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Bumblebees, humble pollinators or assiduous invaders? A population comparison of foraging performance in *Bombus terrestris*

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Abstract Worldwide trade in non-native bumblebees remains largely unrestricted despite well-documented cases where introductions of non-native bees have gone dramatically wrong. Within Europe, indiscriminate importation of non-native populations of bumblebees (*Bombus terrestris*) for the pollination of glasshouse crops continues on a massive scale. However, no risk assessment has been conducted for these introductions, perhaps because *B. terrestris* is considered a native species, so shipping populations from one region to another has been implicitly assumed to present no risk. This view is clearly unjustified because *Bombus terrestris* populations differ significantly in their genetic makeup as demonstrated by strong differences in coat colour and behavioural traits. Therefore, for the first time we compare an important competitive trait, namely foraging performance, between commercially available *B. terrestris* populations in contrasting environments. We test whether commercially reared populations differ in their nectar foraging performance and whether this is influenced by both their source environment and the one they are introduced into. We do this by means of a reciprocal transplant experiment. Strong, consistent inter-population differences in performance occurred irrespective of test location: Canary Island bees (*B. t. canariensis*) were superior to Sardinian bees (*B. t. sassaricus*), which were generally superior to mainland European bees (*B. t. terrestris*). These inter-population differences in performance were largely explained by

inter-population variation in forager size, with larger bees being superior foragers. However, even when body size was accounted for, “native” bees were not superior to transplanted non-native bees in all but one case. We conclude that non-native populations, especially those with large foragers, can be highly competitive foragers. This could lead to their establishment and displacement of native bees. Therefore, we recommend that unregulated movements of non-native *B. terrestris* populations within Europe should not be carried out without a full risk assessment.

Keywords Body size · Bumblebee trade · Invasive potential · Island populations · Local adaptation

Introduction

Bumblebees, notably *Bombus terrestris* L., have been shipped throughout the world in vast numbers (Goka et al. 2001) since they were recognised as commercially valuable pollinators of glasshouse crops in the late 1980s (Velthuis 2002). Unfortunately, this trade in bumblebees remains almost unrestricted despite social insects being identified as potentially highly invasive (Moller 1996). This has been repeatedly demonstrated by several well-publicised cases where such pollinator introductions have gone drastically wrong. For example, since its introduction to Brazil in 1956, the “Africanised” honeybee has spread as far as the southwest United States, readily hybridising with European honeybees along the way (Diniz et al. 2003). In addition, worldwide pollinator movements carry a high risk of introducing non-native parasites: for example, the highly destructive mite *Varroa jacobsoni* now threatens honeybee populations worldwide (Oldroyd 1999) and imported bumblebees carry parasites which potentially threaten native bumblebees (Goka et al. 2001). Furthermore, non-native *B. terrestris* has readily become established and spread in countries outside its native range (e.g. Chile, Ruz and

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Herrera 2001; Tasmania, Hingston et al. 2002; and Japan, Matsumura et al. 2004). However, although there is fierce debate now over further introductions to countries outside the native range of *B. terrestris*, (e.g. Australia, Hergstrom et al. 2002; Carruthers 2003, 2004), little consideration has been given to the potential threats posed by the extensive movements of *B. terrestris* across populations (e.g. Widmer et al. 1998).

The natural range of *B. terrestris* is centred in Europe and North Africa where several distinct populations are found. These populations show a high degree of colour variation (Chittka et al. 2004), and genetic studies by Estoup et al. (1996) and Widmer et al. (1998) revealed that the mainland populations, whilst genetically quite homogeneous, differ significantly from those native to the Mediterranean Islands (e.g. Sardinia, *B. t. sassaricus* Tournier), Canary Islands (*B. t. canariensis* Pérez) and British Isles (*B. t. audax* Harris). Several of these populations have been available to crop growers from commercial breeders, e.g. *B. t. terrestris* L., *B. t. sassaricus*, *B. t. canariensis* and more recently *B. t. dalmatinus* (Dalla Torre). Alarmingly, colonies of these bees have all been shipped in extremely large numbers to regions where other populations are native without appropriate risk assessment. For example, between 1989 and 1996 tens of thousands of colonies of *B. t. sassaricus* (of Sardinian origin) have been transported into Southern and Western European countries (A. Van Doorn, Koppert Biological Systems, personal communication). Unfortunately, both workers (Morandin et al. 2001) and more importantly new queens (gynes) and males (Goulson et al. 2002a) escape from the glasshouses where they are used as crop pollinators. Furthermore, evidence points to the fact that *B. terrestris* is able to naturalise easily, even with limited numbers of founding queens (Buttermore et al. 1998). Therefore, given that the probability of establishment is positively related to propagule pressure (Kolar and Lodge 2001), and that potentially large numbers of sexually reproductive individuals are escaping from imported colonies, establishment of non-native populations is a real threat.

The escape of sexually reproductive bees from non-native populations could impact on native ecosystems in a number of ways. Both males and gynes of non-native populations may interbreed with native bees (De Jonge 1986; Chittka and Wells 2004), resulting in intraspecific hybridisation (Olden et al. 2004), thereby threatening the natural genetic diversity of *B. terrestris* (Widmer et al. 1998) and potentially adding to the global phenomena of biotic homogenisation (McKinney and Lockwood 1999). There is also a risk that non-native bees and/or their hybrids become established, as in Chile (Ruz and Herrera 2001) and Japan (Matsumura et al. 2004). Newly established non-native bees may be superior to native bees in some aspect of their biology, such as their foraging ability, potentially leading to displacement of native bees through competitive exclusion. Such competitive exclusion through nectar depletion could not only affect native populations of *B. terrestris* but could

also impact on other bee species, a phenomenon often observed with honeybee introductions (reviewed in Goulson 2003). Hence, introduced bumblebees could have a significant impact on pollination systems, possibly leading to changes in plant communities: for example through differential seed set from introduced bees pollinating plants that previously received poor pollination services (Stout et al. 2002; Goulson 2003). Therefore, coupled with the potential for spreading parasites (Goka et al. 2001), it is important that a suitable risk assessment is carried out prior to the introduction of non-native populations of *B. terrestris* for pollination purposes. Furthermore, such risk assessments need to be underpinned by high quality scientific research.

A comparison of foraging performance between *B. terrestris* populations would provide valuable information necessary for such a risk assessment of European bumblebee introductions for a number of reasons. Efficient foraging has been recognised as one of the traits that makes social insects particularly invasive (Moller 1996). Furthermore, in order to establish and spread in non-native environments, introduced organisms need to find sufficient food for growth and reproduction. This is particularly important for bumblebees, as food supply affects colony dynamics, with fewer smaller workers being produced in poor environments (Schmid-Hempel and Schmid-Hempel 1998). More importantly, access to more food increases reproductive success with greater numbers of males and disproportionately more gynes being produced (Pelletier and McNeil 2003). Thus, it is reasonable to assume that, although foraging performance is only one component of fitness in bumblebees, it is likely to be a good predictor of potential colony success and invasive potential.

Therefore, the aim of this study is to assess the invasive potential of three commercially available populations of *B. terrestris* by focusing on one important trait, namely their ability to forage efficiently. Furthermore, we intend to ascertain whether the invasive potential of commercial *B. terrestris* populations is influenced by their source environment and that of the region into which they are introduced. We address both aims simultaneously by employing the powerful method of a reciprocal transplant experiment where populations are compared both in their natural and non-native environments (reviewed in Kawecki and Ebert 2004).

Materials and methods

Study species and locations

For this study, we chose three commercially available sub-species (henceforth referred to as populations) of *B. terrestris* sourced from different, widely separated geographic regions: *B. t. canariensis* from the Canary Islands, *B. t. sassaricus* from Sardinia and *B. t. terrestris*

from Central Europe. A reciprocal transplant experiment was used to compare the Central European and Sardinian populations in both their native and non-native habitats. In addition, we added value to our experiments by including the Canary Island population in our comparisons to assess its competitive ability in non-native environments. We could not do a reciprocal transplant in the Canary Islands as the local authorities justifiably prohibit the importation of non-native bumblebees.

The transplant experiments were carried out at two locations in Sardinia (Costa Rei, late autumn 2000, and Monte Padru, spring 2001) and one in Germany (Würzburg, summer 2002). We carried out two experiments in Sardinia, because Mediterranean *B. terrestris* typically has two generations per year (Rasmont 1997), one in spring/summer and one in the autumn. In contrast, only one generation occurs in Central Europe during the spring/summer (Alford 1975). The vegetation at the Costa Rei site was dominated by extended dry shrub land (macchia), and although we found about 10 plant species in bloom, *B. terrestris* foraged almost exclusively from flowers of the strawberry tree (*Arbutus unedo* L.), with occasional visits to a garden species, *Aptenia cordifolia* (L.f.) Schwantes (introduced from South Africa). The vegetation at Monte Padru was dominated by dry meadowland with several dozen plant species in bloom. Here, both low macchia and cork oak forest were within the flight range of *B. terrestris*. At the final test site, near Würzburg, the vegetation was typical of Central Europe: i.e. dry grassland, deciduous forest and some farmland with multiple flower species in bloom.

Bumblebee colonies were purchased from commercial breeders, with all three populations for the Sardinian experiments being obtained from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). For the German experiment, *B. t. canariensis* and *B. t. sassaricus* were still obtained from Koppert but as they no longer supplied *B. t. terrestris* we had to purchase them from Bunting Brinkman Bees (Tilburg, Belgium). However, within mainland Europe there is very little genetic population restructuring (Estoup et al. 1996), so the bees from Holland and Belgium should have been very similar.

Foraging observations

Foraging observations were carried out simultaneously on all three populations. Two populations, *B. t. sassaricus* and *B. t. terrestris*, were compared in both their native and non-native environments (Sardinia and Germany). The third population, *B. t. canariensis*, was compared with the other two populations in both Sardinia and Germany, where it was a non-native population.

Within each location, three sets (blocks) of foraging observations were carried out consecutively. In every block, each of the three populations was represented by one colony of bees (Table 1). All colonies within a block were established in the field at the same time and placed within 5 m of each other, so that they were exposed to the same foraging environment. Prior to placement in the field, all colonies were fed pollen and nectar ad libitum. Only young colonies were placed in the field to reduce the risk of males and gynes being produced during the observations. Each colony contained approximately 30–50 workers and no males or new gynes.

Colonies were housed in the field in specially designed bipartite nest boxes whose entrance consisted of a long Plexiglas tunnel with a system of shutters to enable movements of bees into and out of the nest to be controlled by the observer. All workers in each colony were marked with individually numbered tags (*Opalith Plättchen*, Christian Graze KG, Weinstadt-Endersbach, Germany). Males and gynes, identifiable by lack of tags, were never allowed to leave the colonies to prevent any non-native bees establishing themselves as a result of our experiment. Foraging observations began immediately when colonies were first placed in the field. All colonies were monitored continuously between 08:00 h and 19:00 h during dry weather and all marked bees were allowed to leave and enter the nest at will during these periods. The total duration of observations varied between blocks depending upon the weather and ranged from 3 days to 16 days (Table 1). During each observation period, the following data were recorded for each marked bee: (1) departure time, (2) departure mass, (3) arrival time, and (4) arrival mass. Our focus was on nectar foraging, so bees returning with pollen were not

Table 1 Summary of study duration and the number of bees making more than three foraging trips in each experimental location

Location	Block	Study duration	<i>B. t. canariensis</i>	<i>B. t. sassaricus</i>	<i>B. t. terrestris</i>	Total
Sardinia 2000	A	8/11–10/11	9	8	6	23
	B	18/11–25/11	23	17	3	43
	C	29/11–7/12	17	27	28	72
Sardinia 2001	A	5/4–16/4	11	8	4	23
	B	5/4–18/4	26	11	26	63
	C	22/4–26/4	24	22	19	65
Germany 2002	A	22/7–6/8	13	8	21	42
	B	8/8–11/8	13	15	13	41
	C	13/8–20/8	4	14	–	18
Total			140	130	120	390

evaluated. Body mass was measured by capturing bees at the entrance of the Plexiglas tunnel as they departed/arrived and transferring them to an electronic balance (Ohaus Navigator N20330, Ohaus Corporation, Pine Brook, NJ, USA). Departure time was taken when the bees were released from the vial after weighing and time of arrival was taken when the bees first reappeared at the tunnel.

Data analysis

All foraging data (674 bees making 2,966 trips) were screened prior to analysis and trips shorter than 10 min, i.e. defecation or orientation flights, were discarded (Spaethe and Weidenmüller 2002 and references therein). After screening, only individual bees that foraged on at least three occasions (bouts) were included in subsequent analyses. Data from the *B. t. terrestris* colony in Germany 2002, block C, were also excluded from the analysis as very low foraging activity resulted in too few bees to allow meaningful comparison with other populations. For the remaining bees ($n=390$), mean body mass on departure, duration of foraging bout, net change in body mass, and subsequently, nectar foraging rate (NFR, mg nectar h^{-1}) were calculated. Mean body mass on departure was used as an index of body size as workers only carry very small amounts of nectar when leaving the colony (Allen et al. 1978) and body mass is highly positively correlated with body size (Goulson et al. 2002b; Spaethe and Weidenmüller 2002).

Data exploration revealed that variance in NFR increased proportionally to the mean, so we used generalized linear models (GLM) with a Gamma error distribution and log link function (R 2.0.0 statistical language software, R Development Core Team 2004). As nectar foraging performance is known to be positively related to body size (Goulson et al. 2002b; Spaethe and Weidenmüller 2002), we used body mass as a covariate in all GLMs. Only bees which had been reared in the laboratory with ad libitum nectar and pollen were tested, so their body mass was independent of their foraging performance. Similar models were used to examine variation in flight duration and mass of nectar collected.

Results

The nectar foraging rates of 390 bees making an average of 6.29 ± 0.23 (mean ± 1 SE mean) trips per bee were compared. Nectar foraging rates of all populations varied greatly between locations (Fig. 1) with overall performance substantially higher in Sardinia than Germany (pooled mean NFR ± 1 SE: Sardinia 2000 = 216.3 ± 9.0 mg h^{-1} , Sardinia 2001 = 130.3 ± 9.6 mg h^{-1} , and Germany 2001 = 76.1 ± 4.3 mg h^{-1}). However, the rank order of performance of the three populations was surprisingly consistent in all habitats, with *B. t.*

canariensis performing much better than *B. t. sassaricus* and *B. t. terrestris* in all locations (Fig. 1). Although the relative foraging performance of *B. t. terrestris* and *B. t. sassaricus* was generally similar, *B. t. terrestris* was the worst in the majority (6/8) of cases (Fig. 1). In Sardinia, the differences in foraging performance were much more pronounced than in Germany, with *B. t. canariensis* up to three times better than *B. t. sassaricus* and nine times better than *B. t. terrestris* (Fig. 1; Sardinia 2001 block B).

The nectar foraging rates of native bees (indicated by “N”) was never greater than at least one transplanted population except for Sardinia 2001 block C (Fig. 1b). However, foraging performance of *B. t. sassaricus* was only slightly better than *B. t. canariensis*, which was substantially better than *B. t. sassaricus* in the other two blocks.

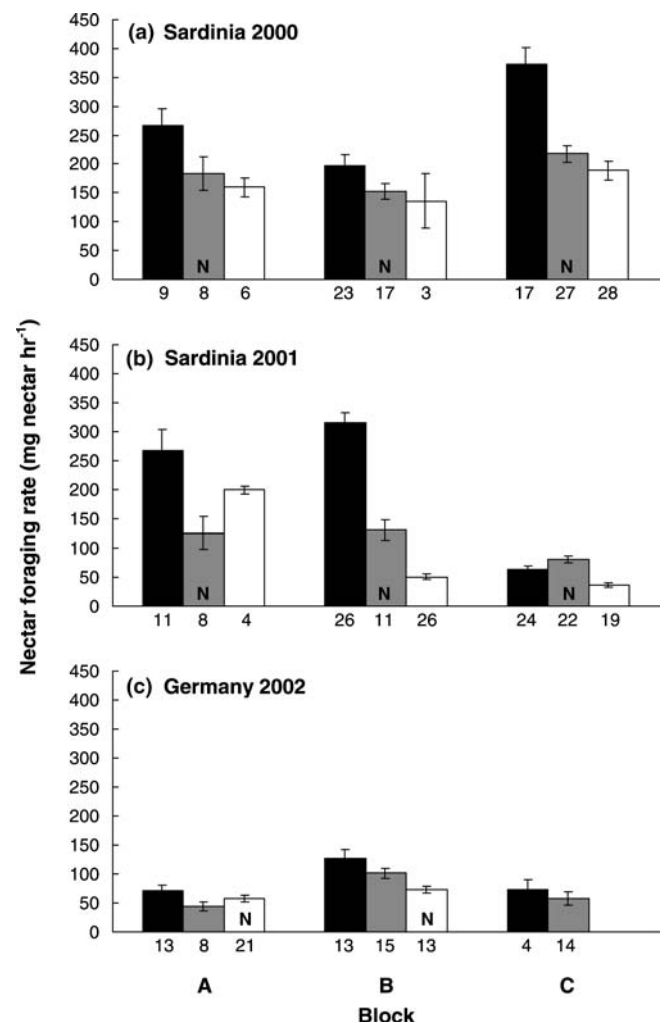


Fig. 1 Comparison of the nectar foraging performance of three populations of *B. terrestris* in **a** Sardinia 2000, **b** Sardinia 2001 and **c** Germany 2002. Bars represent mean (± 1 SE) nectar foraging rate, and numbers under bars indicate the number of foragers observed from each colony. Black bars represent *B. t. canariensis*, grey bars *B. t. sassaricus* and white bars *B. t. terrestris*. Native populations are indicated by an N, inside the bar

Nectar foraging performance of bees in all locations was significantly related to body mass ($F_{1,384}=23.73$, $P<0.001$), with large bees generally performing better than small bees (Fig. 2). Furthermore, the substantial differences in foraging performance between populations could be largely explained by differences in forager body mass ($F_{2,388}=227.07$, $P<0.001$). *B. t. canariensis* foragers were much heavier than *B. t. sassaricus* foragers (1.4 times, Tukey's post-hoc test, $P<0.001$), which were slightly heavier than *B. t. terrestris* foragers (1.1 times, Tukey's post-hoc test, $P<0.001$).

So is body mass the only factor that affects foraging performance? In other words, could native bees actually outperform non-native ones if the effect of body mass is removed? Even after discounting body mass as a factor, there were significant but inconsistent differences (Fig. 2) in the foraging performance between populations (three-way interaction, location:block:population, $F_{11,359}=17.90$, $P<0.001$). Native populations (solid symbols, Fig. 2) never performed better than transplanted bees over the size range of bees tested. Furthermore, inter-population differences were generally small except in Sardinia 2000 block C (Fig. 2a) and Sardinia 2001 block B (Fig. 2b), where *B. t. canariensis* performed substantially better than the other populations irrespective of body mass.

Foraging trip duration was not influenced by body mass of bees ($F_{1,384}=0.07$, $P=0.488$) but varied

significantly between populations (three-way interaction, location:block:population, $F_{11,364}=7.07$, $P<0.001$). However, these differences were inconsistent between blocks and locations. For example, the foraging duration for all populations was similar in Sardinia 2000, but in some locations *B. t. sassaricus* was fastest (Sardinia 2001 block C and Germany 2002 block B) while in other locations (Sardinia 2002 block B and Germany blocks A and C) *B. t. canariensis* was faster. On the other hand, the mass of nectar collected by bees was highly dependent on their body mass ($F_{1,384}=14.59$, $P<0.001$) and corresponded closely to the observed differences in NFR.

Discussion

We found strong and consistent differences in nectar foraging performance between populations. Native populations typically collected nectar at lower rates than at least one of the transplanted non-native populations (Fig. 1), with bees from the Canary Islands (*B. t. canariensis*) being superior irrespective of location. This highly consistent pattern is particularly remarkable bearing in mind that bumblebees show a high degree of inter-colony variation in most traits (Schmid-Hempel and Schmid-Hempel 1998). Furthermore, although most of the observed variation was explained by size

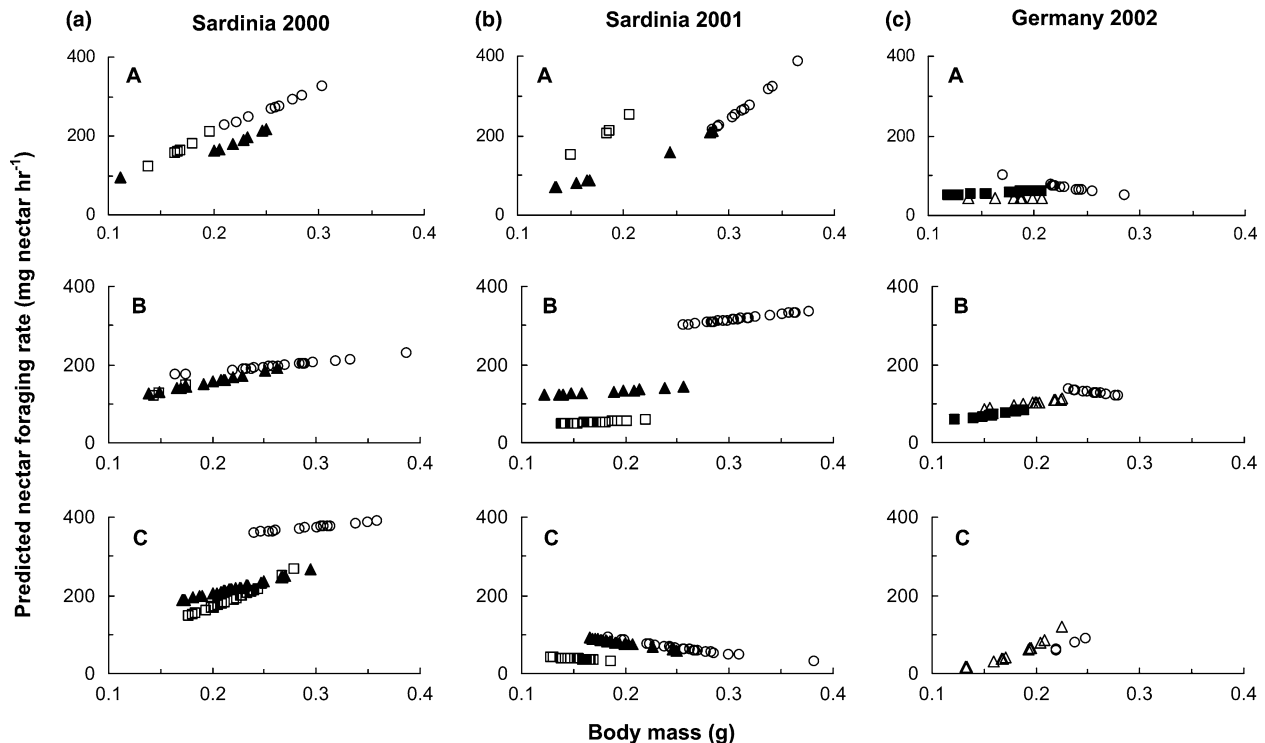


Fig. 2 Summary of predicted nectar foraging performance plotted against body mass (GLM with Gamma error distribution and log link function). Plots in **a** represent Sardinia 2000 blocks A–C, **b** represent Sardinia 2001 blocks A–C and **c** represent Germany 2002

blocks A–C. Circles represent *B. t. canariensis*, triangles are *B. t. sassaricus* and squares are *B. t. terrestris*. In each plot, the native population is represented by solid symbols and non-native populations by open symbols

differences between foragers from the different populations, within the size range of bees tested, native populations never performed better than transplanted populations (Fig. 2). Therefore, we propose that, at least insofar as commercially reared *B. terrestris* are representative of their native population, foraging behaviour does not appear to be strongly adapted to the environment of the source population. More importantly, forager body size in *B. terrestris* populations appears to be a crucial factor determining their foraging performance and potential competitive abilities. Therefore, our results clearly indicate that a risk assessment should be carried out before importing non-native populations of *B. terrestris* for crop pollination.

Clearly, nectar foraging performance is only one component of invasive potential and local adaptation. However, we argue that, as sexual reproduction is closely linked to food supply (Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003), there should be sufficient selection pressure on foraging performance. Also, colony foundation and hibernation/aestivation survival, which are important components of fitness, are strongly linked to food supply, and therefore foraging ability. For example, hibernation survival is positively related to the body size and condition of queen bumblebees (Beekman et al. 1998). Furthermore, colony foundation (in wasps) is also correlated with body size and condition, which are largely a product of food availability during maturation in the parent colony (reviewed in Moller 1996). In addition, other studies suggest that *B. terrestris* is able to rapidly establish itself in a wide variety of non-native habitats both in regions where native bumblebees occur (e.g. Japan, Matsumura et al. 2004) and where they are absent (e.g. Tasmania, Hingston et al. 2002). Furthermore, it is suggested that in Tasmania the thriving population of *B. terrestris* may have originated from a single founding queen (Buttermore et al. 1998).

Although commercially available populations have been bred under artificial conditions for several generations it has been shown that some traits, which differ between natural populations, are preserved in laboratory-reared bees. For example, both natural and commercially reared *B. t. sassaricus* unusually possess a preference for red in addition to the more typical one for blue (Chittka et al. 2004). Hence, it is reasonable to expect that commercial bees sourced from different regions will, to a degree, still possess traits reflecting local adaptation. Furthermore, the main focus of this study was to determine how the relative foraging performance of commercially bred populations was influenced by different environments.

There are a number of important points worth considering when interpreting foraging rate data. Higher rates of nectar collection do not implicitly mean greater efficiency as the quality of nectar collected and energy expenditure during foraging are not known. Therefore, in future studies it would be interesting to measure both energy expenditure and the quality of nectar collected to

get a clearer picture of foraging efficiency. Also, in our study, observations began immediately after colonies were placed in the field, so some of the foraging rates measured could have included less efficient “learning” flights as bees became familiar with their environment. However, this applied to all populations equally and our data are representative of the critical early stages of colony growth.

We found that the most important factor explaining the strong difference in foraging performance between populations was a consistent difference in forager size between the populations. The population with the largest foragers, *B. t. canariensis*, collected nectar at superior rates in all test locations. These superior foraging rates of larger bees were generally the result of large bees collecting more nectar than small bees during foraging trips of a similar duration, which agrees with Spaethe and Weidenmüller (2002). Interestingly, Goulson et al. (2002b) also found that large bees collected more nectar than small bees, but that they did so during shorter foraging trips. This difference is perhaps a reflection of great variability between *B. terrestris* colonies and as such underlines the need to sample a sufficient number of colonies before making population inferences. The fact that the large inter-population differences in foraging performance were explained by forager body size is intriguing. It suggests that bumblebee body size is an important competitive trait leading us to ask why larger bees are better foragers and why island bees are larger.

A number of suggestions have been put forward to explain the superior nectar foraging rates of large workers. Firstly, they have superior spatial visual resolution: a one-third increase in body size leads to doubling in the precision of detecting flowers (Spaethe and Chittka 2003). Hence, larger bees can detect flowers at greater distances, and also detect smaller flowers more easily, thus potentially reducing search times. In addition, Goulson et al. (2002b) proposed that larger workers have higher nectar foraging rates because they may (1) have higher rates of nectar uptake due to stronger muscles, (2) they handle flowers more efficiently, or (3) they may visit more flowers per unit time.

Although a full discussion of why island bees are larger than those on mainland Europe is beyond the scope of this paper, it is interesting to note that this observation neatly fits the “Island Rule” (Foster 1964; Case 1978; Lomolino 1985). This rule states that small-bodied animals, including insects (Palmer 2002), tend to be larger on islands than on the mainland. Favoured explanations for this are that ecological release from predators and competition leads to an increase in body size whilst resource limitation leads to size reductions (e.g. Lomolino 1985; Brown and Lomolino 1998). However, even if we understand why different populations have large workers and why they are better foragers, we still need to examine what implications the strong size-related differences in foraging performance

between populations has for the current trade in *B. terrestris* across Europe.

Larger, non-native bees, especially those from the Canary Islands (*B. t. canariensis*), performed better than smaller native bees in both Sardinia and Germany. Although large bees are clearly superior nectar foragers, there could be a trade-off between the number and size of foragers. For example, the Central European population, *B. t. terrestris*, may produce many small workers whilst the island populations, e.g. *B. t. canariensis*, may produce fewer large foragers. In this case, at the colony level, both could be equally efficient. However, our colonies contained similar numbers of workers and we did not observe substantially more foragers in colonies of *B. t. terrestris* than *B. t. canariensis* (Table 1). Furthermore, a doubling in body mass typically results in a two–threefold increase in nectar foraging rates (see Spaethe and Weidenmüller 2002; Goulson et al 2002). Hence, if we assume that costs of forager production increase linearly with body mass, then production of large workers is still likely to be more energy efficient. Therefore, populations with large foragers are likely to be more competitive as colony success is related to food intake (Pelletier and McNeil 2003).

Even after body size was accounted for, native bees never performed significantly better than introduced bees. This indicates that foraging-related behavioural traits are not strictly adapted to the populations' source environments, or they have been lost through commercial breeding. Of course it is possible that native bees (or smaller bees) were collecting higher quality nectar than non-native bees (or larger bees), resulting in greater energy efficiency. However, it was not possible to measure nectar quality and, at least in Sardinia 2000, foragers were observed almost exclusively at the dominant flowering species *Arbutus unedo*. Therefore, it is reasonable to assume that the quality of nectar collected was similar across populations and in terms of nectar foraging, introduced non-native populations of *B. terrestris* with large foragers are likely to be highly competitive with native populations with small foragers.

If sufficient niche overlap occurs between native and introduced populations, the more competitive introduced bees could displace the local ones through depletion of nectar resources (Hingston and McQuillan 1999). However, even if there is sufficient niche separation for both populations to coexist, the continued release of introduced bees into the wild could increase the dominance of *B. terrestris* in local bumblebee communities. Inter-specific competition between bumblebees does not appear to be a problem in flower-rich habitats (Goulson and Darvill 2004) but resource depletion by introduced bees is likely to become more pronounced when resources are more limiting (Goulson 2003).

Within Central Europe, the loss of flower-rich habitats through intensification of agriculture is believed to be behind the decline of many bumblebee species (Carvell 2002; Mand et al. 2002). Therefore, the introduction of highly competitive populations of *B. terrestris*

into Central Europe may have an even greater impact as floral resources become more limiting. We observed that for all populations, nectar foraging rates were substantially lower in Germany than Sardinia, suggesting that floral resources are more limiting. Indeed, bumblebee declines have been reported in Germany due to loss of floral resources (Edwards 2001). Therefore, the observed superior performance of the larger introduced non-native bees in Germany could have a greater impact than in Sardinia.

Introduced bees may also have other locally adapted traits, which could lead to additional competition between bumblebee species. For example, Mediterranean populations of *B. terrestris* have greater flexibility in their phenology, with at least two generations occurring annually compared to only one in Central Europe (Rasmont 1997). Flowering times of many plant species are becoming increasingly earlier (Fitter and Fitter 2002) and in regions with less harsh winters (e.g. Britain) year round forage is available in gardens. Therefore, flexibility in phenology could allow introduced populations to respond to increased climatic fluctuations, e.g. warm winters, predicted under current climate change scenarios (Hulme et al. 2002). Introduced populations of *B. terrestris* could therefore significantly deplete spring resources before species with more rigid phenologies are able to set up colonies. There is also some evidence that populations have different floral preferences (e.g. floral colour, Chittka et al. 2004), suggesting that they may forage from different flowers than native *B. terrestris* but could overlap with those used by other less common species. Therefore, coupled with continued release of sexually reproductive bees at different times of the year, these traits could result in greater niche overlap between introduced *B. terrestris* and other native species.

As far as we are aware, our study is the first attempt to explore the risks involved with the use of non-native *B. terrestris* populations for European glasshouse crop pollination. By comparing the nectar foraging performance of three populations in three different environments, we have shown that non-native populations can be highly competitive with native bees in their own foraging environment. Differences in body size between populations are of prime importance as the population with the largest foragers, *B. t. canariensis*, was superior at collecting nectar in all test environments. However, even when body size was accounted for, non-native bees performed as well as, or indeed sometimes better than, native bees. Populations with superior nectar foragers have the potential to displace both native *B. terrestris* populations and possibly also other bumblebee species.

We conclude that it is imperative for more high-quality research to be carried out to provide essential information needed for an overdue risk assessment of the use of non-native populations of bumblebees for commercial pollination. In particular, the risks associated with hybridisation, parasite spread and phenological differences between populations need to be explored further. At this stage, we recommend that populations

with large foragers should not be introduced into regions where local populations have smaller foragers. Furthermore, it is also important that careful assessments are carried out before importing bees into environments where local bumblebee populations are already under threat from habitat loss.

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