sites, this nesting behavior may prove useful and could even be beneficial in the management of this wasp. There is potential for these plant protectors to be used as a way to supply preferential wasp nesting sites that can then be easily found and destroyed. Moving forward, considerable work is needed to slow the spread of *P. dominula* to other parts of New Zealand and improve current control strategies for both *Polistes* species.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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