

CATCHING THE THIEF: NECTAR ROBBING BEHAVIOUR BY BUMBLEBEES ON NATURALISED *FUCHSIA MAGELLANICA* IN IRELAND

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Abstract—*Fuchsia magellanica* (Ongaraceae) is a plant with a traditionally ornithophilous pollination system, pollinated primarily by hummingbirds in its native range. As a naturalised alien plant in Ireland, *F. magellanica* is visited largely by bumblebees, with evidence for nectar robbing behaviour of the long-tubed flowers. We aimed to investigate nectar robbing behaviour of bumblebees on *F. magellanica*, and in particular whether floral and pollinator traits (size) determined likelihood of nectar robbing. While *F. magellanica* was visited by a number of bumblebee species, only two with shorter tongue lengths were observed to rob nectar from flowers. Although there was no observed relationship between intra-specific bee body size and nectar robbing behaviour, nectar robbing was observed most frequently in the site with the highest number of bees. Proportions of robbed flowers were low overall and varied between populations, but there was a significant relationship between flower size and whether it was nectar robbed with larger flowers robbed more often. Our work suggests that floral size determines whether a flower-visitor will choose to nectar rob or not in this system. Nectar robbing may also be related to bee density which could suggest this behaviour is driven by competition for resources, or that it is learnt by observing other bees.

Keywords—Bumblebee behaviour, nectar robbing, competition, pollination, floral larceny

INTRODUCTION

Faegri and Van der Pijl (1966, p. 68): "The distinction between simple theft and house-breaking exists in pollination ecology, too; thieves that cannot creep into the flower and steal nectar that way, may bite a hole through the perianth and get at it from the outside"

Plants and the pollinators that visit them have co-evolved over long time periods (Ollerton 2017), resulting in some examples of extreme specialisation between both groups (e.g. Arditto et al. 2012; Weinstein & Graham 2017). The majority of flower-visiting insects visit flowers to feed on nectar and pollen, where many also provide valuable pollination services to plants (Ollerton et al. 2011). However, although many flower visitors visit flowers "legitimately" by coming into contact with the reproductive organs without damaging the flower, some flowers may be prone to having nectar "robbed" from them without the visitor

coming into contact with the reproductive parts (Inouye 1980) which can have consequences for plant pollination (Irwin & Maloof 2002). While nectar robbing can happen in various ways, the majority occurs when a flower visitor makes a hole in the perianth of a flowers to access nectar without "legitimately" visiting the flower (Inouye 1980). Primary nectar robbers are visitors that make the robbing hole themselves, whereas secondary robbers are those that use pre-existing holes (Inouye 1980).

Evidence suggests that both plant and flower-visitor traits could play a role in the likelihood of nectar robbing occurrence, particularly the morphological fit between flower and visitor. For plants, those with long flowers and abundant nectar are more likely to be robbed (Rojas-Nossa et al. 2016). This may occur as nectar robbers are unable to legitimately access the nectar within due to morphological constraints, and robbing results in a large reward. For flower-visitors, visitor size

may also influence the ability of individuals to legitimately visit flowers. This can occur at the species level and some bumblebee species are known to rob because their tongue is simply too short to access nectar legitimately (Irwin & Brody 1998), but it can also happen at the individual level and a negative relationship between intra-specific tongue length and nectar robbing behaviour has also been recorded (e.g. in *Bombus terrestris*; Valdivia et al. 2016). However, some flower-visitor species may act as nectar robbers in situations where morphological fit also allows them to visit legitimately, presumably as the effort of robbing has a high pay off for the robber in terms of reward (Dedej & Delaplane 2005; Irwin & Maloof 2002) although this may not always be the case (Lichtenberg et al. 2018). Nonetheless, more work is needed to understand the relationships between floral and flower-visitor traits, and nectar robbing behaviour.

Fuchsia magellanica Lam. (Onagraceae) is a plant species originally from South America, with a long purple corolla tube containing nectar, and bright red sepals. It is a classically ornithophilous flower, and is primarily pollinated by hummingbirds in its native range with some additional visits from bumblebees (Smith-Ramirez 1993; Traveset et al. 1998). In its native range it can also experience some nectar robbing by a fringillid bird (*Phrygilus patagonicus*; Traveset et al. 1998) and a non-native short-tongued bumblebee, *Bombus terrestris* L. (Valdivia et al. 2016). *Fuchsia magellanica* was initially planted in Ireland as an ornamental plant in the 19th century and is now naturalised countrywide, but especially in the south, west and north (National Biodiversity Data Centre 2020). Although *F. magellanica* is self-compatible, autogamy rates can be low in its native range (Riveros 1991), and anecdotal observations in Ireland suggest that the species here is a cultivar “ricartonii” that does not produce viable seed, thereby deeming any interactions with floral visitors as commensal on behalf of the visitor. In the absence of hummingbirds in Ireland, casual observations suggest *F. magellanica* is primarily visited by bumblebee species but that the flowers are frequently “robbed”.

Here, we investigate nectar robbing in an alien plant species, *F. magellanica* in Ireland, and whether there are associations between floral and

bumblebee-visitor traits such flower and bee size and nectar robbing behaviour (Inoue et al. 2007; Navarro & Medel 2009). In addition, we know that bumblebees can learn nectar robbing behaviour from other individuals of the same species (Leadbeater & Chittka 2008), so nectar robbing may be driven by prior experience and observations of others performing the same behaviour, which could cause variations in robbing per site and season. Therefore, we set out to answer the following questions:

- 1) What are the most abundant bumblebee species visiting *F. magellanica* in Ireland, both legitimately and as robbers, and does bumblebee visitor abundance vary over time?
- 2) What is the extent to which *F. magellanica* flowers are robbed, and does this vary between sites?
- 3) Is there a difference in size between bees that rob *F. magellanica* and those that visit legitimately (i.e. are smaller bees more prone to robbing)?
- 4) Is there a relationship between flower size and robbing behaviour; i.e. are larger flowers robbed more frequently?

MATERIALS AND METHODS

Eleven sites were selected across the west and midlands of Ireland where *F. magellanica* was found growing, including a mixture of urban and rural areas (Fig. 1). We aimed to visit each site three times: once in July, once in August and once in October. One site (West Cork) was only visited in July, while a second (Westport) was only visited in August and October, resulting in 10 sites surveyed in July and August. In October, some sites had finished flowering and so either a nearby *F. magellanica* plant still in flower was chosen (four sites) or no data were collected (three sites; Table S1).

During each site visit, focal observations were carried out to estimate visitation rates of bumblebees to flowers and to quantify any nectar robbing behaviour observed. Two patches of flowers (containing 35 flowers each) were observed for 20 minutes at each site on each visit. Every bumblebee visitor entering the patch during the observation time was identified, as well as whether the individual was legitimately visiting a

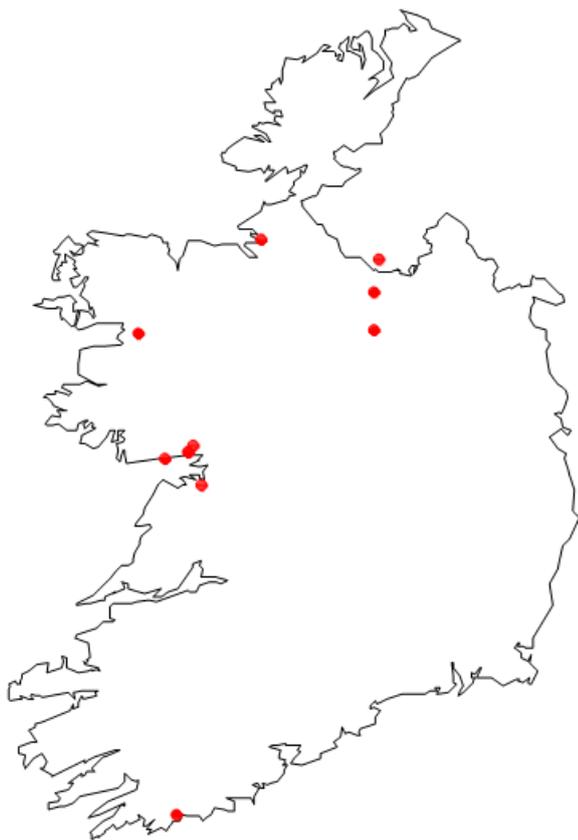


Figure 1. The 11 sampling sites used in the study around the west of Ireland. The closest two sites (Chapel and River Corrib) were 250m apart and so are not differentiated here.

flower or nectar robbing, whether it collected nectar, pollen or both, and the number of flowers visited. Workers of *B. terrestris* and *Bombus lucorum* agg. were grouped as morphological identification is not reliable in the field (Carolan et al. 2012). Observations were carried out in dry, bright conditions (temperatures 11–18°C and wind < 4 on Beaufort scale). Bumblebee abundance was compared between species (abundance pooled per species per site, with $N = 11$ for each species) and sites (abundance pooled per site per sample period, with $N = 10$ for July and August and $n=7$

for October) using Kruskal-Wallis tests as data did not meet parametric assumptions. Bees were only observed nectar robbing at one site in low numbers, and so nectar robbing data are presented graphically but not analysed statistically (Fig. 4).

Following the focal observations, a further 40 minutes was spent collecting bee morphology data on each site visit to assess whether there were any relationships between bee size and nectar robbing behaviour. Bees observed robbing or legitimately visiting flowers were caught using a sweep net and were placed in an insect plunger to hold them still. The inter-tegular wingspan (mm) of each individual was then measured using a Vernier calliper to two decimal places. As sample sizes of bumblebees collected robbing were small, patterns are tabulated but not analysed statistically (Table 1).

To record flower size and percentage of robbed flower in each site, the intactness (robbed or unrobbed) and petal length (mm) was measured of twenty flowers collected at random at each site on each visit using Vernier callipers. Petal length was used as a proxy for overall flower size as it was highly correlated with all other flower variables measured in a pilot study (nectary length, sepal length, stigma length, stamen length, ovary length and total length, Spearman's Rank Correlation $P < 0.05$), except petal width. The proportion of robbed flowers at each site, and the variation between time periods, is present graphically (Fig. 5). The relationship between petal length and whether a flower was robbed or unrobbed was analysed using a linear mixed effects model in the nlme package (Pinheiro et al. 2012) in R v. 3.5.1 (R Core Team 2016), with each data point a flower and site as a random factor. The model was validated by inspecting qq-plots and histograms of residuals, and plotting standardized residuals versus fitted values.

Table 1. Inter-tegular width of bumblebees observed legitimately visiting *F. magellanica* flowers, and robbing them. *Mean tongue lengths are taken from Goulson & Darvill (2004)

Species	Inter-tegular width legitimate (N)	Inter-tegular width robbing (N)	Mean tongue length (mm)*
<i>B. hortorum</i>	4.35 (N = 13)	NA	12.9
<i>B. lucorum</i>	4.1 (N = 9)	4.19 (N = 6)	7.9
<i>B. pascuorum</i>	3.14 (N = 88)	3.37 (N = 1)	8.5

Nectar quantity (g) was measured in a subset of four of the sites closest to the lab. All nectar was extracted from the flowers using a microcapillary tube which was weighed using a fine balance scale to estimate nectar quantity. Nectar sugar percentage was taken from four sites in the first sampling round, but from all sites during the second round. Nectar sugar percentage was obtained using a refractometer from an average of six separate flowers at each site.

RESULTS

Five bumblebee species were observed visiting *F. magellanica*. Across all sampling periods, the most abundant bumblebee visitor was *Bombus pascuorum* Scopoli, whose numbers were significantly higher than the next most common species *Bombus hortorum* L. and *Bombus lucorum* agg. ($X^2 = 16.58$, $df = 2$, $P = 0.00025$; Figs. 2 & 3). *B. hortorum* was the largest of the observed bees which we know from the literature has the longest tongue (Goulson & Darvill 2004), and was followed in tongue length by *B. lucorum* agg. (short-tongued) and *B. pascuorum* (medium-tongued; Table 1). Bumblebee visitor abundance varied between time periods ($X^2 = 10.54$, $df = 2$, $P = 0.005$), with highest abundances in August followed by July and October. Most bumblebee

visitors legitimately visited flowers and robbing behaviour was only observed at one site (River Corrib) by both *B. lucorum* agg. and *B. pascuorum*, where numbers of *B. lucorum* agg. recorded (22 individuals in August) were much higher than any other sampling period in any other site (next highest = 8 individuals). Most of these nectar robbing observations were in August, although one was also seen in July, and both species were also observed legitimately visiting at the same site (Fig. 4).

Robbed *F. magellanica* flowers were recorded in eight sites. Overall, proportions of robbed flowers were low (mean = 11%, range = 2-25%), although the extent of nectar robbing varied among sites and months (Fig. 5). Bees observed robbing did not differ in size to those that visited legitimately (Table 1), although as sample sizes were small and robbing behaviour was only observed at one site statistical analysis could not be completed. Although not recorded, honeybees and wasps were also observed both legitimately visiting and robbing *F. magellanica* in a few sites on some sampling occasions; honeybees were less frequent visitors than bumblebees, but wasps were more abundant than bumblebees at some sites near the end of the season (August and October).



Figure 2. A) *Fuchsia magellanica* flower with a nectar robbing hole, B) *Bombus pascuorum* legitimately visiting *F. magellanica* and C) *Bombus lucorum* agg. nectar robbing *F. magellanica*. Photos EC and DS.

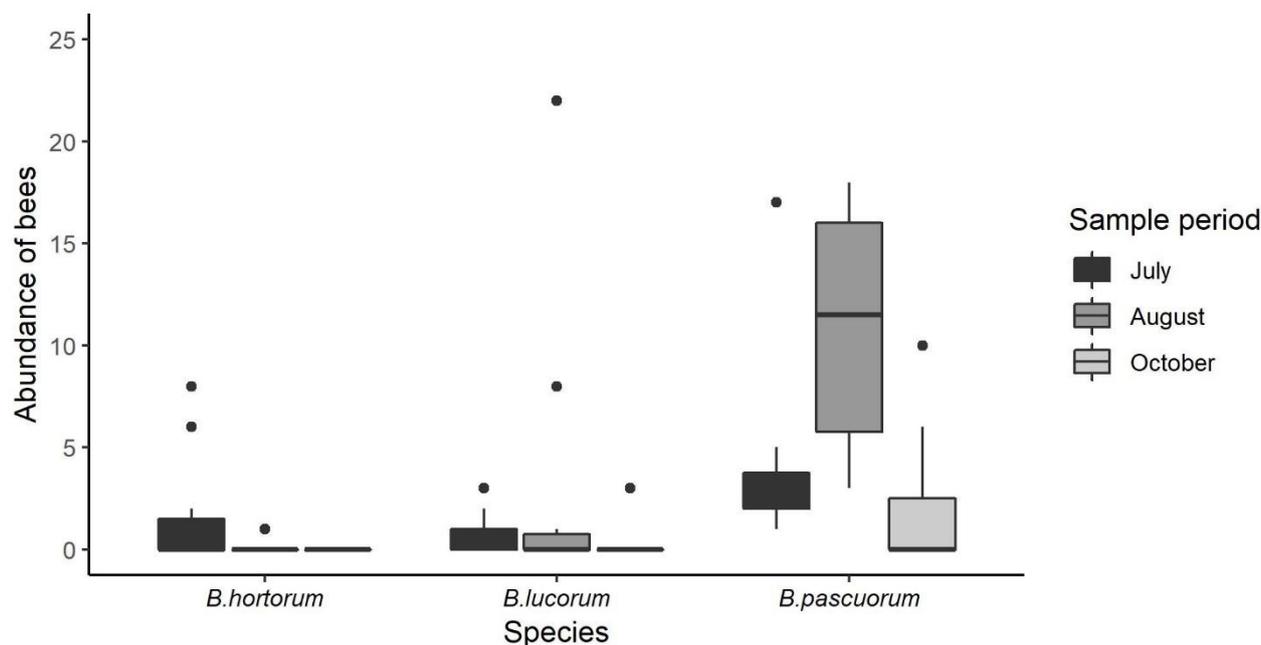


Figure 3. Boxplot showing the abundance of bumblebees observed visiting *F. magellanica* per site in each sampling period. *Bombus jonellus* and *Bombus pratorum* were also observed once each in the Sligo site in August, but were not included in further analyses.

F. magellanica flowers varied in size between sites (mean petal length per site 12.5mm, range 11–15mm). Fuchsia flowers that were robbed were larger than unrobbed flowers (Fig. 6; GLMM $F_{1,568} = 44.35$, $P < 0.0001$). On average, nectar standing crop of *F. magellanica* flowers was 0.014 g ($N = 16$, range = 0.002–0.05) and sugar content was 19% ($N = 127$, range = 3–42).

DISCUSSION

Fuchsia magellanica is a naturalized, alien plant in Ireland. Although it has a classical ornithophilous pollination system and is visited primarily by hummingbirds in its native range, we have shown that in its naturalized range in Ireland it is visited mainly by bumblebees who use it as a forage resource through both legitimate and robbing visits. While floral traits (flower size) influenced likelihood of being robbed and robbing behaviour differed between bumblebee species, we found no evidence that intraspecific flower-visitor traits (body size) affected robbing behaviour.

Bumblebees were frequent visitors to *F. magellanica* in our system, and nectar robbing behaviour differed between species. We only observed robbing in the mid-shorter tongued

bumblebee species (*B. lucorum* agg and *B. pascuorum*), and not the longer tongued *B. hortorum* (although fewer of this species were observed overall). This is consistent with the existing literature; a range of studies have shown that Hymenoptera, and in particular bees, are the most common primary robbers and also commonly use

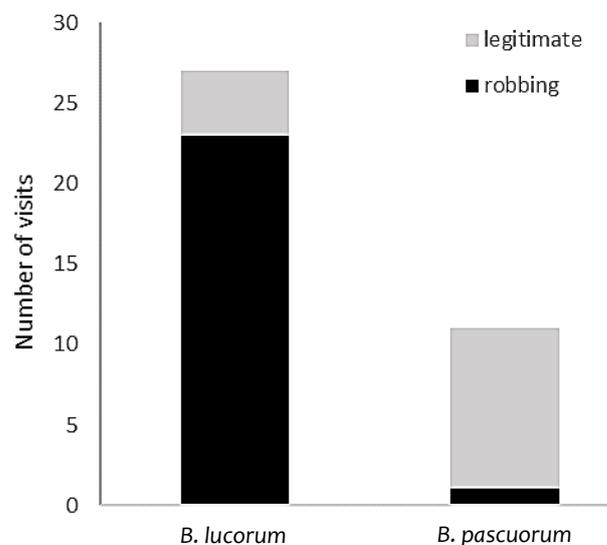


Figure 4. Nectar robbing behavior was only observed at one site: River Corrib. Two species were observed nectar robbing: the medium-tongued *B. pascuorum* and the short-tongued *B. lucorum* agg.

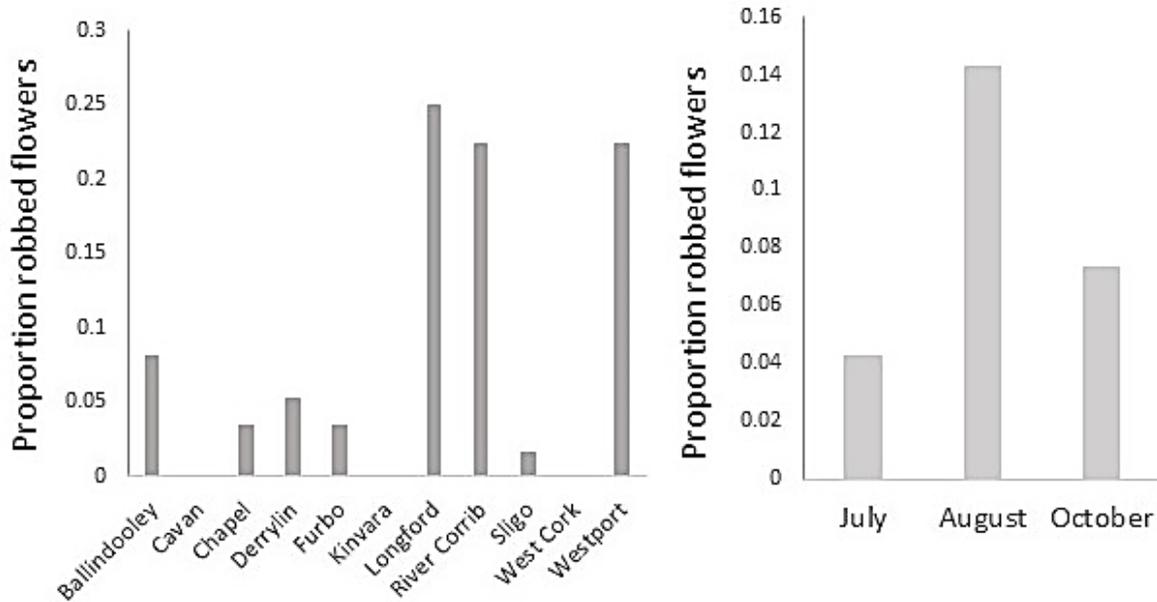


Figure 5. Proportion of all flowers that were robbed varied between (A) sites, and (B) sampling periods.

mixed foraging strategies (i.e. both robbing and legitimately visiting; Irwin et al. 2010). The mean perianth tube length of *F. magellanica* measured in this study (11.7 mm) is longer than the tongue length of both *B. pascuorum* and *B. lucorum* agg. (Table 1), but not that of *B. hortorum*. When visiting *F. magellanica* legitimately, the shorter tongued species appear to be straining to stick their head into the corolla tube to access nectar. This suggests that tongue-length may be a factor limiting legitimate visits from these species, suggesting nectar robbing may be an easier alternative strategy. Short-tongued bumblebees have also been observed to rob nectar in *Linaria vulgaris* in the UK, whereas long-tongued bees visited legitimately (Stout et al. 2000).

Incidence of nectar robbing in *F. magellanica* was low overall (max. 25% flowers per site); this result was similar to that from a study looking at nectar robbing of *F. magellanica* by non-native bumblebees in its native range (Valdivia et al. 2016), but much lower than other studies that investigated other native plant species, in which almost all flowers in some populations can be robbed (Singh et al. 2014; Stout et al. 2000). However, we found variation in proportions of robbed flowers between sites and time periods, with no robbing at all recorded in some sites and differences in robbing among time periods. Few studies have looked at variation in robbing rates between populations and seasons (Irwin et al.

2010) although Valdivia et al. (2016) also found variation in nectar robbing between populations.

The proportion of robbed flowers in our study was highest in August, which is also when numbers of *B. lucorum* agg. and *B. pascuorum* were highest, and we also observed robbing behaviour most frequently in the site with the highest recorded numbers of *B. lucorum* agg. Large numbers of *B. lucorum* agg. visiting *F. magellanica* at this site may be driven by high densities of this species, or competition for resources in the surrounding area, both of which may drive a need

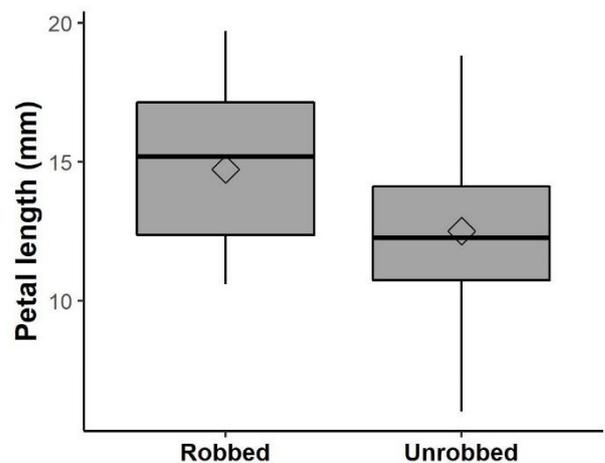


Figure 6. Boxplot of petal length (+/- SE) of flowers that were robbed (with a bitten hole in the corolla tube) or unrobbed across all sites. Diamonds represent mean values (unrobbed N = 535, robbed N = 45).

for easy access to nectar which can be achieved through robbing by this short-tongued species but this deserves further research. Although, for the most part, we were not able to distinguish between primary and secondary robbing, all direct observations of *B. pascuorum* were of secondary robbers, while *B. lucorum* agg. was observed primary robbing. All this may suggest that *B. lucorum* agg. is the key primary robber of this plant, but more data is needed to confirm this and it would be interesting to quantify the rates of primary vs secondary robbing and determine what might be driving these interactions (Irwin et al. 2010). We also know that bumblebees, in particular, can learn nectar robbing behaviour from each other (Leadbeater & Chittka 2008), and so it may be that once a small number of individuals learn to rob at a certain site, the information passes through a number of individuals via social transmission thus increasing the behaviour.

Although sample sizes were too small to formally analyse, we did not observe an influence of intra-specific bee size on nectar robbing behaviour. Other work has found a significant relationship between bee size and nectar robbing with smaller bees robbing more frequently (Valdivia et al. 2016). This may suggest that there is less variation in bee body size in our system, or that other factors such as inter-specific interactions, availability of forage resources, or the variation in floral traits has a stronger effect on nectar robbing behaviour.

We found that larger flowers were more likely to be robbed, which suggests that floral traits, and more specifically the morphological “fit” between a flower visitor and flower, may be driving robbing behaviour. This is concurrent with existing literature that shows that plants with long flowers are more likely to be robbed (but see Irwin & Maloof 2002; Navarro & Medel 2009; Rojas-Nossa et al. 2016). The long corolla of *F. magellanica* is variable in size in this system, and this coupled with the differences in tongue length of the different bumblebee species visitors may be influencing nectar robbing.

In this study, we chose to focus on bumblebees as the most frequent flower visitors to *F. magellanica* in Ireland. Although we directly observed some nectar robbing behaviour, this was

relatively rare. However, both honeybees and wasps were also observed visiting *F. magellanica* flowers, both legitimately and via nectar robbing, with wasps being particularly abundant in October. We also observed a different size and shape of nectar robbing hole in October, which may indicate increased robbing by wasps which would be interesting to investigate further, especially since, historically, wasps have been recorded less often than bees as primary robbers (Irwin et al. 2010).

While we observed the frequency and drivers of nectar robbing, effects on plant reproduction were outside the scope of this study. Reports suggest that *F. magellanica* in Ireland rarely sets viable seed and mainly spreads vegetatively, but reproduction of this species in Ireland requires further investigation. The impacts of nectar robbing on seed and fruit set elsewhere are variable (Maloof & Inouye 2000); for example, robbing can promote foraging and pollinator movement, thus increasing fruit set (Singh et al. 2014), or can negatively affect fruit set in a variety of ways, such as by damaging the flower, as has been demonstrated in *F. magellanica* following nectar robbing by birds (Traveset et al. 1998). However, many nectar-robbing interactions could be described as commensal with pollinators benefitting, but no impacts on reproduction of the plant (Heiling et al. 2018; Stout et al. 2000), and it would be interesting to test this in this system.

Nectar robbing occurs in many plant communities globally (Rojas-Nossa et al. 2016). Here we confirm that it also exists in *F. magellanica* in its non-native range in Ireland, and that there are relationships between floral size and likelihood of nectar robbing which suggests nectar robbing is driven by morphological constraints of bumblebees in the absence of hummingbird pollinators. In addition, we confirm that the naturalized alien *F. magellanica* is providing a nectar source for a variety of bumblebee species in Ireland. However, there is still more to learn about this system in terms of any impacts on plant reproduction, and the role of flower visitors other than bumblebees. This work adds to the growing literature on the ecology of nectar robbing globally (Irwin et al. 2010).

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AUTHOR CONTRIBUTION

Concept and design DS & EC, data collection EC, data analysis DS, writing DS, edits and approval for publication DS & EC

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Site visited, their location and the number of times they were visited

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