

**BUZZING BEES AND THE EVOLUTION
OF SEXUAL FLORAL DIMORPHISM IN
AUSTRALIAN SPINY *SOLANUM***

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ABSTRACT

The flower morphology and reward availability of animal pollinated plants are intrinsically related to the foraging behaviour and preferences of their pollinators. However, it is often difficult to test how pollinator preferences may have helped to shape floral morphology because the morphology of many animal pollinated flowers is an adaptive compromise to optimise both male and female function. This may be overcome by studying the foraging decisions of pollinators in relation to flower morphology of species with unisexual flowers. The inherent difficulty of studying diclinous species is that in nearly all of these species the flowers of different sexes do not only differ in morphology, but also in reward type: male flowers offer pollen and possibly nectar, while female flowers offer nectar only.

Solanum is an ideal genus to investigate evolutionary links between pollinators and flower morphology for two reasons. First, it demonstrates a large variation in sex system with hermaphrodite, andromonoecious and dioecious species. The diclinous species of *Solanum* have evolved sexual dimorphisms involving floral size and the number of flowers per inflorescence. This variation allows the evaluation of floral morphology in a phylogenetically informed way. Second, pollen is the only reward, and is present in apparently equal amounts in both male and hermaphrodite/female flowers. This allows the investigation of sexual floral morphology in the absence of differences in reward type and amount. The genus *Solanum* is further suitable for such investigations because it relies for pollination on a relatively small number of buzz-pollinating bee species.

The main objective of this study was to examine how sexual dimorphisms in floral display and reward availability influence bee foraging behaviour, as this could lead to an understanding of the evolution of floral traits in association with changes in sex systems in the Australian members of *Solanum* subgenus *Leptostemonum*. To investigate this, buzz pollinating bees were tested for their responses to dimorphisms in three floral traits: corolla size, flower number and style length. Although *Amegilla murrayensis* had an initial preference for larger flower size, this preference quickly disappeared in the absence of differences in rewards among flowers. Clusters of flowers were more attractive than solitary flowers, even when the clustered flowers were smaller in size. In another experiment, *Amegilla chlorocyanea* showed no differences in the number of buzzes and time spent on each buzz between two floral morphs of andromonoecious *Solanum elaeagnifolium* that differed in their style length. Furthermore, foraging decisions by individual bees were analysed in relation to variation in pollen availability. *Amegilla chlorocyanea* showed no difference in the total number of times they buzzed pollen-full and pollen-empty flowers before they left the patch. However significant differences observed between first and second visits to flowers indicated that bees could perceive recent visitation by a bee and adjust their visitation behaviour.

Since an overall lack of support was found for the evolution of floral sexual dimorphism as a direct response to bee foraging preferences, a phylogenetic analysis was performed to investigate other possible explanatory models for the evolution of floral dimorphism in the diclinous species of *Solanum*. First, molecular phylogeny was inferred based on three gene region sequences of

71 Australian members of *Solanum* subgenus *Leptostemonum*. The analysis showed that the evolution of andromonoecy from hermaphroditism is most likely preceded by the evolution of large fruit, and thus the selection for large fruit size is the main driving force for the evolution and maintenance of andromonoecy in this group.

DECLARATION

I, Arthur Selwyn Mark, certify that this work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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