Original article

Pollination of invasive *Rhododendron ponticum* (Ericaceae) in Ireland*

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Abstract – Several insect species visited exotic *Rhododendron ponticum* flowers, but bumblebees were most common. Only bumblebees (and one *Vespula*) contacted the flower stigma whilst foraging and are probably the main pollinators. One-third of insect visits resulted in stigma contact and visitation rates were high. This explains the high seed set reported elsewhere. There were significant differences according to the body size of visitors, with large queen bees contacting stigmas more often than smaller workers. There were no significant differences in behaviour of three species (*Bombus jonellus*, *B. lucorum* and *B. monticola*) and all bees tended to move short distances between flowers on a single plant. Longer flights and movements among plants were rare. Pollen carryover was estimated to be high: there was no decline in the amount of pollen deposited on stigmas from the first to fifth flower visited. The impact of bee behaviour on reproduction and invasion by exotic *R. ponticum* is discussed.

body size / exotic plant / invasion / pollen transfer / weeds / pollination / *Bombus* / insect

1. INTRODUCTION

Pollination of exotic plants by insects has recently become recognised as an important issue in invasive species biology (Chittka and Schurkens, 2001; Barthell et al., 2001; Ghazoul, 2002; Parker and Haubensak, 2002; Stout et al., 2002; Hanley and Goulson, 2003; Goulson and Derwent, 2004; Morales and Aizen, 2006). Most angiosperms rely on mutualistic interactions with animal pollinators (usually insects) for seed production and reproduction (Buchmann and Nabhan, 1996). Unless pollinators are also introduced (as, for example, in the case of European honeybees, *Apis mellifera* L., in Asia, America and Australasia; and bumblebees, *Bombus* spp., in Australasia, and Japan), exotic plants often have to rely on forming interactions with native pollinator species (Valentine, 1978; Parker, 1997; Richardson et al., 2000). Failure

to form these interactions with native species can limit reproductive success and establishment. However, successful pollination by generalist native species can facilitate seed set, naturalisation and, in some cases, severe invasion (Parker, 1997; Richardson et al., 2000).

Some flowering plants are visited by a range of generalist taxa which may have varying efficiencies as pollinators (Macior, 1970; Herrera, 1987). Legitimate pollinators are those that not only pick-up pollen from anthers, but also deposit it on a receptive stigma. Several factors influence whether visitors actually pollinate flowers, including body size (e.g. Stout, 2000) and the method by which food (nectar and/or pollen) is collected (Inouye, 1983). Even if a taxon does act as a legitimate pollinator, two further components of pollinator behaviour can affect pollination success: the quantity of visits (visitation rate, abundance of flower visitors) and the quality of visits (in terms of the proportion of visits resulting in out-crossing events).

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The size of the floral display can affect pollinator behaviour, with large plants often attracting more frequent pollinator visitation (Augspurger, 1980; Geber, 1985; Klinkhamer et al., 1989; Klinkhamer and de Jong, 1990; Stout, 2000). However, plants with large floral displays often suffer from increased geitonogamy (within-plant pollen transfer), and hence inbreeding, as pollinators often minimise inter-flower travel and move between adjacent flowers on large plants (Geber, 1985; de Jong et al., 1992, 1993; Klinkhamer and de Jong, 1993). Hence, pollinator behaviour can have profound implications for the genetic structure of invasive plant populations (Levin, 1978).

In this paper, I examine how insect behaviour may affect the pollination success of the ecologically damaging, exotic invasive shrub *Rhododendron ponticum* (Ericaceae) in Ireland. Since its introduction to the British Isles from Spain in the eighteenth century (Elton, 1958), *R. ponticum* has introgressed with other *Rhododendron* species (Milne and Abbott, 2000) and become naturalised and abundant in many Irish habitats. Successful spread in Ireland is caused by effective seedling recruitment (Cross, 1981; Erfmeier and Bruelheide, 2004). Seeds are sexually produced and despite being self-compatible, exclusion of insects from flowers results in very low fruit and seed set (Mejías et al., 2002; Stout, in press). Contrary to findings by Mejías et al. (2002) who studied native *R. ponticum* in Spain, fruit and seed production in naturalised *R. ponticum* in Ireland is significantly improved by out-crossing (pollen transfer between plants) (Stout, in press). *R. ponticum* produces a massive floral display, with large (up to 6 cm corolla), brightly coloured (pink-mauve to the human eye), zygomorphic flowers held in inflorescences of 9–21 flowers (Mejías et al., 2002; personal observations). Flowers produce large volumes of sugar-rich nectar which accumulates in a vertical groove formed by the upper petal (Mejías et al., 2002; Stout et al., 2006). Although pollen is dispensed from anthers through an apical pore, insects do not normally sonicate (buzz) flowers to release pollen because natural vibrations tend to release it (King and

Buchmann, 1995). Pollen is "sticky" and is released in strings, which coat insect visitors (King and Buchmann, 1995; personal observations). Flowers in native populations in Spain and invasive ones across Ireland, are visited by a range of taxa, many of which become coated with strings of pollen whilst foraging (Mejías et al., 2002; Stout et al., 2006).

Since the spread of invasive *R. ponticum* in the British Isles relies largely on seed production (Cross, 1981; Erfmeier and Bruelheide, 2004), the behaviour of pollinating insects has direct implications for the proliferation of this invasive species. However, we do not know which species act as legitimate pollinators in the invasive range, nor how pollinator behaviour may affect population structure. This paper presents the results of the first investigations of pollinator behaviour on invasive *R. ponticum* in the British Isles. The aims are to determine visitation rates of different insect taxa, confirm which species act as legitimate pollinators of *R. ponticum,* and examine how pollinators affect levels of inbreeding and outcrossing.

2. METHODS

2.1. Study sites

Observations were made in naturalised populations of *Rhododendron ponticum* L. plants at Glencullen and Howth Head (Co. Dublin, Ireland) in May and June (peak *R. ponticum* flowering period) in 2002 and at Howth Head in 2003 and 2005 (it was not possible to repeat observations at Glencullen as the population was destroyed in 2003). At Glencullen, plants grew on a steep bracken and heather dominated hillside on the edge of the Wicklow Mountains (N 53°13'28", W 06°16'20", elevation 335 m); and at Howth Head in heathland on the Ben of Howth (N 53°22'36", W 06°04'12", elevation 130 m).

2.2. Visitation rates

To determine visitation rates of different flower-visiting taxa, 72 replicate ten-minute observations were made of small patches of flowers (average of 11.3 inflorescences per patch) between 0930 h

and 1630 h on three days in Glencullen and over five days in Howth in 2002. All insects entering the patch were recorded, along with the number of flowers visited by each individual. Visitation rates for each taxon (*Bombus*, other Hymenoptera, Diptera, Lepidoptera and Coleoptera) were calculated as visits per flower per hour (number of flowers visited in 10 min / number of flowers in the patch × 6).

2.3. Stigma contact

In order to determine which insects might facilitate pollination, 136 insects (117 *Bombus* spp., 5 *Andrena* spp., 10 *Vespula vulgaris*, 1 *Seriocomyia silentis*, 1 *Eristalis tenax*, 1 *Palomena* spp., 1 unidentified Ichneumonidae) visiting *R. ponticum* flowers were observed closely in 2003 and 2005. Insects were observed opportunistically, and so the number of individuals observed of each species reflects the relative abundance of the species at the site. Each individual insect was followed for as many consecutive flower visits as possible (between 1 and 29 flowers, mean = 3.88, SE = 0.29). During each flower visit, I noted whether insects contacted the stigma of flowers whilst foraging and whether insects were collecting nectar only, pollen only or both nectar and pollen from the same flower. The body size of a subset (82 individuals) of the insects observed was noted by categorizing them according to their body length (<15 mm, 15−25 mm, >25 mm). Body lengths were estimated by eye whilst insects were foraging and samples were captured to confirm estimations. The proportion of stigma contacts were compared according to food collected (nectar, pollen or both) and body size, plus the interaction, using a non-parametric equivalent of two-way ANOVA (the Scheirer-Ray-Hare extension of the Kruskal-Wallis test, Sokal and Rohlf, 1995, p. 446). The proportion of stigma contacts were compared among bumblebee species using a Kruskal-Wallis test.

2.4. Time, distance and switching

To determine whether the main flower visitors behaved as a single functional pollinating group and to quantify potential levels of outcrossing, 66 individual bumblebees (which were by far the most abundant and easily observed visitors) of three common species at the Glencullen site in 2002 (19 *Bombus jonellus*, 23 *B. lucorum/magnus* and 24 *B. monticola*) were followed for between 3 and 48 consecutive flower visits (mean = 13.63, SE = 1.08). It was not possible to distinguish between *B. lucorum* and *B. magnus* workers in the field and so these species were grouped. All *B. jonellus* and *B. monticola* individuals were workers, but the *B. lucorum/magnus* group comprised queens, workers and males. Bees were followed until either they finished their foraging bout and flew out of the site, they were lost when flying to the other side of a large plant, or were lost flying between distant plants within the site. If a bee departed from the plant it was foraging on, it was followed to a subsequent plant. If it was not possible to follow it or to determine the subsequent plant, recording ceased and data collected for that particular individual was discarded. Handling times, search times and the distance moved between individual flowers and whether bees switched inflorescence or plant were recorded. The average handling time per flower, search time between flowers and distance between flowers were calculated for each individual bee and compared among castes within *B. lucorum/magnus* and then among bee species using one-way ANOVA. In addition, the proportion of moves between flowers on an inflorescence, between inflorescences on a plant and between plants were calculated for each individual bee and compared among castes within *B. lucorum/magnus* and then among bee species using non-parametric Kruskal-Wallis tests.

2.5. Pollen carryover

In order to assess levels of stigmatic pollen carryover by bumblebees to successively visited flowers, 100 flowers were emasculated prior to anthesis (to avoid contamination of stigmas with self pollen) and bagged with bridal veil material (to prevent insect visits). This method of emasculation and bagging has previously been shown to successfully exclude pollen from stigmas (Stout, 2007). On large, many-flowered plants such as *R. ponticum*, it is very difficult to ensure free-flying insects visit a sequence of emasculated flowers. In order to overcome this problem, once emasculated flowers were fully open, dead *B. terrestris* bumblebees (of all three castes, from a colony which had been kept in a glasshouse, hence not contaminated with *R. ponticum* pollen) were used to simulate the behaviour of live ones to examine levels of pollen carryover (this technique has been successfully used by Waddington, 1981, and Escaravage and Wagner,

2004). The relaxed bumblebees were loaded with pollen by simulating their natural positions during live visits to five unmanipulated *R. ponticum* flowers with dehiscing anthers for 5 seconds (which is slightly longer than the 3.7 seconds average time spent per flower by live foraging bumblebees). The test bee was then inserted into five successive emasculated flowers for 5 s in the same way. Since dead bees were of all three castes, they represented a range of body sizes and so were assumed to pick up pollen and contact stigmas the same proportion of times as live bees. After each "visit" to an emasculated flower, the stigma from that flower was removed and later mounted on a microscope slide, stained with 0.5% safranin solution and the number of *R. ponticum* pollen tetrads counted. The number of tetrads on flowers 1–5 were compared using Friedman's method for randomized blocks (a nonparametric test using ranks, with each block representing a sequence of five flower "visits", Sokal and Rohlf, 1995, p. 440).

3. RESULTS

3.1. Visitation rates

A total of 555 insects were observed foraging on *R. ponticum* patches during 12 hours of observation. Bumblebees of six species (29 *B. jonellus*, 3 *B. lapidarius*, 163 *B. lucorum/magnus*, 110 *B. monticola*, 16 *B. pascuorum* and 121 *B. pratorum*) were recorded. In addition, 32 other Hymenoptera (from 8 taxa), 76 Diptera (11 taxa), 4 Lepidoptera (4 taxa) and 1 Coleoptera were observed. Mean visitation rates were different at the two sites: 1.29 (S.E. = 0.14, n = 40) insects per flower per hour during daylight at Howth, and 4.10 (S.E. = 0.32, n = 32) at Glencullen. At both sites, most visits per flower per hour were made by bumblebees (Howth: mean = 1.10, S.E. = 0.10, n = 40; Glencullen: mean = 3.86, S.E. = 0.22, n = 32), with queens, workers and males observed visiting flowers (15% of individuals recorded were queens, 73% workers and 12% males).

3.2. Stigma contact

On average, 33.3% of visits by insects resulted in contact with the stigma of *R. pon-*
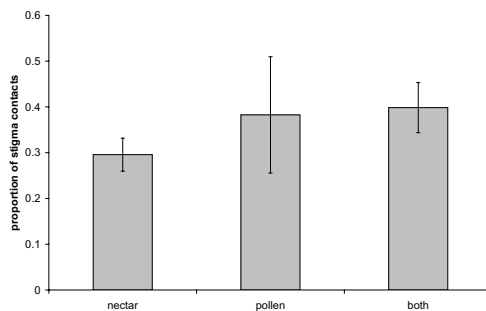

Figure 1. Proportion of flower visits with stigma contact (mean ± S.E.) according to food collected from flowers (nectar, pollen, both).

ticum. Stigma contact was made by various parts of the insects' bodies, depending on the position in which they approached and landed on flowers. Some landed so that the ventral side of the insect contacted the stigma (in the way described by Mejéías et al., 2002), but others flew down into the back of the flowers so that the dorsal side of the insect contacted the stigma. Other contacts were made as the insect flew into or out of the flower. Stigma contacts were only made by bumblebees (38.6% of visits by bumblebees resulted in contact with stigmas) and one *Vespula vulgaris* queen (1.3% of visits made by insects other than bumblebees resulted in contact with stigmas). Of all visits to flowers, 62.5% were to collect nectar only, 10.3% to collect pollen only and 27.2% to collect both. The average proportion of stigma contacts did not vary according to whether insects collected nectar, pollen or both from flowers (Fig. 1, Tab. I). However, the proportion of stigma contacts did vary significantly according to body size (Fig. 2, Tab. I), with larger insects (mostly queen bumblebees) contacting the stigma of *R. ponticum* flowers more frequently than smaller ones (on average, 66.1% of queen bumblebee visits resulted in stigma contact). There were no significant differences among bumblebee species in the proportion of stigma contacts made ($\chi_3^2 = 7.45$, $P = 0.06$).

3.3. Time, distance and switching

There were no differences among castes within the *B. lucorum/magnus* group

Table I. Analysis of proportion of stigma contacts according to body length of insect (size), food collected (nectar, nectar + pollen, pollen) and the interaction. Test statistic given is H (as calculated by the Scheirer-Ray-Hare extension of the Kruskal-Wallis test). ** $P < 0.01$.

	SS	MS_{total}	H	df	P
Size	5533.9	516.8	10.71	2	0.005**
Food	1662.4	516.8	3.22	2	0.200
Size × Food	637.8	516.8	1.23	4	0.872
Error	34546.0			73	

($P > 0.05$ for all tests). There was no difference in the handling or search/flight times of the three bumblebee species nor in the distance flown between successive flowers (Tab. II). There were no differences between species in the proportion of moves made within inflorescences, between inflorescences and between plants (Tab. II). In total, 47.5% of all bumblebee moves observed were within inflorescences, 50.1% of moves between inflorescences, and 2.4% of moves between plants. The distribution of distances moved between successive flower visits was highly leptokurtic, with short-distance movements far more common than longer distance ones (Fig. 3).

3.4. Pollen carryover

There was no decline in the number of pollen tetrads deposited on stigmas of successively "visited" flower (from 1–5) (Tab. III, $\chi^2_4 = 6.59$, $P = 0.16$).

4. DISCUSSION

Visitation by native insects to the invasive exotic, *Rhododendron ponticum*, was very frequent in the populations studied. Even with only a third of visits resulting in stigma contact and hence potential pollen transfer, individual flowers may be pollinated at least once every three hours during the peak flowering season. This explains the high seed set in these populations, reported elsewhere (Erfmeier and Bruelheide, 2004; Stout et al., 2006; Stout,
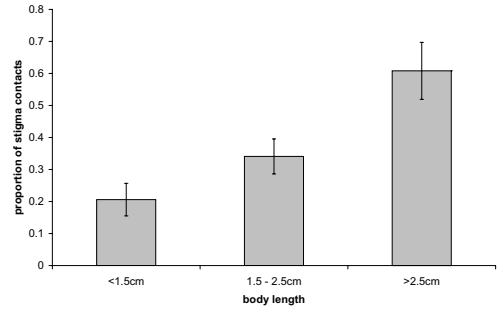

Figure 2. Proportion of flower visits with stigma contact (mean ± S.E.) according to body length of visitor (< 15 mm, 15–25 mm, > 25 mm).

2007) and an absence of pollination limitation (Stout, 2007).

Visitation rates were three times higher at the Glencullen site compared with the Howth site. This may be due to the fact that there were few other flowering plants at the Glencullen site, and *R. ponticum* provided the primary resource to anthophiles in the area. Indeed, *R. ponticum* flowers after *Vaccinium* and before the heathers (*Erica* and *Calluna*) and so may provide an important resource for bees at this time of year. By contrast, the Howth site is close to urban gardens which may compete for pollinator attention.

Queens, workers and males of six bumblebee species, including relatively uncommon heathland specialist species, *B. monticola* and *B. jonellus*, were the most frequent diurnal visitors to flowers, with other taxa rarely seen visiting flowers. Previous studies have also shown that bumblebees comprise the majority of flower visitors and pollen was found on the bodies of most individuals examined (Mejías et al., 2002; Stout et al., 2006). Bumblebees were the only taxon (except the occasional *Vespula* queen) to contact the stigmas of flowers whilst foraging. Since *R. ponticum* flowers are relatively large, small insects, including worker bees, can visit flowers without touching the reproductive structures of the flower by flying directly towards the back of the flower to extract nectar from the groove in which it accumulates. The larger queens, however, many of which are foraging during the peak

Table II. Mean (S.E.) time spent per flower (Handling), time spent searching between flowers (Search), distance between successive flowers (Distance), proportion of moves within inflorescences, between inflorescences and between plants, for *B. jonellus*, *B. lucorum* and *B. monticola*, and results of statistical tests for differences among species (ANOVA for Handling, Search and Distance, Kruskall-Wallis for proportion of moves).

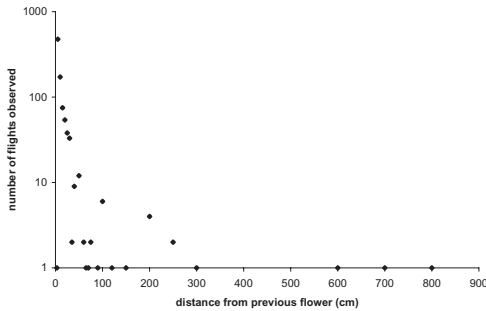|	*B. jonellus*	*B. lucorum*	*B. monticola*	Test statistic	P
Handling (s)	3.51 (0.38)	3.42 (0.29)	4.14 (0.36)	$F_{2,63} = 1.370$	0.262
Search (s)	1.07 (0.06)	1.14 (0.07)	1.18 (0.11)	$F_{2,63} = 0.365$	0.695
Distance (cm)	15.79 (1.97)	34.92 (14.62)	13.11 (1.35)	$F_{2,63} = 1.839$	0.167
Within inflorescence	0.45 (0.04)	0.51 (0.05)	0.46 (0.04)	$\chi^2_2 = 1.58$	0.452
Between inflorescences	0.53 (0.04)	0.44 (0.05)	0.53 (0.04)	$\chi^2_2 = 3.46$	0.178
Between plant	0.01 (0.008)	0.05 (0.03)	0.01 (0.006)	$\chi^2_2 = 1.08$	0.584

Figure 3. The number of flights of different distances made by all bumblebees observed (logarithmic scale).

Table III. Mean (plus standard error) number of pollen tetrads on stigmas of the first to fifth "visited" flowers and mean rank of each flower within each visitation sequence (where flowers receiving least pollen are ranked 1 and those receiving most are ranked 5). Flowers "visits" were simulated using dead bumblebees.

Flower number	Mean number of pollen tetrads (S.E.)	Mean rank
1	53.7 (18.53)	3.3
2	20.75 (11.02)	2.6
3	9.85 (3.51)	2.425
4	26.5 (10.25)	3.25
5	38.55 (17.92)	3.425

flowering for *R. ponticum*, more frequently contact flower stigmas.

No differences were found among three bumblebee species in terms of their search or handling time per flower, distance flown between successive flowers, or proportion of switches within and between plants. These three species have similar, short-medium length probosci (Stout, unpublished data), and seem to forage in a similar way. Although we only examined three species, it is possible that all the bumblebee species visiting *R. ponticum* form a single functional pollinating group (Fenster et al., 2004). If this is the case, even though a wide range of insect species visit *R. ponticum*, tempting us to conclude that the plant-pollinator interaction is a broad, generalised one (Mejías et al., 2002; Stout et al., 2006), bumblebees are the most frequent flower visitors and if several species are comprising a single functional pollinating group, the pollination ecology of *R. ponticum* could be more specialised than previously thought, with specialisation towards pollination by large bees.

Bumblebees are known to be efficient foragers, frequently moving between flowers, often visiting adjacent flowers to reduce flight times, and avoiding re-visitation of depleted flowers (Goulson, 2003). This efficiency on the part of the pollinator can often affect levels of inbreeding and outbreeding, and ultimately, the population structure of the plant. Most (97.6%) successive flower visits recorded in this study were between flowers on the same plant. It is possible that this is an underestimation, as bumblebees are often very difficult to follow if they fly over the top of large *R. ponticum* plants. Nonetheless, with individual plants producing hundreds of flowers

(Cross, 1981), it is likely that within-plant movement accounts for most successive flower visits. This might result in high levels of inbreeding via geitonogamy. Even if bees move between plants, if they move between adjacent individuals, it is possible that they are moving between clones (because *R. ponticum* can spread locally by vegetative layering, Erfmeier and Bruelheide, 2004), causing inbreeding. Indeed, since many exotic species consist of small isolated populations with low genetic diversity, or descend from small founder populations (Lee et al., 2004), inbreeding may be relatively common.

However, relatively high levels of pollen carryover might mitigate the negative impacts of bees visiting many flowers on a single plant and may increase pollen dispersal and outbreeding (Broyles and Wyatt, 1991). In this study, stigmatic pollen carryover was not shown to decline at all over the first five flowers visited. Other studies of pollen carryover have found a rapid decrease in pollen deposition (e.g. Geber, 1985; Cresswell et al., 1995; Cresswell, 2000), with more than half of all pollen deposited going to the first two flowers visited (e.g. Escaravage and Wagner, 2004). However, Carré et al. (1994) also found that the quantity of pollen deposited was very variable and depended on the individual forager, and in 50% of cases the pollen deposition was independent of the visitation order. Pollen carryover may have been overestimated in this study by the use of dead bees to simulate flower "visits". This may have caused two problems: firstly, dead bees may not have been inserted into flowers in the same way that live bees visit flowers (although every attempt was made to mimic natural behaviour) and, secondly, dead bees are unable to groom pollen off their bodies, increasing the chances of pollen deposition in the experiments (Escaravage and Wagner, 2004). However it is quite plausible that the patterns shown in this experiment are an accurate reflection of the natural situation. *R. ponticum* flowers are big, and not all bee visits contact stigmas (depending on the position of the stigma when a bee visits and, as shown above, the size of bee). Therefore, in natural situations, bees may well visit five flowers without ever touching the stigma and depositing pollen. In addition, as *R. ponticum* pollen adheres in "strings" (King and Buchmann, 1995), we would expect a clumped distribution of deposition, not a linear one.

If *R. ponticum* plants are suffering from inbreeding, we might expect a reduction in individual plant fitness through decreased quantity and quality of seed produced (Keller and Waller, 2002; Wallace, 2003). Recent experiments suggest that inbreeding in naturalised *R. ponticum* in Ireland does reduce seed set, but that it has little impact on seed germination (Stout, 2007). In addition, at the population level, inbreeding can affect genetic diversity and the ability of a population to cope with environmental change (Lande, 1995). Although it is possible that introgression with North American *Rhododendron* species has occurred (Milne and Abbott, 2000), currently we know little about the genetic diversity of invasive *R. ponticum* populations in Ireland. Work is currently underway to address this issue (Stout et al., unpubl. data).

In conclusion, invasive exotic *R. ponticum*, which benefits from animal-mediated outcrossing, has succeeded in forming legitimate pollination interactions with native generalist bumblebee species in the British Isles. This is not altogether surprising considering the native range of *R. ponticum* is within the same continent, where it is also pollinated by generalist large bees (Mejías et al., 2002; Stout et al., 2006). It would be interesting to discover what pollinates introduced *R. ponticum* in areas where bumblebees are not native and to examine rates of invasion in these places. Many exotic plants with a large floral display, and copious nectar production form associations with native insects, particularly bumblebees. This may not only promote invasion by the exotic plant, but may disrupt native plant-pollinator mutualisms and so have further impacts on native biodiversity and ecosystem functioning (Traveset and Richardson, 2006). Clearly, there is a need for more research into exotic-plant – native-pollinator interactions.

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Pollinisation de *Rhododendron ponticum* (Ericeceae), plante invasive en Irlande.

Pollinisateur / *Bombus* / Insecta / taille corporelle / plante exotique / plante invasive / transfert de pollen / adventice

Zusammenfassung – **Bestäubung von invasivem *Rhododendron ponticum* (Ericaceae) in Irland.** Das Verhalten von Blüten besuchenden Insekten beeinflusst den Umfang und die Qualität der Bestäubung für Pflanzen und beeinflusst damit sowohl die individuelle Fitness der Pflanze als auch die Populationsdynamik. Entomogame exotische Pflanzen müssen bezüglich ihrer Bestäubung mutualistische Beziehungen mit einheimischen Bestäubern bilden, um sich in fremden Habitaten durchzusetzen und zu verbreiten. Dadurch können einheimische Bestäuber einen direkten Einfluss auf die Verbreitung invasiver exotischer Pflanzen haben. Die invasive Art *Rhododendron ponticum* in Irland wird von einer ganzen Reihe von Insekten besucht, doch hatten bei zwei eingebürgerten Populationen in der Region Dublin lediglich Hummeln und eine Wespenkönigin Kontakt mit der Narbe. Bei einer Erhebung während der Hauptblütezeit im Jahr 2002 waren Hummeln die häufigsten Blütenbesucher mit mehr als einem Besuch pro Stunde. Dies erklärt die enorme Samenproduktion und die erfolgreiche Invasion dieser Art. Sechs Hummelarten (bestehend aus 15 % Königinnen, 73 % Arbeiterinnen und 12 % Drohnen) wurden beim Blütenbesuch und Nektar- bzw. Pollensammeln beobachtet. Es gab keinen signifikanten Unterschied zwischen Pollen und/oder Nektar sammelnden Insekten bezüglich ihrer Bestäubung (bestimmt über den Anteil Besucher mit Kontakt zur Narbe, Abb. 1). Allerdings hatten größere Insekten (meist Königinnen) eher Kontakt mit den Narben als kleinere Insekten wie Arbeiterinnen oder Drohnen (Abb. 2). Die lediglich geringen Unterschiede im Sammelverhalten der verschiedenen Hummelarten (Tab. II) sprechen dafür, dass diese Arten eine einheitliche funktionelle Bestäubergruppe bilden. *R. ponticum* bilden enorme Blütenansammlungen. Analysiert man die Flugaktivitäten der Hummeln, so bewegen sich 47,5 % innerhalb eines Blütenstandes, 50,1 % zwischen Blütenständen und 2,4 % zwischen verschiedenen Pflanzen. Zwischen zwei Blütenbesuchen wurden meist nur kurze Distanzen zurückgelegt (Abb. 3), was zu hohen Inzuchtraten führen könnte. Verstärkt werden könnte dies durch die Fähigkeit von *R. ponticum* zu lokaler vegetativer Verbreitung, wodurch benachbarte Pflanzen Klone sein könnten. Dadurch könnten selbst als Auskreuzung interpretierte Bestäubungsvorgänge zu Inzucht führen. Möglicherweise ist die Pollenübertragung aber sehr weit reichend, da es keine Abnahme der übertragenen Pollenmenge bei aufeinander folgenden Blütenbesuchen gab (Tab. III). Hummeln haben demnach als der primäre Bestäuber für *R. ponticum* in Irland eine wichtige Bedeutung für das Auskreuzen und die Populationsdynamik dieser exotischen Pflanzenart.

***Bombus* / Insekt / Größe / exotische Pflanzen / Invasion / Bestäubung / Unkraut**

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