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The pollination ecology and reproductive success of the Australian shrub *Grevillea macleayana*

Samantha M. Lloyd
University of Wollongong

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**The Pollination Ecology and Reproductive Success of the
Australian shrub *Grevillea macleayana***

**A thesis submitted in fulfillment of the requirements for the award of the
degree**

DOCTOR OF PHILOSOPHY

from the

UNIVERSITY OF WOLLONGONG

by

Samantha M. Lloyd

SCHOOL OF BIOLOGICAL SCIENCES

2006

Certification

I, Samantha M. Lloyd, declare that this thesis, submitted in fulfillment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Samantha Lloyd

6th April 2006

"To describe different groups of plant, Linnaeus had used extraordinary terms like 'bridal chamber' and 'nuptials'. For prudish Britons, this sexualized version of nature verged on the pornographic, and battles over botanical textbooks resembled current debates about allowing children to watch violent videos. Self-appointed moral guardians of society declared that they wanted to protect young women from the corrupting influences of botanical education" (Fara, 2003)....

Fortunately they failed!

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Abstract

Theory predicts that plants that are more attractive to pollinators (via greater floral rewards) should have greater reproductive success, produce higher quality seed, and hence have greater fitness. Within a species, we assume that competition for effective pollinators is more intense because plants look the same, and thus, attracting pollinators may be more difficult. Moreover, plant-pollinator systems are highly variable and, in Australia, they have been subject to disruption by habitat fragmentation and the introduction of the European Honeybee. Ultimately, some individuals within a population will be more fit than others, however, there is little empirical evidence on the relationships between floral traits and plant fitness. This study examines the links between floral rewards, pollinator foraging behaviour, reproductive success, plant mating system parameters, and some non-reproductive plant traits and environmental variables, in an Australian woody shrub.

Variation may be evident in five primary components of plant-pollinator systems: (1) floral traits (e.g. flower, nectar, and pollen production); (2) pollinator foraging behaviour (e.g. insects, honeyeaters, and mammals); (3) reproductive success (e.g. pollen transfer, seed production and viability); (4) plant mating system and genetics (e.g. self-compatible species with low outcrossing rates) and (5) non-reproductive plant traits and environmental variables (e.g. plant size and density, climatic conditions). Our current understanding of the extent of intraspecific variation within these variables and how these variables interact within pollination systems is poor. This study quantifies intraspecific variation among *Grevillea macleayana* plants in each of these five components of the plant-pollination system, using three sites studied over three years. The broad aims are to: (1) quantify variation among plants in characteristics conferring attractiveness to pollinators (floral traits), pollinator foraging behaviour, reproductive success, and mating system variables and (2) determine how these components are related, and identify the interactions most important in explaining variation among plants.

Grevillea macleayana is a rare, hermaphroditic, bird-pollinated, medium to large shrub, with a large floral display. It has a fragmented distribution on the south-east coast of NSW, Australia. *Grevillea macleayana* is self-compatible and has low genetic diversity. It is visited by a suite of potential pollinators including honeybees,

honeyeaters, and the Eastern Pygmy Possum. However, evidence suggests that honeybees do not facilitate pollen transfer.

I quantified variation among *G. macleayana* plants in three floral traits: monthly inflorescence number; nectar production (i.e. volume per inflorescence and sugar concentration); and pollen production. I found substantial variation among plants in inflorescence production at every site. At each site, a small number of plants (three to five) produced over half the inflorescences for the study plants (19 in total), over the survey period. I also found significant variation among plants in nectar volume, but less variation in nectar sugar concentration. I did not detect significant variation among plants in pollen production. These results were consistent with previous studies on other Proteaceae species and provide evidence that floral display and nectar production are the most important floral rewards.

I quantified variation among plants in four aspects of honeybee and honeyeater foraging behaviour: the number of honeybees and honeyeaters; the number of inflorescences visited per plant; the foraging time per inflorescence; and the foraging time per plant. I found significant variation among plants in at least one feature of honeybee and honeyeater foraging behaviour, for one or two survey seasons per site. Contrary to the expectation that all pollinators will respond positively to similar floral traits, there were very few similarities between honeybees and honeyeaters in how they responded to variation in floral characteristics. These results provide some evidence that honeybees and honeyeaters may be responding differently to variation in floral cues and rewards.

I quantified variation among plants in two aspects of female reproductive success: monthly seed number, and nocturnal and diurnal pollen deposition. Plants varied substantially in seed numbers over the study period. Moreover, at each site, a small number of plants contributed to more than half the seed production of the survey population. I detected very low seed-to-inflorescence ratios, and these varied substantially among plants. However, plants with greater inflorescence numbers also had greater reproductive success (maternal seed numbers). Interestingly, there were no significant differences in pollen deposition between diurnal and nocturnal surveys, at two of the three sites. This result indicates that nocturnal pollinators may have an important role in pollinating *G. macleayana* plants.

I quantified variation among plants in two aspects of the *G. macleayana* plant mating system, using six microsatellite loci: family outcrossing rates (i.e. calculated for individual adults and their seed); and levels of biparental inbreeding for outcrossed seed. I found very low outcrossing rates across all families, and some plants were significantly different from zero and from each other. I also found very low biparental inbreeding rates across all families. The very low family outcrossing rates detected in this study indicates that whilst this is a mixed mating system, individuals are predominantly selfed.

I quantified variation among *G. macleayana* plants in six other non-reproductive plant traits and environmental variables that are likely to be related to plant vigour and hence, reproductive success: plant height, plant area, distance to nearest conspecific, canopy cover, leaf moisture content, and leaf photosynthetic yield. I found substantial variation among plants in height, area, and distance to nearest conspecific. I also found significant variation among plants in mean canopy cover, and slight, but significant variation among plants in leaf photosynthetic yield and leaf moisture.

Having detected significant variation among plants (in three populations) in the previously described five key components of pollination ecology, I then explored the strongest relationships among these variables. I used correlation and regression analyses to test for significant or consistent trends between dependent and independent variables. The most important trends in this system were:

- Significant positive regressions between inflorescence production (size) and nectar production (volume) and (non-significant) positive trends between inflorescence production and nectar production, suggesting no immediate trade-offs between resource allocation for inflorescence and nectar production.
- Numerous significant regressions between floral rewards (inflorescence and/or nectar production) and both honeybee and honeyeater foraging behaviour. These results support previous studies that have found greater numbers of pollinators or greater foraging activity associated with greater floral rewards.
- Significant positive correlations between seed production and both inflorescence and nectar production, suggesting: (1) no immediate trade-offs between resource allocation for floral traits and seed production, and (2) plants with greater floral rewards have greater reproductive success.

- Significant negative relationship between outcrossing rates and inflorescence numbers per plant. Plants with more inflorescences may be receiving more honeyeater visits (and within-plant activity), resulting in increased geitonogamous pollen movement and decreased outcrossing rates.
- Significant positive relationships between plant size (area or height) and both inflorescence and seed number, suggesting that larger plants may have greater carbon stores and resource availability.
- Significant negative regressions and (non-significant) negative trends between both inflorescence and seed number and canopy cover, suggesting that increased shade may reduce photosynthetic yield and resource availability for inflorescence and seed production.

The holistic approach used in this study has contributed to our understanding of intraspecific variation in plant-pollination systems and how this variation is related to plant reproductive success. Furthermore, my study has challenged some of the widely held beliefs about plant attraction to pollinators and added to our limited knowledge of some important plant processes (e.g. outcrossing rates) and their role in this pollination system. In trying to determine the most important relationships among the numerous components of the *G. macleayana* system, I have revealed a very complex plant-pollinator system. Whilst some of the relationships I found were as predicted, trends were not always consistent and it is clear that patterns of floral attraction, pollinator behaviour and reproductive success are not always intuitive.

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