

A REVIEW OF THE UNIQUE NESTING CHARACTERISTICS OF *ROPALIDIA PLEBEIANA* (WHITE-FACED BROWN PAPER WASP) – AN ETHOLOGICAL PERSPECTIVE

P.J. Warburton¹ and L. M. Copeland²

¹NSW, AUSTRALIA
ORCID 0009-0009-4603-893X
email: warburtonphil5@gmail.com

²NSW, AUSTRALIA
ORCID 0009-0000-1478-0085

Summary

This study examines the nesting characteristics of *Ropalidia plebeiana* (White-faced Brown Paper Wasp), a species found in southeastern Australia. The species is unusual amongst social vespid wasps in the variety of nesting styles that it exhibits.

This study reviewed scientific and citizen science information, conducted field observations on nest forms, and investigated the possible ecological and behavioural factors that might account for the nest variability across the full geographic range of the species.

In New South Wales (NSW) and southeast Queensland, nesting in large aggregations of nests, or “cities”, is common with northern populations forming the largest aggregations. In contrast, solitary nests are more typical toward the south and in the Australian Capital Territory (ACT) where large aggregations are not present. Aggregation sites appear to be influenced by nesting site availability and the availability of food resources for adults and larvae; warmer regions offer more abundant resources, supporting larger groupings.

Nests exhibit either a stick-style or plate-style configuration and may be suspended in a pendent form or attached flush to the substrate. Non-pendent nests predominate in the northern parts of the range; further south, pendent nests are more common. The form and attachment method of each nest are shaped by its unique developmental progression across multiple seasons. Additionally, nest architecture correlates to location, substrate type, exposure to weather and spatial constraints in the immediate environment.

The observed variability in the construction of various nest types is primarily the result of five main innate behaviours; each being expressed to the extent permitted by prevailing conditions. This results in diverse nesting outcomes across time and geographical locations.

Keywords: *Ropalidia plebeiana*, ethology, nesting.

INTRODUCTION

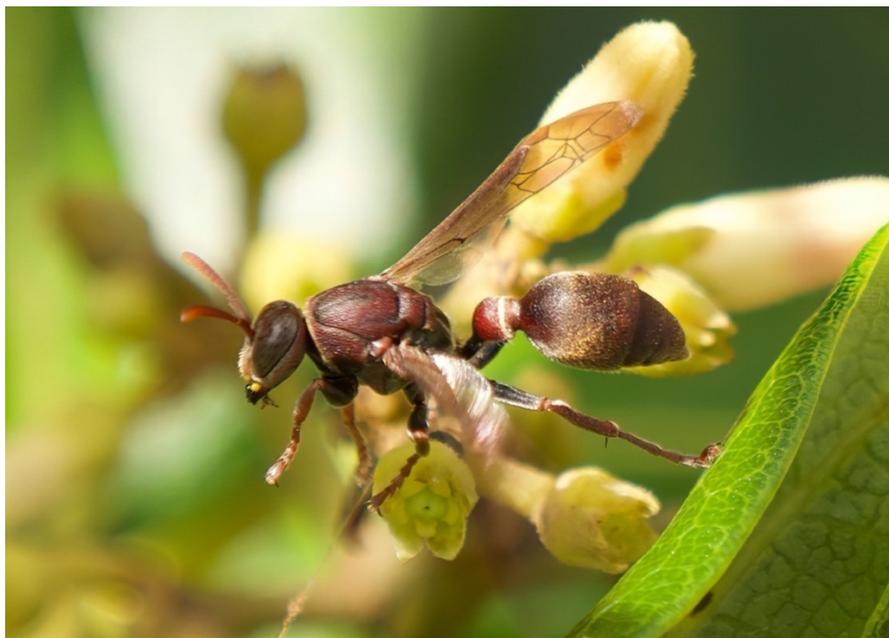
Ropalidia plebeiana (White-faced Brown Paper Wasp) is one of 36 species of social wasps of the subfamily Polistinae in Australia (Australian Faunal Directory, Harris 2025) including two introduced species. It is the only temperate climate species of *Ropalidia* with a distribution spanning the east coast of Australia between Brisbane and Melbourne - the others are all mainly tropical or sub-tropical. They are a small wasp at about 10-12 mm long (Figure 1). They are generally not aggressive and, individually, have only a mildly painful sting. The species has a large window of seasonal activity, emerging early from winter dormancy and rapidly commencing the rearing of young by re-using old nests.

Much of what we know of the species is based on work carried out in the 1970s by Richards and by Itô and others in the 1980s, who studied nests in the South Coast area of New South Wales (Richards, 1978; Itô, 1987).

Historically, the species was found in aggregated nest sites in rocky outcrops. Following the arrival of man-made structures, the species is more likely to be found nesting under more plentiful human constructs such as bridges, making the species an apparent beneficiary of the Anthropocene.

Ropalidia wasps, like other Polistinae, are eusocial. Typically, a single reproductive female gyne (or “queen”) is present per nest, though larger colonies may temporarily have several. Workers, also female and similar in appearance to gynes, handle nest building and caring for young. The establishment of a female in the role of the reproductive gyne, whilst other remain as workers, is mainly determined by size and the process is conducted largely without violent interactions (Fukuda, 2003). Males are often found at the nest but only rarely assist; their main purpose is to seek mates (Kojima 1993).

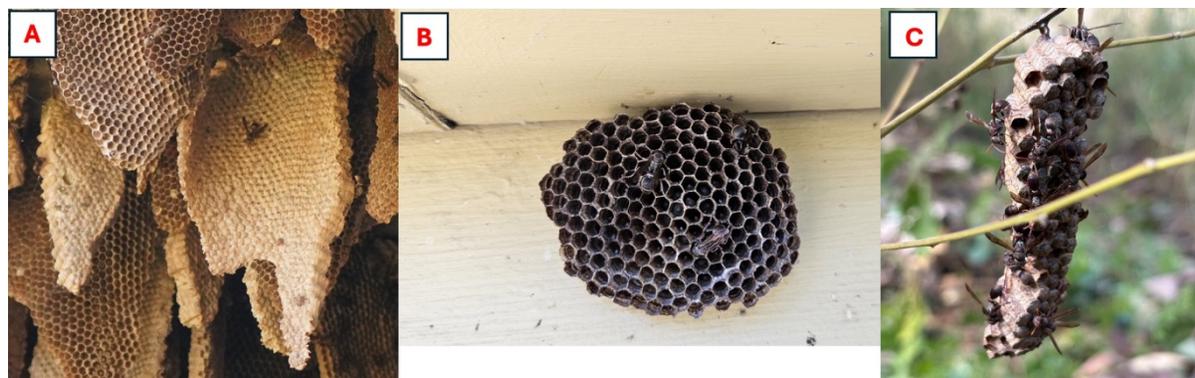
Figure 1. *Ropalidia plebeiana* at Ulladulla, NSW. Photo credit: P. Warburton



Ropalidia plebeiana are also notable for their large, aggregated nesting sites. Such sites are not “super-colonies” but an aggregation of multiple independent nests, usually numbering in the hundreds (Itô 1987). These aggregations, or “cities”, are often in out-of-the-way locations, such as under bridges over creeks and on rocky overhangs on cliffs. Occasionally, these cities are abruptly abandoned, and the wasps relocate to a new nearby site. The preference for nesting in aggregations occasionally extends to *Ropalidia plebeiana* sharing a nesting site with another *Ropalidia* species (Hook 1982).

Most nests are found in the aggregation sites, but there are also some solitary nests positioned apart from others. The nests typically consist of a single layer of cells arranged in a comb. They may be suspended pendulously from an overhead structure with horizontally oriented cells, in an irregular plate-like form (Figure 2A) or instead attached directly to the substrate, with cells oriented horizontally, vertically downward, or at various angles (Figure 2B). Nests may also be in a stick-like form (Figure 2C), again either in a pendent style or attached flush with the substrate.

Figure 2. Three nest styles. Photo Credit: P. Warburton (A) Morpus (B), Chris William (C)



This diversity in nesting styles distinguishes the species, as most other wasp species generally display a

consistent nest architecture with limited variation. It seemingly represents an unusual degree of plasticity in

nest making; insects are more notable for rigidly programmed, innate behaviours in nest building (Sane 2020).

With the modern availability of a wider base of observational data from citizen science (also known as community science) observations, there is now an opportunity to study a larger number of sites and to review the nesting habits over the full geographic range. This study seeks to address that opportunity. The availability of high-resolution cameras and drone technology has allowed a photographic examination of wasp behaviours over a larger number of sites. We address the question of why individuals of this species have multiple different styles of nest building and explain their preference for living in large nest aggregations in northern locations, with a lower propensity for aggregation in more southern locations and highland locations. We consider what leads them to periodically abandon these “cities” and relocate nearby. We address the question as to why they sometimes construct solitary nest sites. We consider these characteristics in light of the innate behaviours of the species.

METHODS AND MATERIALS

Records from the Global Biodiversity Information Facility (GBIF) were examined and taken for analysis in September 2025. A total of 373 photographic observation records of *Ropalidia plebeiana* were extracted and analysed along with records from 28 personal observational visits to 15 sites in September to November 2025. Of those records analysed, 42 aggregated nesting sites and 94 solitary nesting locations had adequate associated photographs for this study. Identifications to species were confirmed by at least two expert identifiers in each case.

The aggregated nesting sites that were visited were at Brogo at the southern-most extent of where aggregations are found, several near Batemans Bay on the New South Wales south coast, Tahmoor in the mid-part of the range, and Coffs Harbour in the northern part of the range. The photographic observations from community science databases provided further information across the entire range of the species from around the Brisbane area to southern Victoria and the Australian Capital Territory (Appendix 2, Figure 15). The 94 solitary nests that were studied were across the range of the species (Appendix 3, Figure 16).

GBIF gathers data from various sources. For *Ropalidia plebeiana*, this includes museum collections and citizen science platforms - predominantly iNaturalist, but also Naturemapr, Questagame, Naturewatch, and

Insect Investigators. These records and their associated photographs were reviewed, the data was checked for accuracy, and each observation was classified according to nesting behaviours. Additional information on sightings was obtained, when necessary, through communication with observers, analysis of Google Maps, and site visits.

Pendent nests were defined to be those that were hanging by one end of the comb from an overhead substrate; the cells of the comb were horizontal or nearly horizontal.

Non-pendent nests were those that were constructed in the plane of the substrate, usually with multiple peduncles throughout the comb. In this case, the cells were either horizontal or pointing vertically downwards, with some at varying angles between the two.

The nests were categorised into groups based on shape. Many of the nests were of an irregular “plate” shape ranging from roughly circular to roughly ovoid, with a flat edge at the point of attachment to the substrate. “Stick” nests were defined to be when the length was greater than 3 times the width.

To avoid disturbing the wasps, and to allow a safe study of the nests, the site activities were studied from about 2 to 5 metres to the nest aggregations using a remotely operated, high-resolution camera with an 800 mm telephoto lens. Activity and location data were logged. A drone was employed to view sites that would otherwise have been inaccessible.

Records were prepared of the details of the nest sites, surrounding vegetation, and topography of the area. Note was taken of any historical information about the nesting site. Botanical studies were carried out in the area around some of the aggregated nesting sites.

Samples of fallen nest combs were obtained from wind damaged nesting sites during the winter dormancy period.

RESULTS AND DISCUSSION

The analysis revealed the very strong tendency to nest in aggregation but with some wasps instead making solitary nests. Nest types vary over time and geography.

Table 1 shows the estimated split between the nest types in the 42 aggregations that were studied (Figure 15 in Appendix 2). Note that these are approximations based on the estimated numbers of nests at each site and the estimated split between the type in each case.

Table 1 Estimated number of nests by type in the aggregation sites studied.

		Number of nests	%
A)	Pendent plate nests	2,000	19%
B)	Non-pendent plates	4,600	42%
C)	Pendent Sticks	4,200	39%
D)	Non-pendent sticks	0	0%
		10,800	100%

The analysis confirmed the paucity of large, aggregated nesting sites in cooler climates; Victoria had just four small aggregation sites that had been recorded on the community science databases, and there were no observations recorded in the Australian Capital Territory. The largest aggregation sites are in Queensland and northern New South Wales. Observations of solitary nests are much more common in Victoria and central/southern New South Wales than in the northern areas of the range.

Aggregation sites in the northern parts of NSW and Queensland were more likely to be relatively exposed to the elements, compared with aggregations in central and southern areas of New South Wales, where overhanging rocks, and similarly sheltered structures under bridges, were strongly preferred.

Botanical surveys of large, aggregated nesting sites confirm the richness of the plant life around large

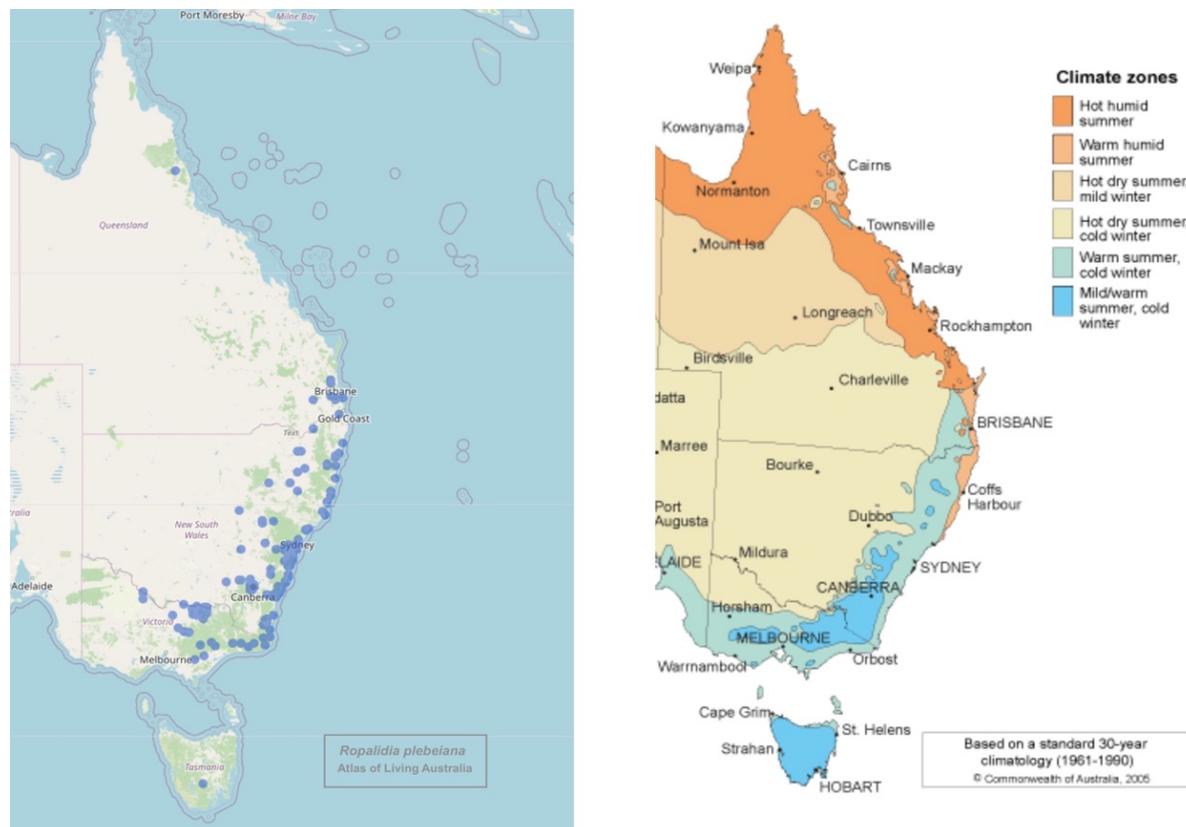
aggregation sites. Eight such surveys were carried out and show that the area within 50 metres of each large site contained many trees, shrubs and smaller plants. These usually included at least a dozen different flowering species that would sustain the colony with nectar and foraging opportunities throughout the active months (Appendix 1).

The timing of the wasps' emergence from dormancy coincided with flowering times for several of the plants mentioned in the surveys, especially *Acacia* species. The emergence from dormancy, in the central areas of New South Wales, lags the northern part of the range by about two weeks. Canberra and the southern parts of the range, in south coast areas of New South Wales and Victoria, lag by a further two weeks. The flowering of *Acacia* and other plants in those areas follows a similar pattern. A minority of the nests studied were solitary nests, constructed outside of aggregations (Table 2).

Table 2. Number of nests by type in the solitary sites studied.

		Number of nests	%
A)	Pendent plates	28	30%
B)	Non-pendent plates	39	41%
C)	Pendent Sticks	24	26%
D)	Non-pendent sticks	3	3%
		94	100%

Figure 3. Range of *Ropalidia plebeiana* (left) compared to climatic regions (right)
 Ref: Atlas of Living Australia and Australia Bureau of Meteorology



Ropalidia plebeiana is the only temperate climate species in the genus (Figure 3) - the other members are mainly confined to tropical and sub-tropical regions.

The species has been able to exploit the arrival of man-made structures as advantageous sites for their nest cities. Several of the sites we observed were mentioned in a 1985 study, indicating that such nest aggregations have survived for decades (Itô 1985), though the exact site of the aggregation within a larger location sometimes changes over time; they may move from one side of a bridge to the other for example.

The nesting aggregation behaviour of this species is a kind of defensive cooperation of independent reproductive units that is rarely found in the animal kingdom.

Importantly, females oviposit in old cells i.e. combs are used for more than one year. This behaviour contributes significantly to the reproductive efficiency in the species, increasing the potential for successful egg development (Itô & Higashi 1987).

A contributing factor in the success of the species is that the active nesting period is long; about 10 months in the northern parts of the range and about 8 months in the southern-most areas, which is longer than typical nesting periods for related temperate polistine wasps (Richards 1978). Most new foundresses are observed to reappear from dormancy at their natal nests in early spring (mid-August to mid-September) to quickly establish colonies by reusing existing nest combs for ovipositing. The pre-emergence stage, referring to the duration before the first adult brood appears, lasts around 3.5 months (Saito 2005).

In Tables 1 and 2, we quantified the three nesting styles that predominate in aggregation sites as well as in solitary sites. These nesting styles are as follows:

A) Pendent-plate nests

Often the pendent nests are in an irregular plate-shape, suspended from an overhead structure, such as the lip of a bridge. Plate-shaped nests typically develop to about 10-20 cells wide and 25-35 cells long, about 450 cells in total, but they can sometimes be as much as six times that size. The orientation is usually with the cells

laid horizontally (Figure 2A). This is the style most common on bridges over creeks between Sydney and Brogo in south New South Wales, for example the

aggregation at Cabbage Tree Creek, on the Kings Highway near Batemans Bay, NSW (Figure 4).

Figure 4. A Nest aggregation at Cabbage Tree Creek, NSW which is mainly pendent plate form nests. Photo credit: P. Warburton



B) Non-pendent plate nests

In most aggregated nest sites, there is a vertical surface that does not lend itself to pendent style combs. In these cases, the combs are attached in the plane of the substrate with multiple peduncles (Figure 2B). In some

cases, this is the predominant form in the aggregation. This type of aggregation, on more exposed flat surfaces, is more likely to be found in the northern parts of the range where it is the preferred style on highway overpasses and vertical rock faces (Figure 5).

Figure 5. An aggregation at Coffs Harbour which is predominantly non-pendent in style. Photo credit: L. Copeland



C) Pendent stick nests

Some pendent nests are more stick-like in shape, and they are found particularly in older, long-established nests. This is the result of a unique process of nest fission. In spring, new foundress females often use their mandibles to cut a prior season's nest-comb, dividing it into two or more independent nests. These reproductive gynes will often do this with subordinate female helpers (Tsuchida, 2022).

The fission of nests into new independent communities is handled with only limited conflict between the females; some pecking and barging but no obvious attempts to sting, confirming prior observations (Fukuda, 2003). This relatively moderate confrontational behaviour is key to the successful operation of such large, cooperative, multi-nest communities (Itô 1985).

Before the nest division, each principal egg-laying female and her subordinates occupy a distinct region of the same comb. These females gnaw at cells within the intermediate zones separating such "territories," eventually resulting in the division of the comb into

independent combs, which they simultaneously secure to the roof with new attachment peduncles (Figure 6). The formation of new nests via comb-cutting has been shown to account for as much as a third of the total increase in nest numbers. This unique form of colony fission has, so far, only been documented in *Ropalidia plebeiana* (Yamane, 1991; Makino, 1994; Oberprieler & Spradbery 2009).

Where nest expansion by fission of old nests predominates, this results in additional nests within the same confined space. The divided nests are longer and narrower than the original nest and there is only room to expand them by extending them in the vertical plane. The result is stick-like nests of variable dimensions but typically 6 to 10 cells wide and 10 to 30 cells long. At the same time, the other females that are starting new nests overwhelmingly do so within the perimeter of the existing aggregation area when there is any space to do so (Figure 8) and so are constrained by congestion into building stick nests that expand in the vertical plane. As time passes, older aggregations increasingly consist of stick type nests if the site has been spared from wind damage for an extended period (Figure 7).

Figure 6. Nest fission taking place. The yellow arrows show where females are dividing older nests. The nest division at the top of the photograph appears to be itself the product of a prior division that included the two segments above it. Photo credit: P. Warburton

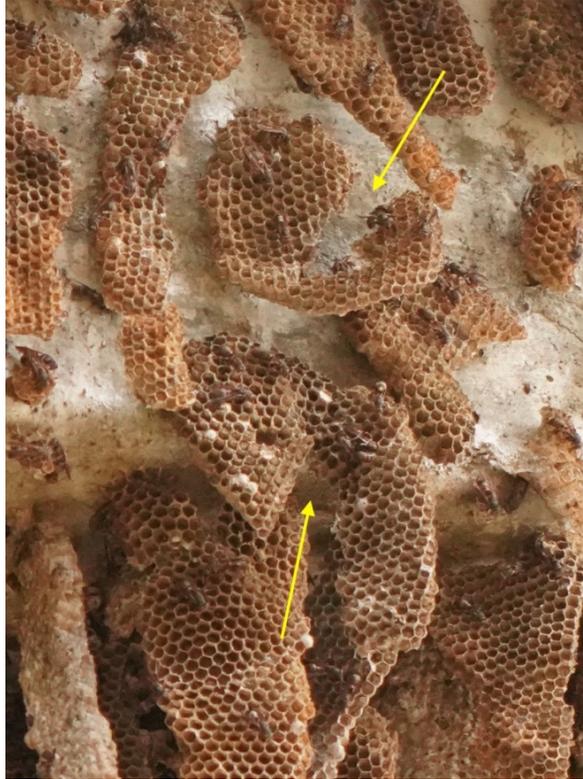


Figure 7. An older aggregation at Tahmoor, NSW with a predominance of stick-like nests. Photo credit: P. Warburton



Apart from wind damage, the nests are well suited to usage over more than one season. The combs are hydrophobic and resistant to water damage. In this study, one of the fallen (unoccupied) nests was immersed in water for 24 hours and then left to dry out. It suffered no visible damage to the structure, and the cells were completely intact.

Pendent stick nests also occur in solitary nest locations. An example is shown in an observation in Prestons, NSW (Figure 2C). Pendent stick nests are usually found in vegetation where there is only a single point of attachment and where obstructions such as twigs constrain development of the nest laterally.

Preference for Aggregated Nesting

Several contributing factors may account for the tendency towards aggregated nesting in *Ropalidia plebeiana*. Aggregations of nests may allow for shared communication about the location of food sources (Richards 1972). The joining of nests in an aggregation provides cooperative protection, for a species possessed of only limited defensive capability at an individual level, making aggregation a successful evolutionary strategy. Certainly, wasps from multiple nests, will fly out to attack any person who gets too close to the aggregation site (Lin and Mitchner 1972).

The species displays notable philopatry, with new adults typically nesting at their natal site. It has been theorised that, throughout the evolutionary history of *Ropalidia plebeiana*, nesting sites under cliff overhangs of a size that facilitates aggregation, may have been relatively limited, making the search for new sites a significant investment. Remaining at

known sites could thus have conferred a selective advantage. This pattern appears to persist even though suitable man-made structures are now more widely available (Itô, 1987). This innate behaviour of philopatry leads to pendent nest structures as the method of using the limited space to the maximum, until resource constraints lead to exploration of alternative sites.

We suggest that the historically limited number of rocky outcrops, that could sustain an aggregation, made this niche too small to support aggregation as an evolutionary strategy more widely in the social wasps.

Aggregated nesting sites in *Ropalidia plebeiana* wasps reflect the “selfish herd” instinct, as individuals prefer central locations in the aggregation for protection, leaving those on the edges at greater risk (Hamilton 1971; Itô 1988). The centripetal tendency to build well within the existing boundaries continues until available inner space is exhausted. At Tahmoor, about 95% of new nests in early spring were built within existing boundaries to fill gaps from lost nests. Similarly, Nelligen Creek saw early-season nest rebuilding focused within the existing aggregation perimeter, after a gale in late winter 2025 caused the loss of about 10% of the nests. (Figure 8).

The periodic abandonment of sites due to excessive wind damage is, in turn, increasingly likely as aggregations age, due to the greater vulnerability of the long, thin stick nests. These increase in prevalence over time due to the nest splitting and congestion within the perimeter of the aggregation.

Figure 8. New nest start-ups predominantly exploited gaps within the existing aggregation perimeter. Photo credit: P. Warburton



Nest city location

Historically, nest aggregations would have been found under overhangs on cliff faces. With the advent of man-made structures, bridges and other similar constructs are more plentiful and have also become preferred nest aggregation locations. Concrete or rock are the preferred substrates for anchoring nests with other materials only occasionally being used. In this study, 22 of the 42 aggregation sites were described as “medium” (100-300 nests) to “very large” (>500 nests) and all of these were attached to rock or concrete (though there were three of those sites that were mainly concrete but included a section of galvanised steel). Metal surfaces are not usually favoured – apparently because nests are more easily blown off when the attachment points are to these materials. Where metal surfaces are used, the nest aggregations are small, and the nests are usually located flush with the substrate with many peduncles used for attachment. On one of the bridges we studied at Nelligan Creek, a small section of steel girder was within the perimeter of the aggregation, the rest of the area being concrete. This area of nest aggregation on steel substrate was impacted disproportionately by wind damage. However, after the winds the wasps set to work to fill the gap, presumably with a future risk of them being blown down again. Apparently, the instinct for centripetal nest building over-rides the aversion for attaching nests to a smooth steel surface.

Botanic surveys indicate that, where there are large aggregations, the surrounding vegetation is consistently rich in flowering plants and provides ample food resources (Appendix 1). A large aggregation of wasps means competition for nectar resources for feeding and for prey resources for the larvae. A study of the site at Tahmoor in early spring revealed that most wasps feeding on nectar were found within 50 m of the nest site; none were found at 100 m from the site, despite the large population of thousands of wasps. This site was typically well provisioned with many flowering shrubs and trees, comprised of over a dozen species within the 50 m radius. Such well-provisioned sites are often available in the warmer northern regions and are fewer in the south of the species' range. Later in the nesting season, when the wasps focus more on finding prey insects for feeding larvae, wasps are found more widely looking for food in the surrounding area.

In the northern parts of the range, there is a clear tendency to nest on vertical surfaces, particularly on concrete bridges including highway overpasses, with non-pendent nests. By contrast, nests in the southern parts of the range tend to be pendent style.

To understand the reasons for the different styles across the range, it is essential to consider the reasons for the nest site development. We propose that the ethological mechanism for the development of aggregations is simply one of trial and error, coupled with complete abandonment of failed sites. Nesting locations are tried, and aggregations develop and become larger over time if the site is successful. Periodically there may be a catastrophic event that destroys a large part of the aggregation. When this occurs, the wasps often completely abandon the site and re-establish in a new location and try again.

The factors that contribute to a site being successful in the north differ from the ones that contribute in the case of more southern locations. In the south, well-sheltered locations with plentiful plant resources nearby are often bridges over creeks with a rich riparian habitat in a sheltered gully. Such sites are relatively scarce and high-density aggregations with pendent nests are prevalent.

Northern regions, with their warmer climates, offer more nesting sites near adequate food sources and these northern areas have more extensive highway infrastructure than the south, hence with more plentiful man-made nesting sites in the form of bridges. However, nests in the flat terrain associated with highway bridges are highly exposed to wind; pendent nests are usually destroyed, while sturdier, non-pendent nests, often attached to a vertical surface, survive. These surviving nests define nest aggregation perimeters and hence define where new nests are built; the wasps' centripetal instincts lead them to expand within the remaining site perimeter rather than into new areas, leading to a predominance of non-pendent forms of the nests.

Most independent solitary nests are amongst vegetation, for example under the shelter of leaves or a branch, and bushfires are a threat to such locations. The extensive 2019/2020 bushfires devastated much of the geographic range of the wasp (Figure 9). However, the preference for nesting in sheltered locations under concrete bridges and under rocky outcrops is clearly beneficial in mitigating fire impacts. In this 2025 study most of the decades-old nest aggregations in the Eurobodalla area of the New South Wales south coast, listed by Itô and Higashi in 1987, were still present and were thriving, despite this area being particularly impacted by the fires. For example, there are still two aggregations under a concrete bridge across Cabbage Tree Creek on the Kings Highway, NSW (Figure 4) that were studied in 1987.

The successful aggregation locations are usually ones that are sheltered from weather with an overhead roof. Usually there is a vertical structure, immediately adjacent to the aggregation site, to provide wind protection laterally. Additional adjacent structural elements, that add further weather protection, are clearly beneficial. Where aggregations are found on bridges, the nest is usually under the lip of the bridge and adjacent to a structural beam providing lateral wind protection.

A representative site is a bridge in Brogo on the far south coast of NSW. The structure provides wind

protection with concrete beams on two sides of the nests, and which also offers some shelter from frost. The location also offers wind protection arising from the local topography; the bridge is in a valley surrounded by hills on all four sides. Observations indicate no evidence of damage from strong gales which took place towards the end of the winter dormancy, and the nest aggregation at this site is large and thriving. The wind and frost protection offered by this location may account for its suitability at the southernmost extent of large nest aggregations (Figure 10).

Figure 9. National Resource Management (NRM) map of the areas of greatest fire intensity in the 2019/2020 bushfires showing the NSW south coast as particularly severely impacted (DAWE, 2020).

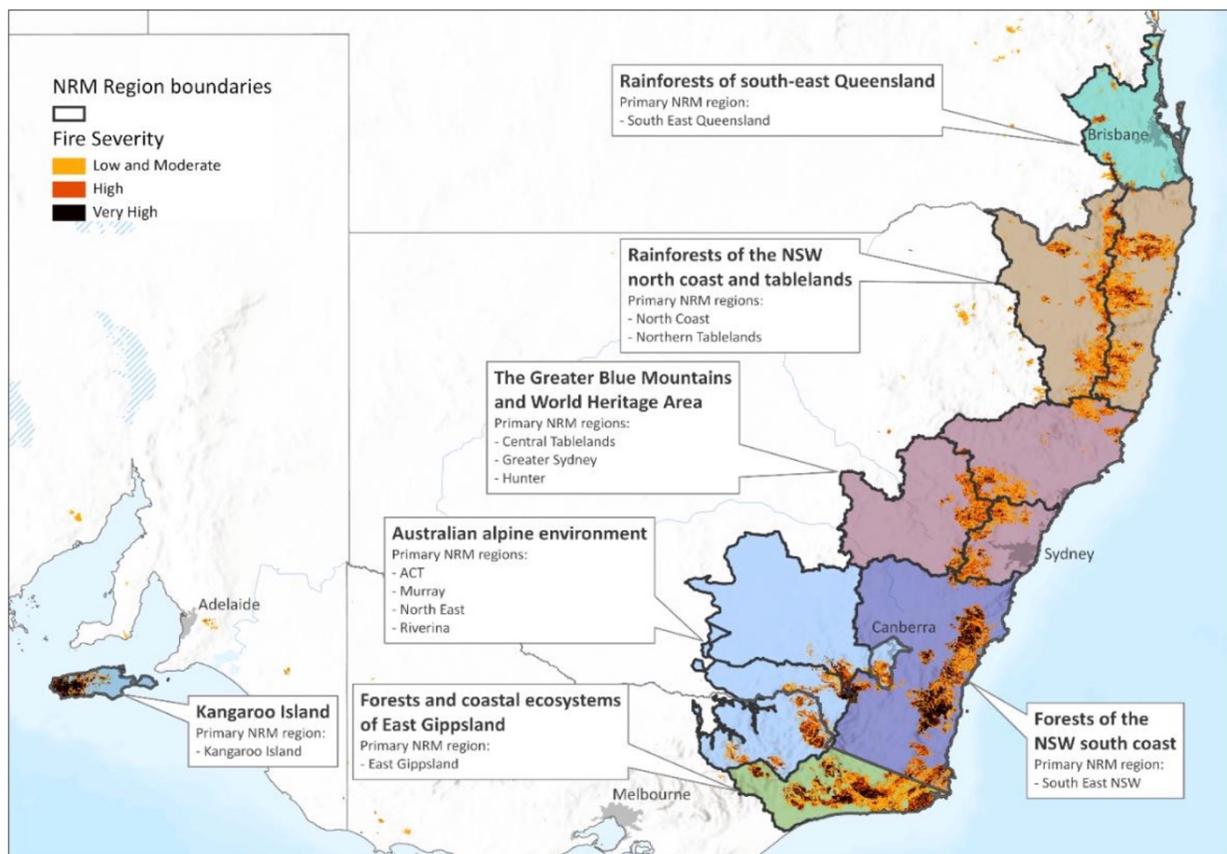


Figure 10. A particularly well sheltered site at Brogo, NSW. Photo credit: P. Warburton



Large nesting groups are mainly found in the northern range, with up to 2,000 nests, while the Australian Capital Territory has none and Victoria has only small aggregations. Solitary nests are more frequent in southern New South Wales and Victoria; 87% of the observations of solitary nests in public databases are south of the mid-point of the species range compared to 13% in the north. Aggregation size decreases further south, giving way ultimately to more solitary nests. Nesting patterns correlate with resource availability and climate.

City layout

Pendent nests near the city's edge are often seen to flap in the breeze, while those farther inside remain protected by outer nests.

The layout of the nests within the city often reflects the degree of wind exposure. Nests at the back of the aggregation and closest to a wind barrier, such as a concrete beam, are often the largest pendent nests. The

nests reduced in size towards the weather-exposed perimeter. In many cases, the pendent style of nests gave way to nests comprised of a single layer of cells in the plane of the substrate, where wind exposure was greatest. For sites that feature pendent nests, the result is a tiering of the nests progressively from the front to the back (Figure 11).

For sites with a high exposure to wind, pendent nests do not persist, and the non-pendent nest form predominates.

Threats to aggregated nesting sites

The main threat to the nests, particularly those at the peripheries of the wasp cities, is wind (Itô, 1987). Significant damage from wind was evidenced in several of the sites studied.

Attacks on the larvae by the ichneumonid parasitoid wasp *Arthula plebeja*, have been reported previously (Ubaidillah et al. 2009). This parasitoid wasp was photographed during our study, apparently for the first time, after it was reared from parasitised *Ropalidia plebeiana* larvae (Figure 12).

Figure 11. At Nelligen Creek - showing that the nests with the least exposure to weather are larger than nests near the perimeter. Photo credit: P. Warburton



Figure 12. The ichneumonid parasitoid, *Arthula plebeja*. Photo credit: P. Warburton



Most observed sites had some spider webs at the edges of the aggregations. In such cases, we observed that the nests with spider webs on them had been abandoned; a single web impacting as many as 6-8 nests. Up to 10% of the nests were abandoned in active aggregations because of spider webs. The spiders were clearly having a significant impact on the wasps confirming earlier reports where spiders were seen capturing wasps (Itô & Hignashi, 1987).

In the case of the Nelligan Creek aggregation, a whole aggregation site had been abandoned and was covered in extensive spider webs (Figure 13). We propose that the most likely explanation for the abandonment was excessive levels of spider webbing and spider activity. No other explanation was apparent as the nests were not significantly damaged. Whilst it is possible that the webs were constructed on the aggregation after abandonment, this seems implausible because there would not have been prey insects around the nests to warrant the spider investment in such extensive webs. This impact by the spiders is unusual as the predation relationship between spiders and wasps is generally asymmetric and favours the wasps. A likely explanation is that the spiders establish themselves with well-developed webs, prior to the wasp's emergence from the dormancy period and have some success in trapping wasps, making the location

worthwhile. The extensive webs provide the spiders sufficient protection to sustain this choice of a web location. The web style of these spiders indicates that they are probably in the *Badumna* genus.

A small spider was reared from the nests which blew down, emerging 23 days after the nests were collected. This was identified as *Intruda signata*. It is possible that this is a second species of spider that is preying on the wasps, though this may have been introduced after the nest fell to the ground. An adult dermestid beetle, *Anthrenus verbasci*, was also found in a fallen nest and was presumed to be feeding on nest material and contents. It is not known if these beetles represent a threat to nests that are in use, however dermestid beetles are a known threat to other hymenopteran nests (Motyka 2022).

The spider threat may be partially reduced by the presence of other wasps. Mud wasp nests, including those of Sphecidae like *Sceliphron*, were often found close to the paper wasp aggregations. These spider predators may benefit from some protection for their larvae by the proximity of the paper wasps, whilst the mud-dauber adult females contribute to constraining the number of spiders threatening the nests of *Ropalidia plebeiana*.

Figure 13. Extensive spider web encroachment of the abandoned aggregation site at Nelligan Creek. Photo credit: P. Warburton



Birds are also a threat to the wasps. For example, the Nelligen Creek site transitioned from dormancy to an active nest site in the period between the 10th and 12th of September 2025, coinciding with the arrival of Welcome Swallows from their migration. These swallows commenced the construction of about a dozen nests in the bridge structure. The birds were making continuous feeding flights around the wasp nest aggregation and certainly would have been making a significant impact on wasp numbers. A Grey Fantail was seen visiting the nests at Nelligen Creek.

The various threats faced by the nesting sites illustrate some of the reasons why the defensive strategies of aggregation and centripetal development have evolved.

Site abandonment

There are several instances where aggregation sites are completely abandoned following a catastrophic event. At Sheep Station Creek, an older aggregation had been abandoned following damage from inundation during heavy rain. Nelligen Creek had two old aggregations that had been abandoned, apparently due to wind damage and a third abandonment was possibly the result of excessive spider incursion. Gales appear to have impacted the aggregation at Tahmoor, causing a relocation of the aggregation to a new position on the bridge.

Eventually, after multiple relocations, a site is found where the risks are minimal, and the site is unaffected by any catastrophic event for an extended period. Some locations on bridges, for example, continue to have nest aggregations for years and even decades, with periodic relocations a few metres along the bridge.

The process of site abandonment appears to be an innate behaviour and an important component of the process for the development of aggregations sites. Over an extended period, the abandonment of unsuitable sites represents a selection process that eventually results in nesting sites with all the ideal characteristics to support large aggregations.

Some questions remain unanswered in this process and require further investigation. It is notable that there do

not seem to be any wasp stragglers that remain at the old nest aggregation sites. When a whole site is abandoned, what is the mechanism that causes the aggregation of wasps to collectively move elsewhere without exceptions? The answer may relate to the centripetal instinct. It maybe that when a majority leave, the remainers find their innate requirement to be at the centre of an aggregation - effectively a herd instinct - is no longer being met. Further study may clarify the mechanism in more detail.

CONCLUSION

Ropalidia plebeiana is an iconic species in temperate regions of Australia. It exhibits some remarkable characteristics in variability in its nest building. This study has clarified the nest behaviours over the full geographic range which had not been possible when the species was studied in the 1970s and 1980s.

The apparent plasticity in nest-type variability is a manifestation of several innate behaviours that are followed as rigidly as circumstances allow. The most important of these innate behaviours are:

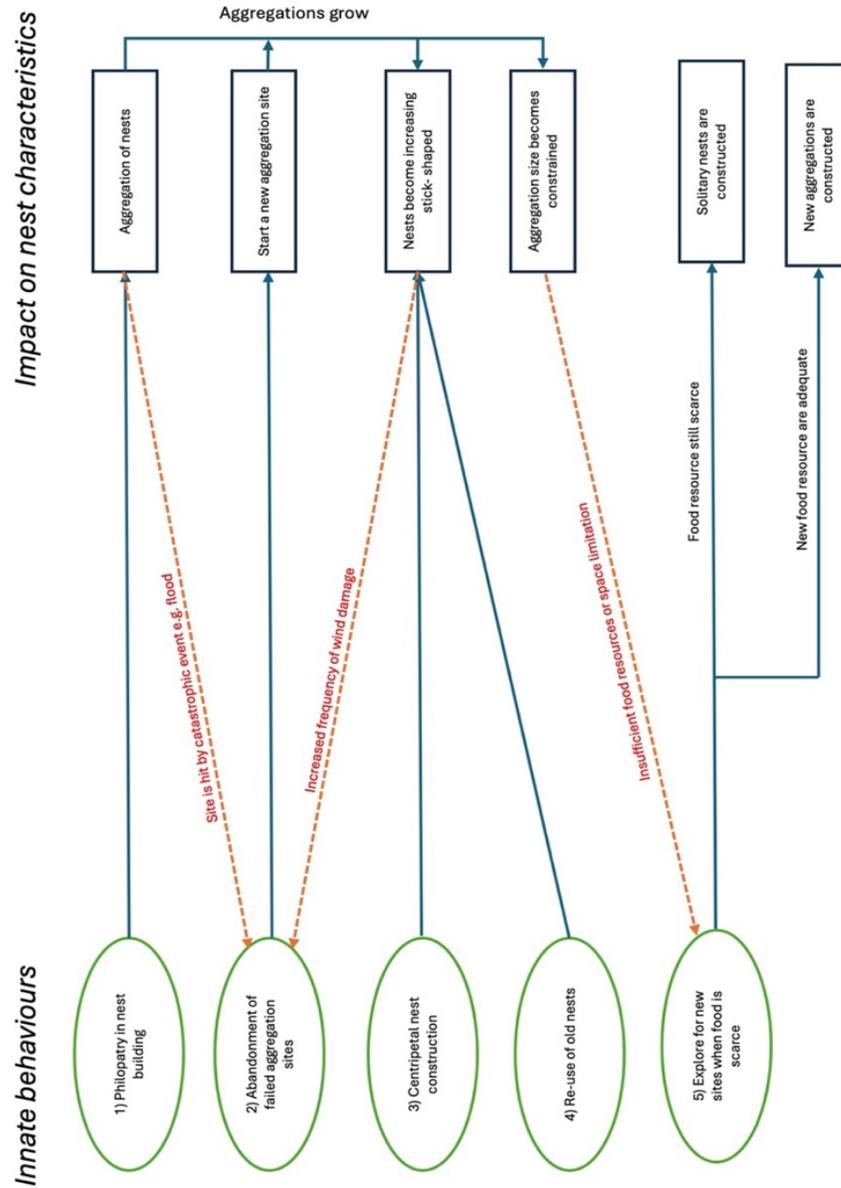
- * the instinct for philopatry in nest choices as the evolutionarily proven method for best dealing with the limited number of suitable sites,
- * the abandonment of a site when hit by catastrophe,
- * the instinct for centripetal nest building for protection,
- * the reuse of old nests when they are available, for reproductive efficiency, and
- * the need to seek new nesting sites when food resource constraints prevent natal site expansion.

These key innate behaviours impact on nest structure, size, location and its development pathway and these are summarised in Figure 14.

We propose that the different nesting styles are simply a reflection of the extent to which these innate behaviours can be acted upon, given the constraints of the wasps' local environment over time and across its geographic range.

Future studies may cast further light on these other innate behaviours that are part of the ethological mechanisms for nesting characteristics.

Figure14. The impact of innate behaviours on nest characteristics



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Appendix 1 – Survey of plants within 30m radius of the aggregated nesting sites

The botanical surveys can be summarised as follows:

Survey site 1 -Tahmoor, NSW

Many flowering plants including a dozen species within 30 m, particularly *Acacia decurrens* and *Acacia longifolia*. Other flowering plants at that location included: *Indigofera*, *Philotheca*, *Clematis*, *Hardenbergia violacea*, *Pomaderris*, *Pseudanthus*, *Dillwynia* as well as some introduced species such as *Senecio madagascariensis* and *Gerbera/Gazania*.

Survey sites 2,3 and 4 on the Pacific Highway in northern NSW

The main plant species flowering during the visit were introduced weeds (e.g. *Lantana camara* and *Ageratum houstonianum*) but there were plenty of native flowering plants (e.g. *Eucalyptus saligna*, *E. microcorys*, *Glochidion ferdinandi*, *Acacia melanoxylon*, *Callicoma serratifolia* and *Synoum glandulosum*) also present, within 30 m of the site, during the September survey and would flower well at other times throughout the year.

Survey site - 5 Brogo in south coast NSW

In the immediate vicinity there were *Acacia*, several *Eucalyptus* and *Casuarina* that were yet to flower and introduced species such as *Senecio madagascariensis* and *Trifolium*. There were a dozen or more flowering *Prunus cerasifera* bushes 100 m away.

Survey site 6 - Nelligen Creek, South Coast NSW

Acacia mearnsii, several *Eucalyptus* species, *Casuarina* spp., *Bursaria spinosa*, *Solanum aviculare*, *Myoporum bateae*, as well as some introduced species including *Acer negundo*, *Lilium formosanum* and *Prunus cerasifera*.

Survey site 7 - Jeramandra Creek, Mogo, South Coast NSW

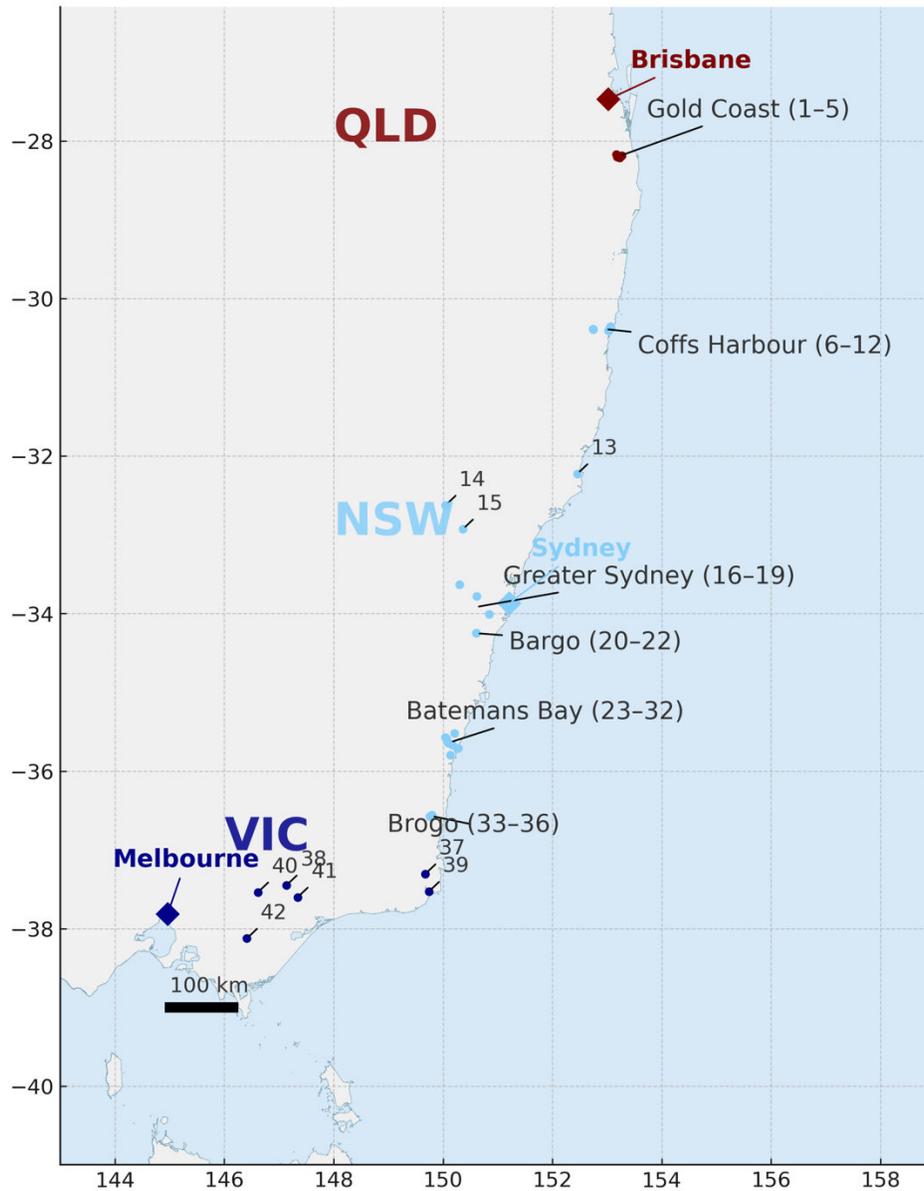
Acacia mearnsii, several *Eucalyptus* species, *Casuarina*, *Gaudium trinervium* and some weed species including *Solanum mauritianum*. There is a domestic garden 100m away with many cultivated flowering shrubs and smaller plants.

Survey site 8 - Lyons Rd overpass over Pacific Hwy, Coffs Harbour

The main plant species flowering during the visit were introduced weeds (e.g. *Ageratina adenophora*, *Ageratum houstonianum* and *Ipomoea cairica*) but plenty of native flowering plants (e.g. *Melaleuca quinquenervia*, *Polyscias sambucifolia*, *Pittosporum undulatum*, *Lomandra longifolia*) are also present within 30m and would flower well at other times throughout the year.

Appendix 2 – Aggregation locations that were studied (see also key below the map)

Figure 15. Aggregation locations (see key below).



Appendix 3. Solitary nest site locations

	Location	State	Latitude	Longitude
1	Binna Burra	Queensland	-28.169958	153.169206
2	Springbrook	Queensland	-28.186817	153.269502
3	Guanaba-Springbrook	Queensland	-28.187241	153.267439
4	Lamington National Park, Binna Burra	Queensland	-28.199550	153.182810
5	Nerrang	Queensland	-28.211660	153.233950
6	Lyons Rd Pacific Highway	New South Wales	-30.354597	153.063179
7	Bonville	New South Wales	-30.376288	153.067135
8	East Bonville	New South Wales	-30.385424	153.042517
9	Dorrigo Mountain	New South Wales	-30.387628	152.740750
10	Dorrigo Mountain	New South Wales	-30.394163	152.745536
11	Northbound Pacific Hwy Coffs Harbour	New South Wales	-30.407588	153.027441
12	Southbound Pacific Hwy Coffs Harbour	New South Wales	-30.408658	153.027571
13	Coomba Park	New South Wales	-32.226185	152.454800
14	Growee	New South Wales	-32.626147	150.044311
15	Wollemi	New South Wales	-32.928911	150.360977
16	Blackheath, Australia	New South Wales	-33.631857	150.304845
17	Near Red hands cave walking track. Blue Mountains	New South Wales	-33.779695	150.616897
18	Obscured	New South Wales	-34.010778	150.844855
19	Bargo River, Rockford Road Bargo	New South Wales	-34.249504	150.607112
20	Rockford Rd Bridge at Tahmoor,	New South Wales	-34.249589	150.607097
21	Rockford Rd Bridge at Tahmoor	New South Wales	-34.249589	150.607097
22	Bargo River, Rockford Road Bargo.	New South Wales	-34.249610	150.607204
23	Mogood	New South Wales	-35.520798	150.208314
24	Cabbage Tree Creek on Kings Highway (1)	New South Wales	-35.572795	150.040711
25	Cabbage Tree Creek on Kings Highway (2)	New South Wales	-35.572795	150.040711
26	Dinner Creek on the Kings Highway, Currawan	New South Wales	-35.591285	150.064419
27	Nelligan Creek Bridge on Kings Highway (1)	New South Wales	-35.641475	150.093876
28	Nelligan Creek Bridge on Kings Highway(2)	New South Wales	-35.641475	150.093876
29	Nelligan Creek Bridge on Kings Highway (3)	New South Wales	-35.641475	150.093876
30	Sheep Station Creek	New South Wales	-35.670084	150.173359
31	Honeysuckle Beach, Murrumurang	New South Wales	-35.710838	150.276425
32	Jeremandra Creek on the Princess Highway near	New South Wales	-35.795869	150.133981
33	Brogo , bridge over Alsops Creek on Hawks Head	New South Wales	-36.560541	149.799268
34	Brogo bridge over Alsops Creek on Hawks Head Rd	New South Wales	-36.560541	149.799268
35	Brogo (3)	New South Wales	-36.577283	149.762578
36	Domestic Porch, Brogo (4)	New South Wales	-36.577324	149.762560
37	Timbillica	New South Wales	-37.306579	149.674346
38	Hawkhurst	Victoria	-37.449134	147.137334
39	Mallacoota	Victoria	-37.530123	149.740175
40	Licola	Victoria	-37.538136	146.614766
41	Mitchell River	Victoria	-37.603000	147.339000
42	Yallourn North	Victoria	-38.125036	146.412214

Figure 16. Solitary nest site Locations

