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RESEARCH

# Moths can transfer pollen between flowers under experimental conditions

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**Abstract:** To be considered an effective pollinator, a floral visitor must not only be able to remove pollen but also transfer this pollen to a receptive conspecific stigma. While studies of diurnal pollination are commonplace, our understanding of the effectiveness of nocturnal pollinators is limited largely because of the difficulties of doing these studies at night. As a result of this, the way in which moths transfer pollen between flowers has been understudied globally, despite many authors suggesting they could be significant contributors to pollination. Here, we tested whether moths are capable of transferring pollen between flowers under experimental conditions using a fluorescent pollen-tracker powder. A flower-feeding taxon (Noctuidae: *Ichneutica plena*) and non-feeding taxon (Hepialidae: *Wiseana* spp.) were contained overnight with flowering shoots of putatively moth-pollinated *Leptospermum scoparium* and *Pimelea prostrata* (*I. plena* only), and putatively bird-pollinated *Crocosmia* × *crocosmiiflora*. Moths were able to transfer pollen tracker between flowers for both of the putatively moth-pollinated species, while no pollen tracker was removed from putatively bird-pollinated flowers. Both the feeding and non-feeding moth taxa were able to transfer pollen tracker between flowers; however, the feeding taxon could be considered a more effective pollinator because of the greater proportion of individuals both carrying and transferring pollen tracker compared with the non-feeding taxon. This study provides experimental evidence that moths may contribute to the pollination of *L. scoparium* and *P. prostrata*, and suggests a reassessment of the pollination ecology for these species is warranted.

**Keywords:** Lepidoptera, *Leptospermum*, mānuka, pollen transfer, pollination, New Zealand, *Pimelea*

## Introduction

Most flowering plants require animal visitors to facilitate pollination, but these visitors vary in their ability to transfer pollen between conspecific flowers (Krenn et al. 2005; Adler & Irwin 2006; Rader et al. 2011; King et al. 2013; Howlett et al. 2017). The removal of pollen without transfer to a conspecific's stigma is detrimental to a plant's overall fitness, through the loss of pollen and resources better utilised by other more effective pollinators ("Opportunity costs" Thomson 2003; Newstrom & Robertson 2005). Thus, quantifying the transfer of pollen is important when determining the effectiveness of a floral visitor. To date, studies on pollination systems in New Zealand have predominantly focused on birds and diurnal insects leaving the role of moths largely unexplored, likely due to the difficulty of conducting surveys at night (Newstrom & Robertson 2005; MacGregor et al. 2014; Robertson et al. 2020). While pollen adhering to moth bodies offers some of the strongest evidence of flower visitation, there is very little information available describing moth pollination and the way in which moths transfer pollen, making this a critically understudied area of research in New Zealand and globally (Buxton et al. 2018; van Zandt et al. 2019). Declines in pollinators are associated with a loss of the plants they interact with, therefore measuring pollen transfer—or the lack thereof—is important in light of conservation and evolution (Baker 1979; Thomas et al. 2004; Newstrom & Robertson 2005; Biesmeijer et al. 2006; Klein et al. 2007).

Pollinator quality (effectiveness of a floral visit) is an area of research that has received less attention than pollinator quantity (frequency of floral visits), likely due to pollinator quantity being substantially easier to record in the field (Fenster et al. 2004). One way of measuring the effectiveness of a pollinator is to quantify pollen transfer, i.e. the degree to which a floral visitor removes pollen from the anther of a flower and deposits it on a conspecific stigma (Herrera 1987; 1989). While pollen transfer itself does not guarantee successful pollination, which is still dependent on pollen viability and successful fertilisation, the ability of a pollinator to deposit conspecific pollen on conspecific stigmatic surfaces is an absolute first requirement for successful pollination to occur. Fluorescent dye particles, often referred to as pollen tracker, have been used as a proxy for pollen grains to quantify the effectiveness and likelihood of pollination across many different animal taxa including

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hummingbirds (Waser & Price 1982; Waser 1988; Rademaker & De Jong 1998), butterflies (Townsend & Levey 2005), bees (Waser 1988; Townsend & Levey 2005) and wasps (Townsend & Levey 2005). However, this method has not been used *in-situ* with moths to our knowledge, apart from a preliminary trial we conducted in subantarctic New Zealand (Buxton et al. 2019). Pollen tracker is easily detectable in minute quantities because of its fluorescent nature, and the transfer of the powder has been shown to be strongly and positively correlated with the transfer of pollen grains (Waser & Price 1982; Dudash 1991; Kearns & Inouye 1993; Townsend & Levey 2005).

The aim of this study was to determine if moths are capable of transferring pollen *in-situ* using pollen tracker as an analogue for pollen. This paper will address three questions:
(1) Can moths be documented removing pollen tracker from flowers under experimental conditions and transferring it to a conspecific stigma?
(2) Do feeding and non-feeding moth taxa transfer different amounts of pollen tracker?
(3) Where on the moth body is pollen tracker most commonly located?

## Methods

### Moth and plant collection

Heath moth traps were deployed in two private gardens in Dunedin, New Zealand, to capture moths for use in experiments. The captured moths were stored in a refrigerator at 4°C the following day and live moths were used in experimentation the next night; no moths were kept in the fridge for more than 12 hours.

Fresh flowers of all species were collected as close to the beginning of the experiment as possible, with all flowers used being collected within 1 hour of the beginning of each experiment.

### Study species

*Ichneutica plena* (Lepidoptera: Noctuidae), formerly *Graphania plena* (Hoare 2019), and *Wiseana* spp. (Lepidoptera: Hepialidae) were selected for experiments because of the contrast in their feeding and non-feeding adult life-histories, and because both species were locally abundant and readily identifiable. *Ichneutica plena* is a nectar-feeding moth endemic to New Zealand. All *Wiseana* species are endemic to New Zealand, but the adult moth has no functioning mouthparts and thus were not expected to be floral visitors. All species in the *Wiseana* genus are very variable in their wing patterning and often require microscopic examination to obtain accurate species-level identification (Hoare 2014), so will be referred to collectively as *Wiseana* hereafter.

We used three plant species in experimental trials: two were selected based on known or suggested associations with moths and one was selected as a negative control. The New Zealand endemic subshrub *Pimelea prostrata* (Thymeleaceae) is thought to be pollinated by moths to some extent (Burrows 1960). Inflorescences are composed of 3–10 white sweet-scented florets. The c. 3–4 mm long corolla of each floret is silky-hairy, with 1–2.5 mm long corolla lobes (Allan 1961). Moths have also been reported as pollinators for New Zealand mānuka *Leptospermum scoparium* (Myrtaceae) (Primack 1978; Stephens et al. 2005). *Leptospermum scoparium* is indigenous to New Zealand and Australia. In New Zealand, flowers are axillary or occasionally terminal on branchlets, sessile or nearly so, usually solitary and up to 12 mm in diameter or more (Allan 1961). Stamens are numerous, the receptacle is dark red–crimson–pink, and the five free petals are white or occasionally pink (de Lange 2021). *Crocosmia* × *crocosmiiflora* (Iridaceae) was used as a negative control in experimental trials because of local availability, flowers displaying adaptations for bird pollination, moths not being known to visit the flowers, and because the reproductive parts of the flowers cannot be reached by settling moths (Goldblatt & Manning 2006). *Crocosmia* × *crocosmiiflora* inflorescences are 15–30 cm long, cymose and 'zigzag' in shape (Healy & Edgar 1980). The flowers are solitary at each inflorescence node, with six perianth lobes c. 3 cm long, a narrow basal tube with an overall perianth diameter of 4–5 cm and orange–crimson coloured (Healy & Edgar 1980).

### Measuring pollen retention and transfer on moth bodies

For each replicate experiment, one live moth individual was placed in a purpose built 'moth cage' containing two flowering shoots from one plant species and left overnight in a room where blinds were drawn over windows to reduce interference from streetlights. The number of flowers on each shoot was not altered from what was naturally occurring and so varied between experiments but flowering shoots used in each comparison were selected to present approximately equal amounts of floral material. The cage measured L 15 cm × W 15 cm × H 19 cm (total volume of 4.4 L) and was a clear plastic container with a removable lid with ventilation holes in the corners (2 mm diameter). The flowering material was arranged as follows in each moth cage: two flowers/inflorescences were removed from the same species and placed in separate 30 mL universal jars with water. All flowers and florets had fluorescent dye particles (pollen tracker) applied to the anthers with a fine haired paintbrush, with flowers in separate jars having a different colour dye applied. Jars containing flowers were then placed in the moth cage c. 5 cm apart, ensuring that flowers in separate jars were not touching. The moths were then anaesthetised with $CO_2$, and one moth was gently placed in each moth cage. The moths were left in the cages for the duration of the night and anaesthetised with the use of $CO_2$ the following morning before being removed from the cage and euthanised in an ammonia killing jar. Moth bodies and flowers were examined with an ultraviolet light for the presence of pollen tracker. The number of times this experiment was run each night was based on the number of target moths that were caught the previous night and so varied between nights. Each cage was treated as a separate experiment, and in total *P. prostrata* was replicated 27 times, *L. scoparium* was replicated 33 times, and the negative control *C. crocosmiiflora* was replicated 43 times. Replicate number for each plant species differed due to the variability in the number of moths caught at the time each of these species were flowering.

### Statistical analysis

Analyses were performed with Statistix Analytical Software (v. 9.0). Pearson's Chi-Square was conducted to test for a difference in the number of moths in the two genera that were able to transfer pollen between flowers of *Leptospermum scoparium*. No such analyses were carried out on *Pimelea prostrata* as only one moth species was captured in Heath traps at the time of flowering. No analyses were performed on experiments involving *Crocosmia* × *crocosmiiflora* because all values equalled zero.

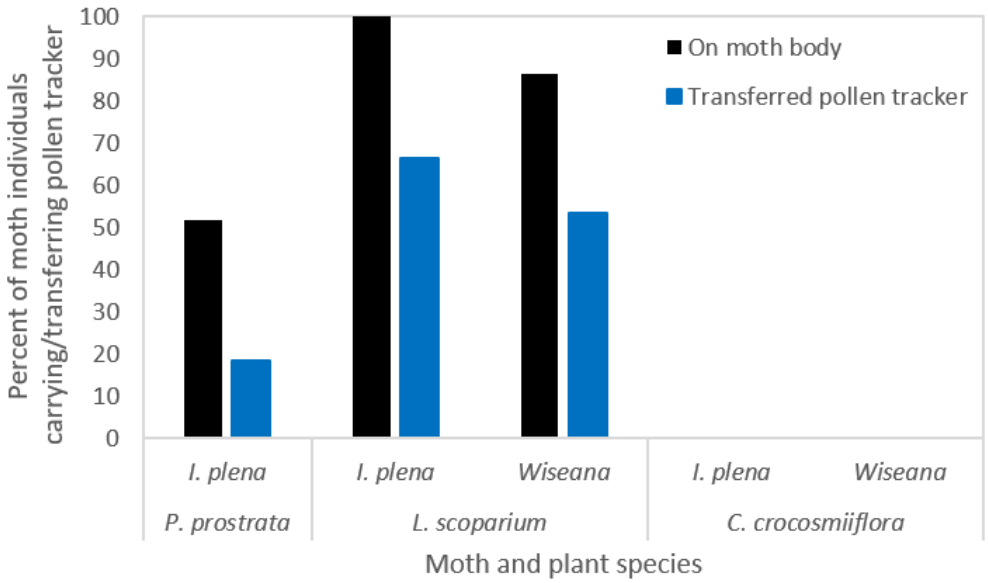


**Figure 1.** The ability of *Ichneutica plena* and *Wiseana* moths to carry and transfer pollen tracker to flowers of *Pimelea prostrata*, *Leptospermum scoparium* and *Crocosmia* × *crocosmiiflora*. The black bars refer to the percentage of moth individuals that had pollen tracker on their body for each plant species, and blue bars refer to the percentage of moth individuals that transferred pollen tracker between flowers. No moths carried or transferred pollen tracker for *C. crocosmiiflora*.

## Results

### Plant species

*Pimelea prostrata*

Twenty-seven *Ichneutica plena* individuals were used in conjunction with *Pimelea prostrata* in cage experiments. Fourteen *I. plena* individuals (52%) had pollen tracker from *P. prostrata* on their body, while five of these moths (19%) transferred pollen tracker grains to a conspecific stigma (Fig. 1). No pollen tracker was found to have been transferred onto the stigma of the same bouquet from which the pollen tracker originated (i.e. no self-pollination was observed).

*Leptospermum scoparium*

This trial involved flower-feeding and non-feeding moth taxa and was replicated 33 times. All 18 *I. plena* individuals (feeding taxon) removed pollen tracker from *L. scoparium*, as did 13 of the 15 *Wiseana* individuals (non-feeding taxon). There was no difference between species in the proportion of moths that carried pollen tracker on their bodies (Pearson's chi-squared; $X^2_{(1, 33)} = 2.55$, $P = 0.11$; Fig. 1). There was also no difference between moth species in the proportion of moths that transferred pollen tracker between *L. scoparium* flowers (Pearson's chi-squared; $X^2_{(1, 33)} = 2.25$, $P = 0.134$; Fig. 1). No pollen tracker was found to have been transferred onto the stigma of the same bouquet from which the painted anther originated (i.e. no self-pollination was observed).

*Crocosmia* × *crocosmiiflora*

Neither *I. plena* (40 individuals) nor *Wiseana* (three individuals) removed or transferred pollen tracker from our negative control *C. crocosmiiflora*; thus transfer rates between the three plant species are significantly different (Fig. 1).

### Pollen tracker on moth bodies

All anatomical parts of *I. plena* contained pollen tracker after visiting *L. scoparium*, but tracker particles were most frequently located on the proboscis (Table 1; Fig. 2). Pollen tracker was also located on all anatomical parts of *Wiseana*, yet less frequently than for *I. plena* (Table 1).

**Table 1.** Location of pollen tracker on moth bodies after visiting *Leptospermum scoparium*. The fractions presented refer to the number of individuals that carried pollen tracker on the respective body part for both species.

| Location on moth body | *Ichneutica plena* | *Wiseana* spp. |
|---|---|---|
| Proboscis | 18/18 | N/A |
| Fore-legs | 16/18 | 10/15 |
| Mid-legs | 16/18 | 8/15 |
| Hind-legs | 16/18 | 6/15 |
| Antennae | 15/18 | 5/15 |
| Abdomen | 14/18 | 10/15 |
| Wings | 13/18 | 6/15 |
| Head | 9/18 | 2/15 |
| Thorax | 8/18 | 2/15 |

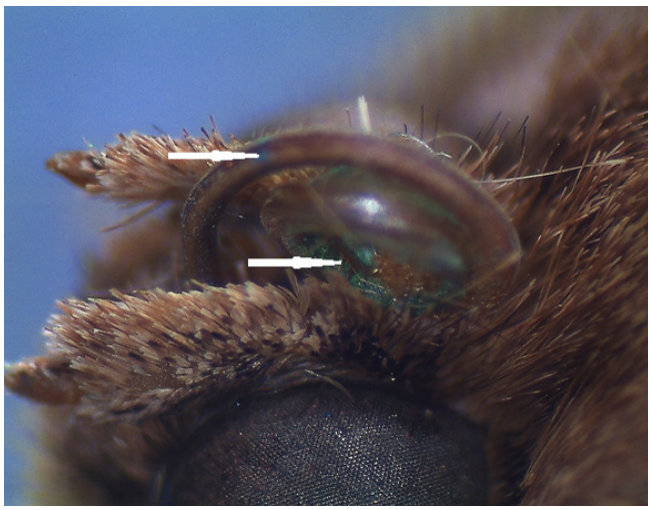

**Figure 2.** *Ichneutica plena* under a dissecting microscope with green and blue pollen tracker present on the proboscis after visiting *Leptospermum scoparium*.

## Discussion

To determine if moths are able to act as pollen vectors, *I. plena* (a feeding moth species) and *Wiseana* (a non-feeding moth species) were used in experiments with putatively moth pollinated *P. prostrata* (Burrows 1960) and *L. scoparium* (Primack 1978; Stephens et al. 2005). *Ichneutica plena* individuals were able to remove pollen tracker from *P. prostrata* and transfer it to a conspecific stigma, offering further evidence that moths are able to pollinate *P. prostrata*. No *Wiseana* spp. were caught during *P. prostrata* flowering, thus their ability to transfer pollen for this species remains unknown. Both *I. plena* and *Wiseana* individuals were able to move pollen tracker after visiting *L. scoparium*, offering further evidence that moths can act as pollinators for this species.

While both moth species were able to transfer pollen tracker, *I. plena* transferred the tracker more often (*I. plena*: 100%, *Wiseana*: 86.6%) and as such could be considered a more effective pollinator although more research is required to add weight to this claim. Waser (1988) emphasised the value of a moderate sample size when using pollen tracker to measure transfer in detail and as only two moth and three plant species were used in the trials, these data should be treated as preliminary and care taken when making generalisations about other moth and plant species. Our results indicate that moths can act as pollinators for *L. scoparium* and *P. prostrata*, data that complement flower visitation records from Burrows (1960), Primack (1978), and Stephens et al. (2005).

Neither moth species was found to have pollen tracker on their bodies in trials using the putatively bird-pollinated *Crocosmia*, despite one *I. plena* individual being observed to visit the flowers through chance observation. However, whether this visit was to feed or perch is unclear, and it is uncertain whether *Wiseana* visited these flowers. *Crocosmia* × *crocosmiiflora* flowers have extremely exerted anthers, which moth bodies would likely not contact, potentially explaining why no pollen tracker was removed. This result demonstrates that the accidental movement of pollen tracker from these flowers is unlikely.

The effectiveness of a pollinator is determined not only by its behaviour but also by the location of the pollen grains on the insect body and how that interacts with floral morphology. For Lepidoptera, pollen is most often located on the faces and proboscises as these body parts are more likely to come into contact with the sex organs of the flowers (Turnock et al. 1978; Merrett et al. 2002; Fenster et al. 2004) although not exclusively, see Funamoto (2019). Both *I. plena* and *Wiseana* carried pollen tracker on all anatomical body parts after visiting *L. scoparium* and the proboscis of *I. plena* had pollen tracker on it in every instance which aligns with previous studies. Pollen tracker was also often located on ventral parts of moth bodies for both species in our study, as has been documented for other Lepidoptera species (More et al. 2006; Atwater 2013; Weller et al. 2017; Funamoto 2019; Robertson et al. 2020). Pollen deposition from the ventral side of moth bodies (sternotribic pollination) may also contribute to the pollination of open-access flowers such as *L. scoparium* and *P. prostrata*.

Despite our own pilot trial using pollen tracker in subantarctic New Zealand (Buxton et al. 2019), this is the first experimental evidence of pollen transfer via moths in New Zealand to our knowledge, and with some refining provides a useful method by which moths can be tested as pollinators for a range of flowering plants. Our lab-based approach complements a field-based approach where a range of pollination experiments and observations can be followed through to seed set. By employing both laboratory and field methods, future research can quantify pollen transfer and investigate how this pollen transfer translates into seed production (Baker 1979). These experiments would allow for moth contribution to seed set to be measured and compared with other pollinating taxa, improving our understanding of the reproductive biology of plants at the species level and wider pollination systems at the community level.

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## Author contributions

MB, BA and JL conceptualised the research and method development; MB undertook field and lab work; JL and BA provided supervision; JL undertook the analysis; all authors involved in writing, reviewing and editing.

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