

The potential management of the drone fly (*Eristalis tenax*) as a crop pollinator in New Zealand

Brad G. Howlett* and Megan Gee

*The New Zealand Institute for Plant and Food Research Limited, Private Bag 4704,
Christchurch Mail Centre, Christchurch 8140, New Zealand*

*Corresponding author: brad.howlett@plantandfood.co.nz

Abstract The drone fly (*Eristalis tenax*) pollinates many crops and is found almost worldwide. Its successful management as a field-crop pollinator would provide an additional option to augment bee pollination. We reviewed literature to assess their management potential. A literature search was conducted for information on drone-fly abundance across New Zealand crops, pollinator effectiveness, lifecycle-requirements and potential for mass rearing. Relevant literature was then evaluated to assess the feasibility, benefits and limitations of their management. *Eristalis tenax* is a proven pollinator of pak choi (*Brassica rapa* spp. *chinensis*), kiwifruit (*Actinidia deliciosa*) and onion (*Allium cepa*), and visits the flowers of several more crops in New Zealand. It readily completes its lifecycle under laboratory conditions when reared on various organic materials. No reviewed studies were identified that showed successful management of populations for the purpose of field-crop pollination. Key challenges for their management as field-crop pollinators include: being able to mass rear them at an appropriate scale; retaining numbers within targeted areas in the field; and ensuring their use does not significantly impact on non-target species and land-user interests.

Keywords honey bees, pollination, pollinator management, non-bees, Diptera, pollinator diversity, Syrphidae, hover fly, wild pollinators

INTRODUCTION

Wild pollinating species can provide valuable crop pollination services (Garibaldi et al. 2013); however, most growers of crops that are dependent on insect pollination rely solely on the managed honey bee (*Apis mellifera* Lineaus, 1758) for pollination (Rollin & Garibaldi 2019). This dependence leaves growers vulnerable because hive availability can be affected unpredictably by factors such as sudden outbreaks of honey-bee pests and diseases as well as other environmental stressors such as pesticide use (Potts et al. 2010). Developing viable alternative pollinators that could replace or augment honey-bee pollination could create resilience in the supply of pollination services.

Few studies have examined the possibility of flies (Diptera) as potential managed-crop pollinators. However, a recent study by Rader et al. (2016) found that flies do indeed contribute to the pollination of many crops grown across the world. To date, the use of flies for pollination has been largely restricted to enclosed spaces, with Free (1993) describing several studies of blow flies (Calliphoridae) being used successfully to pollinate various crops under these conditions. In New Zealand, Howlett (2012) demonstrated that the blowfly, *Calliphora vicina* Robineau-Desvoidy, 1830, is an effective pollinator of hybrid carrot under caged conditions. Hover flies (Syrphidae) can also pollinate crops within enclosed spaces (Garratt et al. 2014; Garratt et

al. 2016); however, we are unaware of studies demonstrating successful management of flies for field crop pollination.

The drone fly (*Eristalis tenax* Linnaeus, 1758) is a species that may offer potential as a managed pollinator of field crops. It is a cosmopolitan hover fly species occurring across Europe (Francuski et al. 2013a), China (Zhang et al. 2011; Guo et al. 2017), Japan (Buckton 1895), the Indian subcontinent and throughout the New World (Mehrabi & Ssymank 2008; Patnaik et al. 2012). It is found visiting the flowers of various New Zealand native plants (Schmidlin et al. 2018) and can pollinate various crops including pak choi (*Brassica rapa* subsp. *chinensis* (L.) Hanelt) and onion (*Allium cepa* L.) in New Zealand (Rader et al. 2009; Howlett et al. 2017a), kiwifruit (*Actinida deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson) in Italy (Barbattini et al. 1994), soybeans (*Glycine max* (L.) Merr) in Poland (Karnkowski 1999), sweet pepper (*Capsicum annuum* L.) in greenhouses in Canada (Jarlan et al. 1997a) and onion, spring turnip rape (*Brassica rapa* L.) and carrot (*Daucus carota* subsp. *sativus* (Hoffm.) Schübl. & G. Martens)) in isolation cages in Germany (Schittenhelm et al. 1997).

There do not appear to be any developed strategies for the management of the drone fly as a field-crop pollinator despite it being easy to rear and maintain in the laboratory (Nicholas et al. 2018) as well as being common in agro-ecosystems (Wilson et al. 2009; Stavert et al. 2017). To evaluate the potential of managing *E. tenax* in New Zealand field crops, we reviewed literature describing the efficiency of this species as a crop pollinator, its abundance in New Zealand crops, and those key factors likely to influence abundances, distributions and lifecycle.

MATERIALS AND METHODS

The initial systematic search was conducted in February 2019 as part of a larger review of factors influencing life-histories, abundances and distribution of New Zealand bee and non-bee crop pollinators. As part of this, we searched for literature likely to contain relevant information on drone-fly abundance and

efficiency as pollinators across New Zealand crops, lifecycle-requirements and key factors likely to influence their life history. We also searched for information on their potential to be reared. Our systematic search utilised three bibliographic databases: Web of Science Core Collection (WoS); CAB Direct; and ProQuest. Our search strategy included the terms (season* or climat* or habitat or habitats or distribution or climat* or Food or feeds or Zealand or nz or "n.z.") AND ((Lasioglossum and (sordidum or cognatum))) OR (Leioproctus and (huakiwi or fulvescens or imitatus or vestitus or monticola or boltani)) OR ("Lucilia sericata" or (Calliphora and (vicina or stygia or quadrimaculata))) OR ("Pollenia pseudorudis" or "Hydrotaea rostrata" or "Oxysarcodexia varia" or "Delia platura" or Proscissio or pales or Protohystricia) OR ("Dilophus nigrostigma" or "Eristalis tenax" or Odontomyia or "Melangyna novaezealandiae" or "Melanostoma fasciatum").

We found 2607, 4439 and 3083 references respectively from each of the three databases listed above and reviewed the title of each record. If they contained information of potential relevance, then the abstracts were reviewed. We selected 204 CAB records and, after duplicates were removed, 39 WoS and 37 ProQuest records. We then assessed the reference lists of all 280 documents, which resulted in 69 further additional published documents and cited grey literature considered likely to contain relevant information. Further assessment of the articles beyond the abstract reduced the number of relevant documents to 17 sources with information relating to New Zealand and a further 17 sources that were not New Zealand-specific. These 34 sources were included in our analysis.

RESULTS

Life history and factors affecting abundances and distributions of the drone fly

A summary of some key factors likely to influence *E. tenax* abundances and distribution throughout New Zealand is provided in Table 1. These are seasonality, habitat and distribution,

Table 1 A summary of some factors likely to influence or constrain abundances and distribution of drone fly (*Eristalis tenax*) throughout New Zealand. More detailed descriptions and references are provided in the text.

Factor	Influence and/or constraints
Seasonality	Adults active all seasons but less so in winter.
Habitat & distribution	Present across North, South and Stewart Islands, capable of travelling distances >75 km, common across many habitats including intensively managed agroecosystems
Lifecycle, generations, adult longevity, fecundity	Multiple generations/year, females can lay about 3000 eggs over 2 months, have a lifespan of about 3 months, with time from egg to adult 24–36 days under laboratory conditions ~21.5°C.
Food requirements	Adults feed on nectar and pollen. Larvae feed on decaying organic material in stagnant water.
Climate	Adults seek shade when > 30°C but can forage on crop flowers 5–10°C and under windy conditions (>30 km/h). Larvae develop rapidly at > 20°C.

lifecycle, generations, adult longevity, fecundity, food requirements and climate. These factors are non-exclusive and may include many additional interacting factors about which knowledge of their effect remains poor (e.g. pesticide use, presence of predators and parasitoids, interspecific competition for resources and phenotypic variation among individuals).

Eristalis tenax is found throughout New Zealand's North, South and Stewart Islands (iNaturalist [n.d.]) and uses a wide range of habitats (Francuski et al. 2013b). The fly can be particularly common in intensively farmed agroecosystems (Stavert et al. 2018a). Adults can be active across all seasons in New Zealand but are generally less active during winter, at which time females are more abundant than males (Irvin et al. 1999). Adults are capable of extensive, long-distance migration (Bailes et al. 2018) and can fly continuously over distances of at least 75 km across open ocean (Krčmar et al. 2010). In Europe, they will migrate north to avoid hot summers before returning south in autumn (Francuski et al. 2013a; Francuski & Milankov 2015). However, males can become territorial with home ranges of around 500 m² (Wellington & Fitzpatrick 1981).

Eristalis tenax normally has multiple generations per year (Dziocck 2006). In the laboratory, females were found to produce around 3000 eggs over a 2-month period and their lifespan without hibernation was approximately 3 months at around 21.5°C (Nicholas et al. 2018). This result contrasts with earlier findings by Jarlan et al. (1997b), who found females survived under greenhouse conditions for 2–4 weeks, and males rarely beyond 3 weeks (temperature uncontrolled). The time to develop from egg to adult took just 24–36 days in the laboratory when kept around 21.5°C. (Nicholas et al. 2018). Eggs were observed to be deposited on various surfaces near water or on water, and typically hatched 2–3 days following deposition (Boughalmi et al. 2013).

Adults, particularly newly emerged imagos, showed preferences for yellow flowers (Ilse 1949; Lunau et al. 2018) but this was not exclusive (An et al. 2018). In New Zealand, Bensemman (2013) found no significant differences in their preferences for flower colour, native or exotic species, or temperature and shade requirements although, subsequently, McGimpsey and Lord (2015) found them only on white alpine flowers. Along with nectar, adults were found to require

pollen protein to mature their gonads and allow for the development of eggs (Gilbert 1986; Dyer 2006). They are generalist pollen feeders and consume pollen from many plant species in New Zealand (Irvin et al. 1999). In contrast to adults, larvae feed on decaying organic material in stagnant water (Dyer 2006) and can be phytophagous, mycophagous or zoophagous (Francuski et al. 2011). In New Zealand, they have been noted to be particularly abundant within dairy effluent (Wilson et al. 2009).

After several moults, the mature larvae crawl out of the liquid material to pupate for 6–10 days (Fischer et al. 2006; Nicholas et al. 2018). They pupate in surrounding soil and vegetation (Wilson et al. 2009). Drone-fly larvae were found to be excellent climbers, moving rapidly (>1 m/min) and able to scale 4-cm vertical bands of Fluon®, a synthetic fluoropolymer coating (<https://www.agcce.com/fluon-ptfe/>) that inhibits most insect movement (Wilson et al. 2009). Pupae preferred moist sand, moist soil or moist sawdust. Sawdust has been successfully used to hatch pupae in laboratory studies (Nicholas et al. 2018), but survival of pupae placed in vials at 20°C was poor (Wilson et al. 2009).

Flies tended to stop foraging and seek shade at temperatures above 30°C (Jarlan et al. 1997b). Males have been noted to become active at temperatures above 10°C in Canadian field studies (Wellington & Fitzpatrick 1981); however, adults have been observed foraging on crop flowers at temperatures between 5–10°C and under windy conditions (>30 km/h) in New Zealand (Howlett et al. 2013). Cloudy conditions or a high midday sun tended to increase the aggression of territorial males towards other insects (Wellington & Fitzpatrick 1981).

The drone fly as a crop pollinator

Only three peer-reviewed studies from New Zealand were found that contain original data indicating that *E. tenax* acts as a crop pollinator. All three studies used single-visit pollen deposition as their measure of pollination ability. Rader et al. (2009) found that *E. tenax* placed similar numbers of pak choi pollen grains onto

stigmas as honey bees (107 vs. 123), as did Howlett et al. (2017a) on onions (18 vs. 21). Conversely, for kiwifruit, *E. tenax* placed fewer pollen grains on stigmas (as measured from the first stigma/flower contacted) than honey bees (17 vs. 110) (Stavert et al. 2016). A further non-peer reviewed publication provided further findings that *E. tenax* can be an important pollinator (measured as stigmatic pollen deposited/minute) of hybrid vegetable carrot seed crops (Foundation for Arable Research 2012).

The drone fly as a crop flower visitor

Four studies were found that provided count data for *E. tenax* visiting crop flowers through either observation or sweep netting, but honeybees generally greatly outnumbered *E. tenax* when both species were assessed (Table 2). Of those studies with honeybee counts, managed hives were present in or within 500 m of fields. Further studies recorded *E. tenax* as crop flower visitors but did not including actual count data. For pak choi, Rader et al. (2009; 2012) measured pollinator flower visitation frequency (flower visits/ min) finding honeybees to be on average 1–8 times more prevalent than *E. tenax* across 15 fields, while Howlett et al. (2017a) reported low numbers of *E. tenax* visiting kiwifruit flowers but had grouped their counts with other rat-tailed hoverflies (i.e. *Helophilus* spp.). Window trap data found *E. tenax* to be present within flowering fields of pak choi (Mesa et al. 2013), turnip (*Brassica rapa* var. *rapa* L.) and rape (*B. napus* L.) (Howlett et al. 2018a).

DISCUSSION

This review highlights: (1) that a number of studies have shown drone-fly abundance to be very variable across crops (Table 2); and (2) that there is potential for better exploitation of the species as a pollinator of several different crops grown throughout New Zealand. It is capable of pollinating a range of crops including pak choi, onion seed and kiwifruit (Table 2), and hybrid vegetable carrot seed crops (Foundation for Arable Research 2012). Moreover, it is of similar efficiency as the honeybee in terms of stigmatic

Table 2 Studies containing counts of drone flies (*Eristalis tenax*) observed or collected from different crops in New Zealand. Total insect and honey bee counts are provided for comparison. All studies employed observers to record flower visit except for Stavert et al. (20018a, 2018b), who used sweep nets to collect insects from flowers.

Crop	Total Insects	Drone Flies	Honey Bees	No. fields	Study
Pak choi	15303	425	3942	11	Howlett et al. (2009)
Pak choi	3653	1010	not included	12	Stavert et al. (2018 a,b)
Onion	20765	84	10147	16	Howlett et al. (2009)
Carrot	3058	148	884	14	Howlett et al. (2013)
Radish	1103	18	1103	6	Howlett et al. (2013)
Avocado	3674	2	3414	4	Read et al. (2017)

pollen deposition in some crops (pak choi and onion), although not always (kiwifruit). There is also significant potential to rear large populations of *E. tenax* rapidly. Females have high fecundity, the development time from egg to pupae is short providing an ability to rear several generations per year, larvae are easily reared under laboratory conditions using a variety of organic materials (Table 1) and adults are easy to maintain as overwintering populations (Francuski et al. 2014; Nicholas et al. 2018).

No studies describing techniques to mass-reared *E. tenax* in open crop field conditions were found but larvae are known to naturally occur in very large numbers within cattle effluent on dairy farms in New Zealand (Wilson et al. 2009). Moreover, the willingness of drone-fly larvae to feed on a wide range of organic material offers flexibility to rear the species in large numbers at potentially low cost.

Challenges and benefits to developing the drone fly as a managed pollinator of field crops

The development of managed *E. tenax* as field-crop pollinators is likely to face challenges, which may become apparent only through field trials. To be effective pollinators it is important that flies are retained in sufficient numbers within the crops they are intended to pollinate. *Eristalis tenax* do not care for their brood during their development nor do they create nests as many bee species do so are not restricted in their movement

and distribution. Moreover, drone-fly larvae use different food resources than adults, and adult females need to locate suitable oviposition sites. *E. tenax* are also capable of long-distance flights and may therefore migrate quickly from fields if conditions do not suit their retention.

The territorial nature of some male flies could potentially cause dispersal of *E. tenax* and other insects, thereby reducing the efficiency of the full pollinator assemblage. On the other hand, male drone-fly aggression could potentially improve the efficiency of pollinators with subsequent interspecific interactions creating varied and extensive movement patterns leading to improved cross pollination rates (Brittain et al. 2013).

The use of *E. tenax* as a managed pollinator could also potentially have unintentional effects on surrounding land users. The pre-pupae of *E. tenax* have been considered a nuisance on dairy farms that use certain types of cattle housing as they may interfere with the mechanical operation of dairy equipment (Wilson 2009) or contaminate livestock feed (Day 2019). Therefore, the migration of large numbers of adult flies to these farms and their subsequent oviposition within effluent could exacerbate problems. Moreover, in very rare cases, drone-fly larvae can cause myiasis (particularly gastrointestinal) in humans ((Raffray & Malvy 2014) and references within).

To date, the lack of published research into the potential management of *E. tenax* as open field

crop pollinators makes it difficult to assess the scale of the possible challenges outlined. However, if appropriate management strategies can be developed that provide controlled predictable drone fly numbers in target fields, it will provide crop growers with the option to select a new managed pollinator that may be used in tandem with honey bees. This may be of particular benefit for the pollination of crops where honey bees are inefficient pollinators. For example, drone flies may be a more efficient pollinator of hybrid vegetable seed crops than honey bees as they will more readily move between hybrid lines (Gaffney et al. 2018). This movement is necessary to transport pollen from male fertile to male sterile umbels (Howlett et al. 2015). There is also potential for crop growers to rear them *en-masse* on readily available substrates, including effluent or decaying plant material.

Future research

The potential to better utilise non-bee species as crop pollinators has gained attention by growers reliant on insect pollination (Howlett et al. 2018b). Research into managing flies for crop pollination is currently being undertaken in New Zealand by the Sustainable Farming Fund Project No. 405657: Alternative pollinators for seed production (<http://mpiportal.force.com/public/SFFPublicPortal>). Key aims of the project include addressing current knowledge gaps (outlined in this manuscript) that prevent the use of *E. tenax* as a managed field crop pollinator. These include: 1) whether it is possible to mass rear *E. tenax* in crop fields and retain flies effectively for pollination; 2) the suitability of different organic substrates for rearing larvae; 3) the potential to mass rear flies under control laboratory conditions for release into targeted field crops; and 4) the monitoring of fly movements away from target fields into landuses that could potentially be negatively impacted. A video describing research currently being undertaken to manage *E. tenax* within this project can be found: <https://www.youtube.com/watch?v=ezqTsCqaaEI>.

CONCLUSIONS

The effectiveness of *E. tenax* as a crop pollinator along with an ability to easily rear its larvae on a variety of readily available organic materials, including waste products (e.g. effluent), are useful attributes for developing a managed pollinator for broad-acre crops. However, research and development will need to focus on methods to retain adequate numbers of flies within fields during crop flowering, and to identify and minimise potential negative impacts to surrounding land users (e.g. farms, industrial) and the environment.

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REFERENCES

- An LN, Neimann A, Eberling E, Algora H, Brings S, Lunau K 2018. The yellow specialist: dronefly *Eristalis tenax* prefers different yellow colours for landing and proboscis extension. *Journal of Experimental Biology* 221, jeb184788.
- Bailes EJ, Deutsch KR, Bagi J, Rondissone L, Brown MJF, Lewis OT 2018. First detection of bee viruses in hoverfly (syrphid) pollinators. *Biology Letters* 14, 2018001.
- Barbattini R, Greatti M, Zandigiaco P, Costa G, Testolin R, Vizzotto G 1994. Insect pollinators of kiwifruit and their role in crop pollination. *Atti XVII Congresso Nazionale Italiano di Entomologia, Udine, Italy, 13-18 Giugno 1994: 855-858.*

- Bensemann LL 2013. Patterns in flower visitation of flying insects in urban Christchurch. Master's Thesis, University of Canterbury.
- Boughalmi M, Pagnier I, Aherfi S, Colson P, Raoult D, La Scola B 2013. First isolation of a Marseillevirus in the Diptera Syrphidae *Eristalis tenax*. *Intervirology* 56: 386–394.
- Brittain C, Williams N, Kremen C, Klein AM 2013. Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proceedings of the Royal Society B-Biological Sciences* 280, e20122767.
- Buckton GB 1895. The natural history of *Eristalis tenax* or the drone-fly. MacMillan, London, UK. 140 p.
- Day 2019 ER Livestock Area Fly Control. Chapter 2. In: Flessner M, Taylor SV Eds. *Pest Management Guide*, Virginia Cooperative Extension. Pp. 7–8. https://www.pubs.ext.vt.edu/content/dam/pubs_ext_vt.edu/456/456-016/ENTO-288.pdf (accessed 2 May 2019)
- Dyer JA 2006. Raising awareness among Canadians about plant pollinators and the importance of monitoring and conserving them. https://seeds.ca/d/?n=pc/Dyer2006_Pollinator_Awareness_Paper.pdf (accessed 8 April 2019).
- Dziok F 2006. Life-history data in bioindication procedures, using the example of hoverflies (Diptera, Syrphidae) in the Elbe floodplain. *International Review of Hydrobiology* 91: 341–363.
- Fischer OA, Matlova L, Dvorska L, Svastova P, Bartos M, Weston RT, Pavlik I 2006. Various stages in the life cycle of syrphid flies (*Eristalis tenax*; Diptera: Syrphidae) as potential mechanical vectors of pathogens causing mycobacterial infections in pig herds. *Folia Microbiologica* 51: 147–153.
- Foundation for Arable Research 2012. *Crop Pollination*, FAR focus, Issue 7. https://www.far.org.nz/assets/files/uploads/25801_FAR_focus_7_-_crop_pollination.pdf. (accessed 5 April 2019)
- Francuski L, Matic I, Ludoski J, Milankov V 2011. Temporal patterns of genetic and phenotypic variation in the epidemiologically important drone fly, *Eristalis tenax*. *Medical and Veterinary Entomology* 25: 135–147.
- Francuski L, Djurakic M, Ludoski J, Milankov V 2013a. Landscape genetics and spatial pattern of phenotypic variation of *Eristalis tenax* across Europe. *Journal of Zoological Systematics and Evolutionary Research* 51: 227–238.
- Francuski L, Ludoski J, Milankov V 2013b. Phenotypic diversity and landscape genetics of *Eristalis tenax* in a spatially heterogeneous environment, Durmitor Mountain (Montenegro). *Annales Zoologici Fennici* 50: 262–278.
- Francuski L, Djurakic M, Hurtado P, Ludoški J, Milankov V, Pérez-Bañón C, Rojo S, Ståhls G 2014. Shift in phenotypic variation coupled with rapid loss of genetic diversity in captive populations of *Eristalis tenax* (Diptera: Syrphidae): consequences for rearing and potential commercial use. *Journal of Economic Entomology* 107: 821–832.
- Francuski L, Milankov V 2015. Assessing spatial population structure and heterogeneity in the dronefly. *Journal of Zoology* 297: 286–300.
- Free JB 1993. *Insect Pollination of Crops*. Academic Press, Harcourt Brace Jovanovich, Publishers, London. 684 p.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey-bee abundance. *Science* 339: 1608–1611.
- Garratt MPD, Coston DJ, Truslove CL, Lappage MG, Polce C, Dean R, Biesmeijer JC, Potts SG 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation* 169: 128–135.
- Garratt MPD, Breeze TD, Boreux V, Fountain MT, McKerchar M, Webber SM, Coston DJ, Jenner N, Dean R, Westbury DB, Biesmeijer JC, Potts SG 2016. Apple pollination: Demand depends on variety and supply depends on pollinator identity. *Plos One* 11, e15.
- Gilbert FS 1986. *Hoverflies*. Cambridge

- University Press, London, Cambridge, New York. 72 p.
- Guo Y, Zhang X, Shao Y, Li J 2017. Evaluation of diversity and abundance of pollinating insects on oilseed rape in major planting area of China. *International Journal of Agricultural Policy and Research* 5: 117–124.
- Hort Innovation 2018. Managing flies for crop pollination (PH16002). <https://www.horticulture.com.au/growers/help-your-business-grow/research-reports-publications-fact-sheets-and-more/ph16002/> (accessed 24 April 2019).
- Howlett BG, Walker MK, Newstrom-Lloyd LE, Donovan BJ, Teulon DAJ 2009. Window traps and direct observations record similar arthropod flower visitor assemblages in two mass flowering crops. *Journal of Applied Entomology* 133: 553–564.
- Howlett BG 2012. Hybrid carrot seed crop pollination by the fly *Calliphora vicina* (Diptera: Calliphoridae). *Journal of Applied Entomology* 136: 421–430.
- Howlett BG, Butler RC, Nelson WR, Donovan BJ 2013. Impact of climate change on crop pollinator activity in New Zealand. MPI Technical Paper No: 2013/30. Ministry for Primary Industries, Wellington, New Zealand. 45p. www.mpi.govt.nz/document-vault/4101 (accessed 24 April 2019).
- Howlett BG, Lankin-Vega GO, Pattermore DE 2015. Native and introduced bee abundances on carrot seed crops in New Zealand. *New Zealand Plant Protection* 68: 373–379.
- Howlett BG, Evans LJ, Pattermore DE, Nelson WR 2017a. Stigmatic pollen delivery by flies and bees: Methods comparing multiple species within a pollinator community. *Basic and Applied Ecology* 19: 19–25.
- Howlett BG, Read SFJ, Jesson LK, Benoist A, Evans LE, Pattermore DE 2017b. Diurnal insect visitation patterns to ‘Hayward’ kiwifruit flowers in New Zealand. *New Zealand Plant Protection* 70: 52–57.
- Howlett BG, Butler RC, Walker MK, Teulon DAJ 2018a. Are insect flower visitor assemblages distinguishable between *Brassica napus* and *B. rapa*? *New Zealand Plant Protection* 71: 189–197.
- Howlett BG, Gee M, Garratt MP 2018b. Growers believe non-bee insects are important pollinators. *Talking Avocados* 29: 60–63.
- Gaffney A, Bohman B, Quarrell SR, Brown PH, Allen GR 2018. Frequent insect visitors are not always pollen carriers in hybrid carrot pollination. *Insects* 9: 61.
- Ilse D 1949. Colour discrimination in the dronefly, *Eristalis tenax*. *Nature* 163: 255–256.
- iNaturalist No Date. Common Drone Fly (*Eristalis tenax*) <https://www.inaturalist.org/taxa/55719-Eristalis-tenax>. (accessed 24 April 2019).
- Irvin NA, Wratten SD, Frampton CM, Bowie MH, Evans AM, Moar NT 1999. The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. *New Zealand Journal of Zoology* 26: 105–115.
- Jarlan A, de Oliveira D, Gingras J 1997a. Pollination of sweet pepper (*Capsicum annuum* L.) in green-house by the syrphid fly *Eristalis tenax* (L.). *Acta Horticulturae*: 335–339.
- Jarlan A, de Oliveira D, Gingras J 1997b. Pollination by *Eristalis tenax* (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. *Journal of Economic Entomology* 90: 1646–1649.
- Karnkowski W 1999. The occurrence of larvae and pupae of *Eristalis tenax* Diptera Syrphidae on the soya bean. *Wszechswiat. Lipiec-Sierpien* 1007: 159–160.
- Krčmar S, Kučinić M, Durbešić P, Benović A 2010. Insects from the middle of the Adriatic Sea. *Entomologia Croatica* 14: 75–84.
- Lunau K, An LN, Donda M, Hohmann M, Sermon L, Stegmanns V 2018. Limitations of learning in the proboscis reflex of the flower visiting syrphid fly *Eristalis tenax*. *Plos One* 13, e20.
- McGimpsey VJ, Lord JM 2015. In a world of white, flower colour matters: A white-purple transition signals lack of reward in an alpine *Euphrasia*. *Austral Ecology* 40: 701–708.

- Mehrabi R, Ssymank A 2008. Species composition and flower visiting by Syrphidae (Diptera) in north-eastern Iran. *Zoology in the Middle East* 45: 73–78.
- Mesa LA, Howlett BG, Grant JE, Didham RK 2013. Changes in the relative abundance and movement of insect pollinators during the flowering cycle of *Brassica rapa* crops: implications for gene flow. *Journal of Insect Science* 13, e13.
- Nicholas S, Thyselius M, Holden M, Nordstrom K 2018. Rearing and long-term maintenance of *Eristalis tenax* hoverflies for research studies. *Journal of Visualized Experiments* 135: 1–8.
- Patnaik HP, Satapathy CR, Panda NN 2012. Prevalence, species richness and diversity of flower visiting insects at Bhubaneswar (Odisha). *Journal of Plant Protection and Environment* 9: 1–10.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* 25: 345–353.
- Rader R, Howlett B, Cunningham S, Westcott D, Newstrom-Lloyd L, Walker M, Teulon D, Edwards W 2009. Alternative pollinator taxa are equally efficient, but not as effective as the honeybee in a mass flowering crop. *Journal of Applied Ecology* 46: 1080–1087.
- Rader R, Howlett BG, Cunningham SA, Westcott DA, Edwards W 2012. Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? *Journal of Applied Ecology* 49: 126–134.
- Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R, Cunningham SA, Mayfield MM, Arthur AD, Andersson et al. 2016. Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America* 113: 146–151.
- Raffray L, Malvy D 2014. Accidental intestinal myiasis caused by *Eristalis tenax* in France. *Travel Medicine and Infectious Disease* 12: 109–110.
- Read SFJ, Howlett BG, Jesson LK, Pattermore DE 2017. Insect visitors to avocado flowers in the Bay of Plenty, New Zealand. *New Zealand Plant Protection* 70: 38–44.
- Rollin O, Garibaldi GA 2019. Impacts of honeybee density on crop yield: A meta-analysis. *Journal of Applied Ecology* 56: 1152–1163.
- Schittenhelm S, Gladis T, Rao VR 1997. Efficiency of various insects in germplasm regeneration of carrot, onion and turnip rape accessions. *Plant Breeding* 116: 369–375.
- Schmidlin FG, Sullivan JJ, Bowie MH, Howlett BG 2018. Insect flower visitors of planted native species within the arable landscape on the Canterbury Plains, New Zealand. *New Zealand Plant Protection* 71: 198–206.
- Stavert JR, Linan-Cembrano G, Beggs JR, Howlett BG, Pattermore DE, Bartomeus I 2016. Hairiness: the missing link between pollinators and pollination. *PeerJ* 4, e18.
- Stavert JR, Pattermore DE, Bartomeus I, Gaskell AC, Beggs JR 2018a. Data from: Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. Dryad Digital Repository. <https://datadryad.org/resource/doi:10.5061/dryad.rf510> (accessed 10 November 2018).
- Stavert JR, Pattermore DE, Bartomeus I, Gaskell AC, Beggs JR 2018b. Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. *Journal of Applied Ecology* 55: 1737–1746.
- Wellington WG, Fitzpatrick SM 1981. Territoriality in the drone fly, *Eristalis tenax* (Diptera: Syrphidae). *Canadian Entomologist* 113: 695–704.
- Wilson DJ, Gerard PJ, de Villiers JE 2009. Preventing rat-tailed maggot incursion into dairy sheds. *New Zealand Plant Protection* 62: 99–102.
- Zhang S, Chen L, Zhang H, Chen R, Huo K 2011. Flower-visiting habitus of three common syrphids in farmland of Hanzhong area in early spring. *Agricultural Science & Technology - Hunan* 12: 1355–1358.