Pollination biology of the sclerophyllous shrub
*Pultenaea villosa* Willd. (Fabaceae) in southeast
Queensland, Australia

JANE E. OGILVIE,1 JACINTA M. ZALUCKI and SARAH L. BOULTER
Centre for Innovative Conservation Strategies, Griffith University, Nathan, Queensland 4111, Australia

Abstract

The pollination biology of the common shrub *Pultenaea villosa* Willd. was examined in a subtropical dry sclerophyll forest in eastern Australia. We determined floral phenology and morphology, the timing of stigma receptivity and anther dehiscence, nectar availability, the plant breeding system, and flower visitors. The shrub’s flowers are typical zygomorphic pea flowers with hidden floral rewards and reproductive structures. These flowers require special manipulation for insect access. A range of insects visited the flowers, although bees are predicted to be the principle pollinators based on their frequency on the flowers and their exclusive ability to operate the wing and keel petals to access the reproductive structures. Nectar and pollen are offered as rewards and were actively collected by bees. Nectar is offered to visitors in minute amounts at the base of the corolla. In Toohey Forest, *P. villosa* flowers in spring and is the most abundant floral resource in the understory of the forest at this time. The breeding system experiment revealed that *P. villosa* requires outcrossing for high levels of seed set and that the overlap of stigma receptivity and pollen dehiscence within the flower suggests the potential for self-incompatibility.

Keywords: bees, dry sclerophyll forest, melittophily, Mirbelieae, self-incompatible.

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Introduction

The fabaceous tribe Mirbelieae is a large and diverse group of approximately 690 species in 25 genera that is endemic to Australia, except for two species that extend to Papua New Guinea and the Lesser Sunda Islands (Crisp et al. 2005). Species in this tribe are mostly ericoid shrubs that make up a conspicuous component of the understory in sclerophyll eucalypt-dominated open forest and woodland and in heath communities, to which they are largely confined (Crisp et al. 2005). The floral morphology among members of the Mirbelieae is remarkably uniform, consisting of mostly zygomorphic pea flowers that are yellow to orange in color, with reddish nectar guides and markings. The only exceptions appear to be species in the genera *Leptosema* and some species in *Gastrolobium*, where flowers are entirely red and elongated (Crisp 1994; Chandler et al. 2002; Crisp et al. 2005). Members in the Mirbelieae group appear to be largely self-incompatible, relying on animal pollinators to transfer pollen to compatible stigmas for successful seed set (six out of seven species in which the breeding system has been examined; Gross 1990, 2001; Young and Brown 1998; but see Rymer et al. 2002). In particular, the flowers appear to be mainly entomophilous and bees are the most frequent visitors and most likely pollinators (Beardsell et al. 1986; Gross 1992, 2001; Young & Brown 1998; Rymer et al. 2002, and see table 5 in Armstrong 1979). There are exceptions of course, for example, *Stonesiella (Pultenaea) selaginoides* (Hook. f.) Crisp & P. H. Weston is most likely to be pollinated by nitidulid and clerid beetles (Lynch 1999), and species in *Leptosema* and some species in *Gastrolobium* that have red elongated pea flowers are most likely to be pollinated by birds (Crisp et al. 2005), for example,


*Gastrolobium formosum* (Kippist ex Lindl.) G. Chandler & Crisp is pollinated by honeyeaters (Keighery 1984).

*Pultenaea villosa* Willd., a member of the Mirbelieae, is a perennial shrub that is common and widespread in the understory of dry sclerophyll forests of southeast Queensland and eastern New South Wales (Stanley & Ross 1983; Henderson 2002; Ryan 2003). In these fire-prone dry sclerophyll forests, *P. villosa* shrubs are killed during fire, but require the heat of fire to break through the hard seed coat of soil-stored seeds to trigger seed germination (Coutts 1987; Hill & French 2003). In the absence of fire, the shrub has a lifespan of 6–8 years, at which point populations begin to decline. As a result of this germination response to fire, *P. villosa* often dominates regularly burnt areas and can be a good indicator of fire frequency and time since fire at a site (Coutts 1987; Ryan 2003). Despite a good understanding of this aspect of the plant’s life history, nothing is known of its pollination biology.

In the present study, we describe the pollination biology of *P. villosa* in dry sclerophyll forest. Specifically we: (i) examine the floral morphology and determine the floral phenology at both the population and flower levels, including the timing of stigma receptivity and anther dehiscence; (ii) assess the availability of the nectar reward within flowers; (iii) measure the level of self-incompatibility by experimentally testing the plant breeding system; and (iv) observe flower visitors to evaluate likely pollinators.

**Methods**

**Study species**

*Pultenaea villosa* (Fabaceae: Faboideae: Mirbelieae) is a perennial shrub 1–3 m in height. The shrub has zygomorphic pea flowers that are axillary and yellow-orange in color, with reddish nectar guides at the base of the upper standard petal. The shrub flowers from autumn until spring, with its main peak of flowering in spring (Stanley & Ross 1983). *Pultenaea villosa* produces turgid pods containing one to two seeds (Stanley & Ross 1983).

**Study site**

We studied *P. villosa* during spring flowering and summer fruiting in 2006 in Toohey Forest, Brisbane, southeast Queensland, Australia, a remnant subtropical dry sclerophyll forest of approximately 640 ha. The area has a subtropical climate with summer dominant rainfall and an average annual rainfall of 1151 mm (Dale & Stock 1987). Four sites were selected that had substantial numbers of *P. villosa*; *Pultenaea Track*, Nathan, Toohey Ridge and Mimosa Ridge. All sites were characterized by woodland or open forest with the tree layer dominated by myrtaceous species in the genera *Eucalyptus*, *Corymbia* and *Angophora* (Coutts & Dale 1987). Botanical nomenclature follows that of Henderson (2002). All methods described hereafter were carried out at each of the four sites.

**Floral phenology and morphology**

The flowering phenology of the *P. villosa* populations at each site in Toohey Forest was monitored over the entire 2006 flowering season, from August until it largely ceased in November. A permanent transect, measuring 100 m in length and 10 m in width, traversing a representative area of the habitat was established at each site (Dafni 1992). The transects were visited every 2 weeks and the number of flowering individuals and open flowers per plant was counted.

The floral development of 102 *P. villosa* flowers from 20 shrubs (five per site) was followed from opening to senescence. Between three and seven buds from a branch on each shrub were individually labeled with numbered merchandise tags. Visitors were excluded from buds through the use of small plastic acetate exclusion cages covered with fine mesh bags (see Boulter et al. 2006 for the design). The progress of each bud was monitored daily in the morning and afternoon and was recorded as ‘closed bud’, ‘splitting bud’, ‘open flower’ or ‘senescent flower’. From this data an average measure of the floral lifetime, or floral longevity, was made. Accompanying notes were made of the position of the reproductive structures when they were visible, the wilting order of the floral organs, the presence or absence of odor, and any visible changes in the floral organs. At each visit the temperature and relative humidity were measured using a whirling psychrometer (G. H. Zeal, London, England).

Floral longevity in hours was compared among sites using a general linear model *anova* with least squares means to account for unbalanced data; *ANOVAs* were carried out using the statistical program SAS (SAS Institute 2003). Type III sums of squares were used in the analysis (Sokal & Rohlf 1995).

The timing of stigma receptivity and anther dehiscence over the floral lifetime was determined by testing 255 flowers of varying known ages from five shrubs at each of the four sites. To test stigma receptivity the minute style was removed from the flowers, placed in a glass capillary tube and a 3% hydrogen peroxide solution was added to test for peroxidase activity (Kearns & Inouye 1993). The stigma was viewed under a field hand-held microscope and the presence of bubbling at the style tip was used to indicate stigma receptivity (Kearns & Inouye 1993). When the flowers were collected the number of dehisced anthers was recorded to determine the timing of pollen release and any possible overlap with stigma receptivity within the flower.
A further 80 labeled and bagged flowers were collected and placed in 70% ethanol 24 h after they had opened to obtain basic morphological measurements. After returning to the laboratory, the flowers were dissected and measurements were made of corolla length, style and stamen length, standard petal length and width, wing petal length, and corolla tube depth to obtain mean flower measurements.

**Nectar production**

The floral nectar of *P. villosa* was sampled to assess the volume and concentration of nectar available to floral visitors. Nectar was sampled from a total of 80 flowers, four flowers from five shrubs per site that were bagged prior to opening to exclude flower visitors. Individual flowers were numbered with merchandise tags and monitored for timing of flower opening and age. Nectar was allowed to accumulate for 24 h (Gross 1992) and at this point flowers were removed and immediately sampled. One microliter of water was placed at the base of the corolla tube to dilute the minute and viscous amount of nectar to enable extraction (Gross 1992). The solution was gently mixed and then extracted using a 10 μL microsyringe to calculate the volume of nectar. This solution was then placed on the surface of a hand-held 0–32% BRIX refractometer (Atago, Tokyo, Japan) for a reading of sugar concentration. The % BRIX measurement (or gram solute per 100 gram solution) was then converted to milligrams of sugar per flower (Bolten et al. 1979; Gross 1992). The nectar volume and sugar concentration per flower were compared among sites using a one-way ANOVA, after the sugar concentration data were transformed using a log(x + 1) transformation (Sokal & Rohlf 1995). After the initial analysis it was obvious that the nectar sugar concentration differed among sites and that this was most likely the result of a single shrub; thus, shrub identity was then included as a factor nested within site in a nested ANOVA.

**Plant breeding system**

To test for the level of self-incompatibility in *P. villosa* a set of six experimental treatments were applied, modified from the protocol proposed in Dafni (1992). These experimental treatments involved combinations of visitor exclusion, emasculation and hand pollination. Each set of six treatments was randomly split across two shrubs to ensure sufficient flowers, as *P. villosa* plants have only a few main branches. Three sets of treatments (six shrubs) each at Nathan and Mimosa Ridge and two sets of treatments (four shrubs) each at Pultenaea Track and Toohey Ridge were carried out. For each set of treatments, six budding branches were selected, an initial bud count was made and any open flowers were removed. The six treatments were as follows:

1. **Open pollination:** flowering branches were left open to natural pollinators and the flowers were unmanipulated.
2. **Spontaneous selfing:** flowering branches were covered with an exclusion cage and fine-mesh bag to exclude visitors and the flowers were unmanipulated.
3. **Induced selfing:** flowering branches were covered with an exclusion cage and fine-mesh bag to exclude visitors, and the flowers were emasculated and then hand pollinated with pollen from within the flower.
4. **Geitonogamy:** flowering branches were covered with an exclusion cage and fine-mesh bag to exclude visitors, and the flowers were emasculated before anthesis and hand pollinated with pollen from a few flowers on the same plant.
5. **Cross-artificial:** flowering branches were covered with an exclusion cage and fine-mesh bag to exclude visitors, and flowers were emasculated before anthesis and hand pollinated with pollen from a few flowers from different plants.
6. **Cross-natural:** flowering branches were left open to natural pollinators and flowers were emasculated with no supplemental hand pollination.

All flowers were visited daily and all open flowers received the allocated pollen. This continued until the last flower to open was pollinated twice. The flowers were visited 2 months later and the presence of a developed pod was used to indicate successful pollination and the seeds within each pod were collected and counted. The proportion of flowers setting fruit was compared among the six treatments, four sites and plant identity within sites using a general linear model ANOVA with least squares means to account for unbalanced data and a Tukey–Kramer test to pinpoint the differences. The proportional data were arcsine transformed using a modified version of the Freedman and Tukey arcsine transformation recommended by Zar (1999). Type III sums of squares were used in the analysis (Sokal & Rohlf 1995). In addition, we calculated the mean seed : ovule ratio for open-pollinated flowers.

**Flower visitors**

We documented visitors to flowers during observational surveys conducted in September and October 2006 on clear and warm days between 0900 and 1700 hours. Each flowering shrub was observed for 10 min and every visitor was identified as it visited the flowers. A record was made of the number of flowers visited and the time spent at the plant by each visitor. To distinguish pollinators from flower visitors, additional notes were made on whether the visitor sipped nectar, collected pollen and...
touched the stigma. Visitors were collected when possible with a hand net and killing jar for later identification. At each observation period the temperature and relative humidity were measured using a whirling psychrometer (G. H. Zeal). Voucher specimens of the bees collected were lodged at the Queensland Museum. In this paper, we only present data on the identity of the visitors. Further analysis of the density dependence of pollinator visitation will be made in a later paper.

Results

Floral phenology and morphology

The *P. villosa* populations in Toohey Forest commenced flowering in the middle of August and continued until mid-November in 2006 (Fig. 1). The main peak of flowering occurred in early to mid-October and the pattern of flowering was similar among sites (Fig. 1).

*Pultenaea villosa* flowers opened in the morning and remained open for approximately 3 days (70 ± 1 h [mean ± standard error], across sites). Floral longevity did not differ significantly among the sites (one-way ANOVA, *P* > 0.05). On opening, the standard petal would pull up from the wing and keel complex and come to rest perpendicular to it. Throughout the lifetime of the flower the style and stamens would remain enclosed within the keel and wing complex and were only exposed when insects manipulated the petals open. The flowers produced no scent detectable by nose. On senescence, the standard petal was the first to drop, followed by the wing and keel petals, and finally the stamens. The style remained and if successfully pollinated and fertilized became part of the seed pod. Each flower had two ovules with up to two seeds produced per pod.

The yellow-orange corollas (6.32 ± 0.08 mm in length) were composed of an upright standard petal (4.61 ± 0.07 mm in length and 5.35 ± 0.09 mm in width) often with reddish nectar guides at the base, two lateral wing petals (4.93 ± 0.08 mm in length) that enclosed two fused keel petals, together the wing and keel complex that concealed the gynoecium and androecium. The corolla tube measured 2.35 ± 0.04 mm in depth. Within the wing and keel complex, 10 free stamens encircled the style with anthers and stigma held closely together just below the tip of the petals (Fig. 2). The stamens were of varying lengths around the style (the shortest was 4.29 ± 0.10 mm and the longest was 6.07 ± 0.50 mm) and the style measured 5.60 ± 0.10 mm in length; that is, the style and the longest stamens were similar in length. Receptivity testing indicated that the stigma was usually receptive at bud splitting (approximately 12–24 h before flower opening), and remained receptive, in general, until senescence (Fig. 3). Pollen was released from longitudinal slits in the anthers and the majority of anthers were dehisced at flower opening and were entirely dehisced within 6 h of opening (Fig. 3). The timing of stigma receptivity and anther dehiscence overlapped within the flower.

Nectar production

Nectar was produced in minute amounts by *P. villosa* and was located at the bottom of the corolla tube around the base of the androecium and gynoecium. Some flowers sampled had no detectable nectar present. After 24 h, the mean nectar volume per flower across the sites was 0.93 ± 0.03 μL and this amount did not differ among the four sites (one-way ANOVA, *P* > 0.05; Fig. 4a). The sugar concentration of the flowers was also low and varied greatly, ranging from 0 to 0.16 mg of sugar per flower with a mean of 0.019 ± 0.003 mg or 2.06 ± 0.45% BRIX across the sites. The sugar concentration per flower was similar among the sites (nested ANOVA, *P* > 0.05; Fig. 4b), but the sugar concentration differed among shrubs within sites; these differences arose from a single shrub at Toohey Ridge with a high nectar sugar concentration (nested ANOVA, *P* = 0.0003).

Plant breeding system

Approximately 28% of *P. villosa* flowers were successfully pollinated and produced pods when left open to natural vectors (Fig. 5). The mean seed : ovule ratio for flowers set in the open-pollination treatment was 0.84 ± 0.04. The proportion of fruit set in all within-plant pollination treatments, that is, induced selfing, geitonogamy and spontaneous selfing, was significantly lower than the remaining cross-pollination treatments (two-way ANOVA, *P* < 0.0001...
and Tukey–Kramer tests, $P < 0.05$). The pollination success of flowers from the cross-natural treatment did not differ significantly from the open-pollinated flowers, indicating that emasculation had no adverse effect on pollination. Flowers cross pollinated artificially had significantly lower fruit set than open-pollinated flowers, but a similar fruit set to cross-natural flowers (Fig. 5).

**Flower visitors**

*Pultenaea villosa* plants were visited by a total of 324 insects during 30 h of observations. Visitors to *P. villosa* flowers were from a diverse range of taxonomic groups, including bees (both social and solitary), wasps, ants, beetles, flies and hard bugs (Table 1). Many of these
insects were infrequent visitors. All bees (superfamily Apoidea) combined were by far the most frequent taxonomic group of visitors. Only a select few of the flower visitors were able to gain access to the hidden rewards and reproductive structures of the *P. villosa* flowers and therefore be potential pollinators. For example, the muscid flies, wasps, ants, chrysomelid beetle and bug observed crawled over the flowers without contacting the reproductive structures. Buprestid beetles were often seen eating the petals. The bombyliid flies hovered above the flowers, attempted to land and often inserted their proboscis down at the base of the standard petal. In addition, early on in the flowering season, thrips were observed in the keel of the flowers (J. E. Ogilvie, pers. obs., 2006).

Eleven bee species were observed on the flowers. Five of these species were common visitors, whereas the remaining visitors were rarely observed (Table 1). The introduced European honeybee *Apis (Apis) mellifera* Linnaeus (Apidae) was by far the most frequent visitor, accounting for 54% of bee visits (Fig. 6). The remaining common bee visitors (observed on more than two occasions) were native solitary bees from the family Halictidae, including *Lipotriches (Austronomia)* sp. 1, *Lipotriches (Austronomia)* sp. 2, *Lasiosglossum (Chilalictus) convexum* Smith (Walker 1995), and the native social bee *Trigona (Heterotrigona) carbonaria* Smith from the family Apidae (Fig. 6).

Bees were the only visitors capable of manipulating the lower petals open. The larger bees would alight on the wing and keel complex and insert their proboscis down below the standard to sip nectar. In this action the keel would move downward and the reproductive column would stay fixed so that the anthers and stigma would become exposed. Using force and with the action of their legs the bees could collect pollen. After suitable rewards were collected the bees would pull away from the flower and the keel would retract back to its original position. Smaller bees, more specifically *T. carbonaria*, foraged at the tip of the flowers by prying the petals open to collect pollen and contact the stigma.

**Discussion**

*Pultenaea villosa* presented a typical set of floral traits associated with bee pollination or ‘melittophily’ (Fægri & van der Pijl 1979), which are traits also typical of the Mirbeliaceae tribe (Crisp et al. 2005). The flowers have striking yellow-orange petals, diurnal anthesis, nectar guides, offer pollen and nectar rewards, and produce nectar at the base of the corolla (Proctor & Yeo 1972; Fægri & van der Pijl 1979). Bees were certainly common flower visitors, but for flower visitors to be considered likely pollinators they must demonstrate the ability to both actively collect pollen and contact the stigma when visiting the flowers. In the case of *P. villosa*, the morphology of the flowers meant that not all observed visitors could achieve this. Pollinators need to be capable of operating the wing and keel complex to access the concealed reproductive struc-
tures, which requires a great amount of force (Westerkamp 1997). In general, bees appear to be the only visitors capable of applying the force needed to access flowers of this form (Fægri & van der Pijl 1979; Westerkamp 1997), and indeed bees were the only visitor capable of operating the flowers of *P. villosa*. This suggests that there is a morphological ‘match’ between bees and these particular pea flowers (Waser 1983). Once it landed on a flower, a bee would force itself into the flower to forage and in doing so it would depress the wing and keel complex to expose the stamens and style, which would contact the ventral side of the bee. After the bee departed, the wing and keel complex would spring back into its original position. This pollination mechanism, which we observed in *P. villosa*, is known as ‘tripping’ and is the most basic and widespread pollination mechanism in pea flowers (Fægri & van der Pijl 1979; Arroyo 1981; Westerkamp 1997).

On the part of the flower, concealing the reproductive structures maximizes the conservation of pollen and nectar. However, the trade-off is that it requires special manipulation on the part of the flower visitor to gain

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Mean no. individuals per 10 min</th>
<th>Total no. individuals during 30 h of observation</th>
<th>Collect pollen</th>
<th>Sip nectar</th>
<th>Contact stigma</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apis mellifera</em> (Apidae)</td>
<td>0.817</td>
<td>147</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Trigona carbonaria</em> (Apidae)</td>
<td>0.089</td>
<td>16</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Lasioglossum (Chilalictus) convexum</em> (Halictidae)</td>
<td>0.139</td>
<td>25</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Lipotriches (Austronomia) sp. 1</em> (Halictidae)</td>
<td>0.372</td>
<td>67</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Lipotriches (Austronomia) sp. 2</em> (Halictidae)</td>
<td>0.067</td>
<td>12</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Unknown solitary bee sp. 1</td>
<td>0.005</td>
<td>1</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Unknown solitary bee sp. 2</td>
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<tr>
<td>Unknown solitary bee sp. 3</td>
<td>0.005</td>
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<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Unknown solitary bee sp. 4</td>
<td>0.005</td>
<td>1</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Unknown solitary bee sp. 5</td>
<td>0.011</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Hyleoides</em> sp. (Colletidae)</td>
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<td>1</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Family Vespidae</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Family Formicidae</td>
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<tr>
<td>Family Buprestidae</td>
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<td></td>
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<tr>
<td>Family Chrysomelidae</td>
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</tbody>
</table>

+, indicates that the specified action was consistently performed by that flower visitor; –, indicates that the action was performed occasionally, but not at all visits to flowers by that flower visitor.

**Table 1** Flower visitors by taxonomic group to *Pultenaea villosa* during 10-min observations of shrubs throughout the day.

**Fig. 6** Pollinators at flowers of *Pultenaea villosa*. (a) *Apis mellifera* (Apidae), (b) *Trigona carbonaria* (Apidae) and (c) *Lipotriches (Austronomia)* sp. 2 (Halictidae). Scale bar = 5 mm.
access to the floral rewards and reproductive structures (Arroyo 1981; Westerkamp 1997). Although this might not always be the case. In the legume *Anthyllis vulneraria* subsp. *vulgaris*, *Bombus* spp. are nectar robbers and access nectar illegitimately by avoiding ‘proper’ manipulation of the flower, yet they still promote legitimate pollination (Navarro 2000). Despite such an exception, it is expected that by imposing a mechanically constraining morphology, the flower will restrict access to particular, although supposedly more effective, flower visitors (Heinrich 1975; Tucker 2003). Providing that visitors are flower constant (Chittka et al. 1999), this pollination mechanism is believed to promote outcrossing (Faegri & van der Pijl 1979; Arroyo 1981; Westerkamp 1997). It would be an interesting exercise to test the hypothesis that the wing and keel complex of the pea flower restricts access to more effective pollinators by removing the keel of the flowers and comparing flower visitation, visitor composition and the subsequent seed set of these flowers to intact flowers.

*Pultenaea villosa* is a xenogamous plant, that is, it requires the services of pollinators to transfer and deposit pollen among plants for high levels of pollination and seed set. Although stigma receptivity and anther dehiscence overlapped within the hermaphroditic flowers, making selfing a physical possibility, the breeding system experiment revealed that very few seeds are set from self-pollen. This suggests the presence of a biochemical self-incompatibility mechanism (Dafni 1992). It is possible, however, that maximal pollen germinability could have occurred after anther dehiscence and hence after stigma receptivity within a flower (Navarro 1997). However, we regard this dichogamy unlikely because very little seed was set from flowers hand pollinated with self-pollen. Self-incompatibility in *P. villosa* is supported by the prevalence of self-incompatible species in the Mirbelieae, with most published accounts of plant breeding systems finding a reliance on pollen vectors to effect seed set (Gross 1990, 2001; Young & Brown 1998; but see Rymer et al. 2002).

Both pollen and nectar were offered by *P. villosa* as floral rewards to flower visitors. Nectar was produced in very small amounts and at low concentrations by the flowers so that the amount of sugar available for foraging visitors was minute. The production of nectar by flowers present suggests that nectar was still a valuable reward and that the plant is likely to be an important source of floral resources for anthophilous insects, in particular bees, at this time of year. Although pollen was not quantified in the present study, it is likely to be an important reward collected by foraging bees, as female solitary bees and worker social bees forage for both nectar and pollen to provision their nests.

Floral morphological differences in plants are often found in different populations and in different habitats for the same species (e.g. Ehlers et al. 2002). In the present study, no such differences were found across populations. The floral morphology of *P. villosa* was consistent across all sites. The only difference detected was the concentration of sugar at one site. This difference, however, can be directly attributed to one individual shrub, which had nectar of a high sugar concentration. The reasons for this individual’s high nectar sugar concentration are not known, but might relate to localized effects. To determine if the floral characteristics of *P. villosa* are consistent throughout the distribution of this species, further comparative studies are needed, but we believe that the data presented here is representative of this species.

The present study has demonstrated that *P. villosa* is dependent on pollinators for seed set and that bees are likely to be the only visitors capable of effecting pollination. The *P. villosa* populations studied in Tooloom Forest exist in an already fragmented system and the introduced honeybee (*Apis mellifera*) is a common flower visitor. Fragmentation and introduced pollinators are known threats to the pollination success of native plants (Goulson 2003; Tscharntke & Brandl 2004); however, it is difficult to speculate on the possible impact of either of these processes on the *P. villosa* populations examined without knowledge of the pollination condition prior to their establishment.

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