

Reproductive Biology of Pointleaf Manzanita (*Arctostaphylospungens*) and the Pollinator-Nectar Robber Spectrum

by Leif L. Richardson And Judith L. Bronstein

Mutualism is a biological phenomenon in which two species interact to their mutual benefit. A classic example is pollination, in which plants exchange a food reward (usually pollen or nectar) for pollen transport between flowers. Mutualisms are ubiquitous in nature, but so is their exploitation by organisms (often individuals of the mutualist species pair) that benefit from the exchange while not reciprocating with either partner. Despite their prevalence, theoretical models predict that these 'cheaters' should drive mutualisms to extinction because deriving a benefit without paying a cost should spread. How do mutualisms persist in the face of this pervasive exploitation?

Nectar robbing, in which flower visitors access nectar through holes torn in corolla tissue, either by themselves (primary nectar robbing) or by others (secondary nectar robbing), is a model system for studying exploitation of mutualism. Because this behavior is intrinsically damaging, it was long thought that nectar robbing must be detrimental to plants. However, many studies report either a neutral or even positive effect of nectar robbing on plant fitness. One reason that we do not fully understand how exploitation shapes mutualism may be that we have failed to appreciate the spectrum of outcomes for plants when they interact with apparently non-mutualist flower

visitors. Here we document a broad spectrum of potentially mutualistic and antagonistic behaviours by flower visitors. We report that many visitor species and even individuals employ flexible foraging strategies, and that nectar robbing may affect behaviour of apparent pollinators.



A female mason bee (Osmia species) foraging at manzanita flowers that have been previously nectar robbed. Photograph by Dorit Eliyahu.

We studied the mating system, pollination and nectar robbing of point-leaf manzanita (*Arctostaphylospungens*) in southern Arizona, USA in 1998-1999. Flowers of this plant are apparently adapted to pollination by long-tongued nectar feeders and pollen foragers who shake ("buzz") the anthersto release pollen. We found that the plant requires pollinators to set seed. We documented visits by 46

species, including hummingbirds, bees, wasps, flies and butterflies, although 12 species made up nearly all of our observations. The most common foraging behavior was 'legitimate' nectar collection, in which insects inserted their mouthparts through the floral opening, feeding in a way that could result in pollination. Five of the bees buzzed flowers for pollen, another behavior likely to cause pollination. Primary and secondary nectar robbing were pervasive, however, especially the latter, a behavior employed by more than 30 species of insects. In manzanita, neither nectar robbing behavior is likely to result in pollination. Many species employed two or more foraging

strategies, sometimes in the same foraging bout. Nearly all animals that foraged legitimately for pollen or nectar were also recorded as primary or secondary nectar robbers.

This study demonstrates that foraging behavior on flowers can be much more flexible than previously reported. A plant's mutualists may change behaviors in the presence of cheaters, and we predict that this indirect interaction effect could have profound consequences for plant reproduction. Theoretical and empirical studies of mutualism should consider the continuum of cooperative and antagonistic behaviors it may include.