

The birds and the bees

SIR — Many Loranthaceae mistletoes, including *Peraxilla* in New Zealand, have 'explosive' flowers which cannot open themselves; birds pop the buds open and pollinate them¹. However, a reduction in bird density has decreased visitation rates in some areas and depressed seed production in these plants². Here we report that tiny native solitary bees (*Hylaeus* sp.) can successfully prise open *Peraxilla tetrapetala* buds, which is to our knowledge the first documented case of an invertebrate opening an explosive, bird-pollinated flower. The bee is inefficient at pollen transfer, but still doubles the number of seeds ripened per flower. This example is an extreme case of ecological replacement of vertebrates by an invertebrate in a depauperate island fauna.

Peraxilla flowers are relatively large (27–42 mm); ripe buds open only with considerable force, from a beak or a human hand, for example. The main pollinators are honeyeaters¹: tui (*Prosthemadera novaeseelandiae*, mass 120 g) and bellbirds (*Anthornis melanura*, 30 g). Explosive flowers worldwide are usually bird-opened, exclusively so in the Loranthaceae³. Insect-tripped explosive flowers occur in several families, such as *Cytisus scoparius* (Fabaceae)^{4,5}, but there are no previous reports of any explosive flower that can be

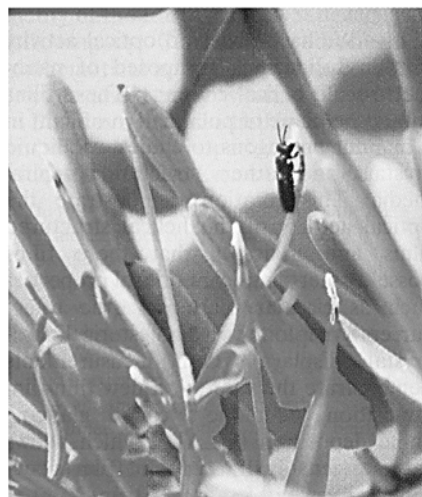
opened by both birds and insects.

We have observed native solitary bees (*Hylaeus* sp.; Hymenoptera, Colletidae) opening flowers of *P. tetrapetala* at two sites, Craigieburn and Lake Ohau. The small bees (body length 7 mm) are dwarfed by mistletoe buds (see figure), yet at Lake Ohau bees successfully opened about one bud in four by attacking the tip of the bud with their mandibles. This takes considerable effort and time (20–40 seconds), whereas tui open buds in 0.23 ± 0.06 seconds¹. As *Hylaeus* weigh only 0.01 g (1/3,000 of the bellbird mass) it is remarkable that they can open buds at all. Insect-explosive flowers like *Cytisus scoparius* are much more restrictive; bumblebees trip them easily, whereas slightly lighter honeybees have difficulty⁶.

Peraxilla stigmas are well placed to collect pollen from an approaching bird, but *Hylaeus* are pollen harvesters⁷ and are so small that they often do not touch the stigma, reducing pollination effectiveness. Our experiments on plants in the absence of birds show that bees cannot open *P. colensoi* flower buds, even though they visit flowers frequently. *P. colensoi* buds require more force to open than *P. tetrapetala*, and may be beyond the strength of these bees.

In contrast, bees open many *P. tetrapetala* buds inside our experimental wire-mesh bird-exlosures; significantly more of these opened flowers ripen a seed (see table). A few unopened buds set seeds by self-pollination in both *Peraxilla* species¹, but by opening *P. tetrapetala* buds *Hylaeus* doubles the fruit-set. As *Hylaeus* cannot readily contact the stigma, it could improve the fruit-set partly by giving other invertebrates access to open flowers. Introduced wasps (*Vespula* spp.) and honeybees (*Apis mellifera*) were present at all sites that we studied, but do not open *Peraxilla* flowers. These flowers are opened only by native animals (whether birds or insects).

New Zealand generally has unspecialized pollination syndromes⁸ and a depauperate fauna (there are no land mammals). This could explain why the only invertebrate known to open bird-adapted explosive flowers is found in New Zealand. Elsewhere, changes in pollinator availability in isolated



A native bee (*Hylaeus* sp.) harvesting pollen from the explosive-flowered mistletoe *P. colensoi* at Wakefield, New Zealand. Although the flowers are normally bird-opened, *Hylaeus* can open flowers of *P. tetrapetala*, but not *P. colensoi*. The bee is so small that it may not regularly contact the stigma in either species, but *P. tetrapetala* flowers opened by these bees do ripen more seeds.

populations may promote speciation via pollination syndrome shifts, like the one recently analysed genetically in *Mimulus*⁹. The tiny *Hylaeus* is an unlikely substitute for birds on large flowers like *P. tetrapetala*, yet we have found that in the absence of birds it can double seed production. Because habitat clearance and introduced mammalian predators in New Zealand have lowered both bird¹⁰ and mistletoe¹¹ densities, this small pollen harvester provides important conservation benefits.

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Fruit-set in *Peraxilla* under various pollination treatments

Pollination treatment	<i>P. tetrapetala</i>	<i>P. colensoi</i>
Unopened	16.3*	11.0*
Bee-opened, birds excluded	30.7†	not applicable
Hand-opened, birds excluded	48.2††	15.8†
Control, naturally opened	28.3††	35.4†
Hand-opened, hand-pollinated	66.3‡	not done
Residual variance (with residual d.f.)		
Model: Null	176.8 (34)	177.8 (17)
Plant	88.55 (27)	107.2 (12)
Plant, treatment	31.44 (23)	33.7 (10)
Probability (treatment)	< 0.001	< 0.001

Fruit-set is defined as the percentage of flowers ripening their solitary ovule. We carried out treatments in summer 1995–96 in the field at Craigieburn, Canterbury (43° 9.2' S, 171° 42.7' E) for *P. tetrapetala* and at Wakefield, Nelson (41° 25.5' S, 173° 2.5' E) for *P. colensoi*. Pollination treatments were as follows. Unopened: buds within wire-mesh bird-exlosures which remained unopened until petal abscission, see ref. 1; bee-opened, birds excluded: opened by bees within the enclosures; hand-opened, birds excluded: buds were opened with human pollen transfer minimized and left accessible to insects; controls: flowers accessible to birds and insects and naturally opened; hand-opened hand-pollinated: abundant outcross pollen but birds excluded. All treatments were replicated within plants as blocks ($n=6$ for *P. colensoi* and 7 for *P. tetrapetala*) and analysed for each species using a generalized linear model with binomial error and logit link function. In each species treatment was highly significant. Comparisons among means were done using *t*-tests on generalized linear model-generated means (and s.e.m.) for pairs of treatment groups; means within a species indicated by the same symbols (*†‡) do not differ significantly ($P > 0.05$).

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