Original article

A failed invasion? Commercially introduced pollinators in Southern France*

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Abstract – The natural diversity of *Bombus terrestris* subspecies could be under threat from the commercialisation of bumblebees. Therefore, to determine whether commercially imported bumblebees are able to establish and spread, we carried out long-term observations of bumblebees in southern France. Our surveys occurred before, during, and after the importation (between 1989 and 1996) of thousands of colonies of the Sardinian subspecies *B. t. sassaricus*. Queens and males of *B. t. sassaricus* were observed foraging outside commercial greenhouses in 1991, 1993, and 1994 and feral workers were observed foraging on native vegetation nearly two years after the importation of *B. t. sassaricus* ceased. However, no *B. t. sassaricus*, or F1 hybrids were observed after 1998. We conclude that *B. t. sassaricus* remains inconspicuous in France and competition from the three native subspecies may have prevented it from becoming invasive. However, genetic interference through introgression cannot be ruled out.

Bombus terrestris sassaricus / bumble bee trade / establishment / introduced subspecies / niche availability

1. INTRODUCTION

Biological invasions resulting from the introduction of non-native organisms generate potentially large economic and ecological costs (Pimentel, 2002; Perrings et al., 2005; Pimentel et al., 2005). Despite this, strong economic pressures are driving the introduction of non-native pollinators, particularly honeybees and bumblebees, throughout the world (Delaplane and Mayer, 2000; Thorp 2003; Velthuis and van Doorn, 2006). Given the scale of these introductions, as well as documented population declines in many natural pollinators across the globe (Kearns et al., 1998; Sarospataki et al., 2005; Steffan-Dewenter et al., 2005; Williams, 2005;

Biesmeijer et al., 2006), and the potential invasiveness of social insects (Moller, 1996; Schneider et al., 2004), it is surprising that relatively few studies have actually attempted to monitor the establishment and spread of non-native pollinators (Ruz, 2002; Diniz et al., 2003; Matsumura, 2003; Inari et al., 2005; Schmid-Hempel et al., 2007). A common feature of these, and other studies on invasive organisms, is that they concern introduced *species*. However, the introduction of non-native *subspecies* (or populations) is more likely to impact on population diversity through hybridisation and introgression, and possibly competitive exclusion (Schneider et al., 2004; Moritz et al., 2005), than the introduction of non-native species.

Bumblebees provide an excellent model system to explore these risks further. After honeybees, bumblebees are the most important species for crop pollination (Delaplane

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and Mayer, 2000). Furthermore, the trade in bumblebees involves introductions of both non-native species and subspecies (Inari et al., 2005; Hingston, 2006; Ings et al., 2006; Inoue et al., 2008; Rasmont et al., 2008).

One of the most important commercially reared bumblebee species, particularly for the European and Asian markets, is *Bombus terrestris* (L.). Worldwide, nearly one million colonies of *B. terrestris* are being used by growers each year (Velthuis and van Doorn, 2006). To date, *B. terrestris* has been imported into over 57 countries, including 16 outside of its native range (Ings, 2007). In fact, *B. terrestris* has now become established in the wild in at least two of these countries as the result of recent commercial introductions: Japan (Matsumura, 2003; Inari et al., 2005; Inoue et al., 2008) and Chile (Ruz, 2002). *B. terrestris* also became well established in New Zealand following purposeful introductions during late 19th and early 20th centuries, and more recently has spread into Tasmania, although it is not known whether the latter introduction was intentional or accidental (Schmid-Hempel et al., 2007). Within Europe, the situation is more complex because the commercial trade in *B. terrestris* involves introduction of non-native subspecies (Ings et al., 2005b; Velthuis and van Doorn, 2006) which could have consequences for the natural population diversity of the species in Europe (Ortiz-Sánchez, 1993; Estoup et al., 1996; Widmer et al., 1998).

There are nine subspecies of *B. terrestris* found within Europe and N. Africa (Rasmont et al., 2008). The continental (e.g. French and German) and island (e.g. Sardinian) populations are recognised as distinct subspecies because they differ significantly in their genotype (Estoup et al., 1996; Widmer et al., 1998) and phenotype; e.g. coat colour and colour preferences (Chittka et al., 2004), pheromones (Coppée et al., 2008), and behaviourally related traits such as foraging ability (Ings et al., 2005a; Ings et al., 2006). In fact, bumblebee breeders have utilised this diversity during the commercialisation of bumblebees by carefully selecting the best suited subspecies for their breeding programs (Velthuis, 2002; Velthuis and van Doorn, 2006). One of these was *B. t.*

sassaricus Tournier, 1890, which naturally occurs in Sardinia. The initial breeding program was very successful and thousands of colonies of *B. t. sassaricus* were produced and shipped outside their native range into southern mainland Europe, including southern France, between 1989 and 1996 to pollinate tomatoes (Ings et al., 2005a; Velthuis and van Doorn, 2006). Since then, commercial breeders have largely been producing and exporting *B. t. dalmatinus* (Velthuis and van Doorn, 2006).

The first step in assessing the potential impacts of introducing non-native subspecies is to determine if they are able to establish themselves in the wild (i.e. establish colonies outside greenhouses) and spread beyond the areas into which they have been directly introduced. The importation of *B. t. sassaricus* into France provides an excellent opportunity to do this. Although the natural population of *B. t. sassaricus* is geographically isolated from the mainland French populations, climatic conditions of N. Sardinia and Mediterranean France are quite similar. Furthermore, a comprehensive survey of the bumblebees of France was undertaken by Rasmont (1988) prior to importation of *B. t. sassaricus*. He established that three subspecies of *B. terrestris* naturally coexist in southern France: *B. t. terrestris* (L. 1758), *B. t. lusitanicus* (Krüger 1956 [= *ferrugineus* auct. nec. Schmiedeknecht, 1878]) and *B. t. dalmatinus* Dalla Torre (1882) (Fig. 1). They exhibit the same annual cycle as *B. t. sassaricus* and *B. t. xanthopus* (Kriechbaumer, 1870) from Corsica (Ferton, 1901; Krausse, 1910), i.e. they have two generations per year, one in the spring and another in the autumn/winter (Rasmont, 1985; Duhayon and Rasmont, 1993). Finally, distinct differences in coat colour patterns of Sardinian and mainland subspecies (described fully in the methods) allow them to be readily distinguished in the field.

Therefore, in this study we use long-term observations of *B. terrestris* in southern France (covering a 15 year period since the initial importation of *B. t. sassaricus*) coupled with recent targeted surveys, to track the potential establishment and spread of an introduced non-native bumblebee subspecies.
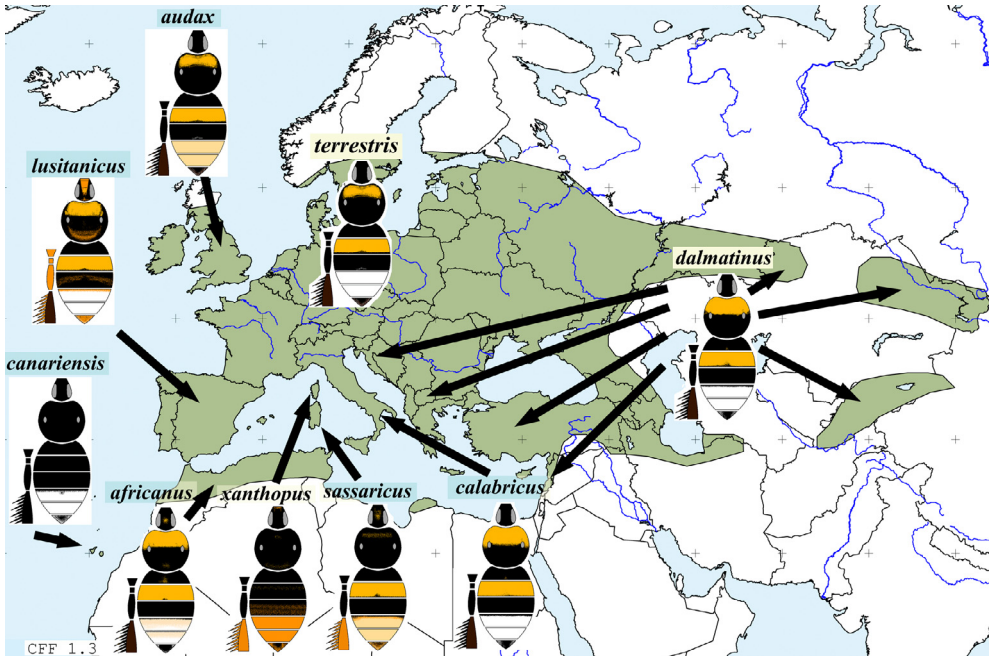
Figure 1. The natural distribution of *B. terrestris* subspecies. The shaded area indicates the range over which *B. terrestris* occurs and the arrows point to the approximate centres of distribution of the nine subspecies. This figure was reproduced with permission from Rasmont et al. (2008).

2. MATERIALS AND METHODS

2.1. Study subspecies

Five subspecies of *Bombus terrestris* L. occur along the southern coast of France and on the Tyrrhenian islands (Sardinia, Corsica and Elba): *B. t. dalmatinus, B. t. terrestris, B. t. lusitanicus, B. t. sassaricus* and *B. t. xanthopus.* The subspecies from the islands show highly distinct colour patterns from those on the mainland (Rasmont et al., 2008). In particular, the Sardinian subspecies of *B. terrestris* can easily be distinguished from all other subspecies found in southern France. The native French subspecies (*B. t. terrestris, B. t. lusitanicus* and *B. t. dalmatinus*) have a black coat with a yellow collar at the front of the thorax, a yellow band on the front of the abdomen (which has a white tip), and black legs (although *B. t. lusitanicus* has black legs with reddish-brown hair). However, *B. t. sassaricus* females (workers and queens) have no yellow band on the thorax and the cuticle on their legs is conspicuously reddish-brown. These characters therefore make field identification of *B. t. sassaricus* easy (Fig. 1). Subspecies of *B. terrestris* are able to

hybridise in the laboratory and in the wild (Rasmont and Adamski, 1996; Rasmont and Quaranta, 1997; Rasmont et al., 2008). We have observed intermediate forms of the three native subspecies in France, indicating that they also hybridise naturally, if infrequently. Coat coloration seems to be controlled by a single locus (Velthuis and van Doorn, 2006) and the red colouration of the legs of *B. t. sassaricus* is carried forward into hybrids, with 50% of males from hybrid matings and all F1 workers maintaining this character (Chittka and Wells, 2004; Velthuis and van Doorn, 2006).

2.2. Area surveyed

During the course of this study (1988–2004) we surveyed all departments of Continental France adjacent to the Mediterranean, from West to East: Pyrénées-Orientales (Postcode 66), Aude (11), Hérault (34), Gard (30), Bouches-du-Rhône (13), Vaucluse (84), Var (83) and Alpes-Maritimes (06) (see Figs. 2–5). This area encompasses the entire range of the autumn/winter generation of *B.*
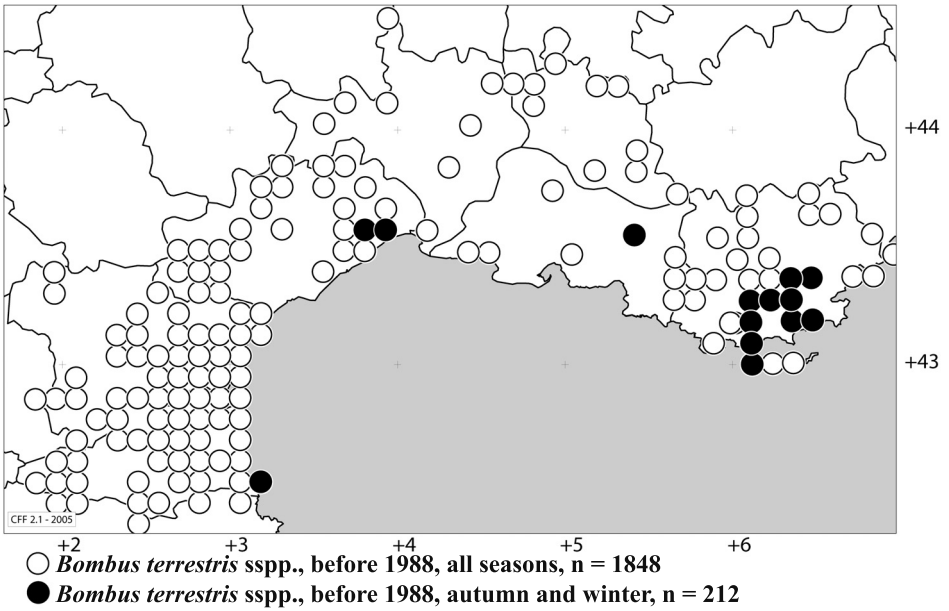
Figure 2. Pre 1988 observations of native *B. terrestris* subspecies in southern France prior to the importation of *B. t. sassaricus*.
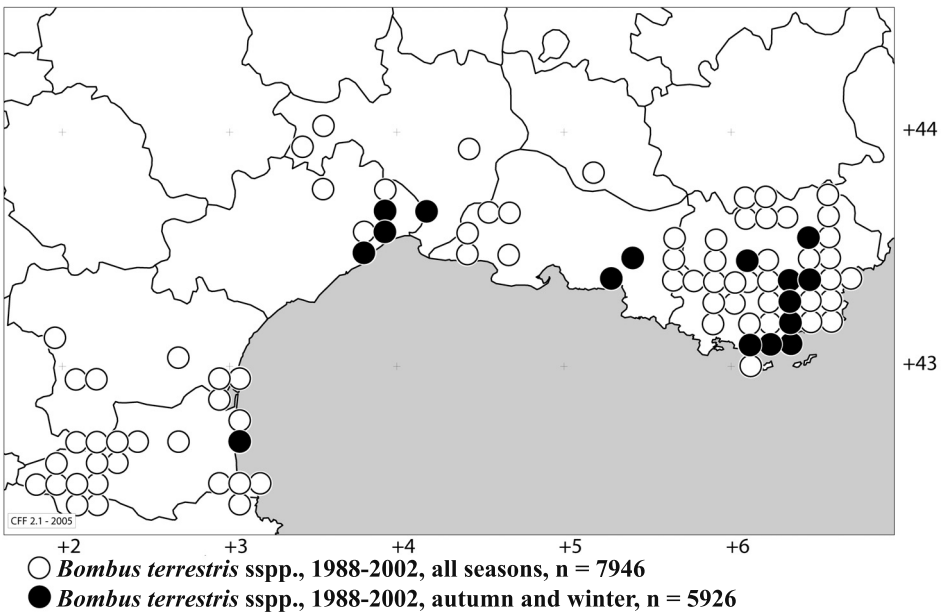

Figure 3. Observations of *B. terrestris* subspecies made between 1988 and 2002. NB. *B. t. sassaricus* was recorded at four localities (see Fig. 5).
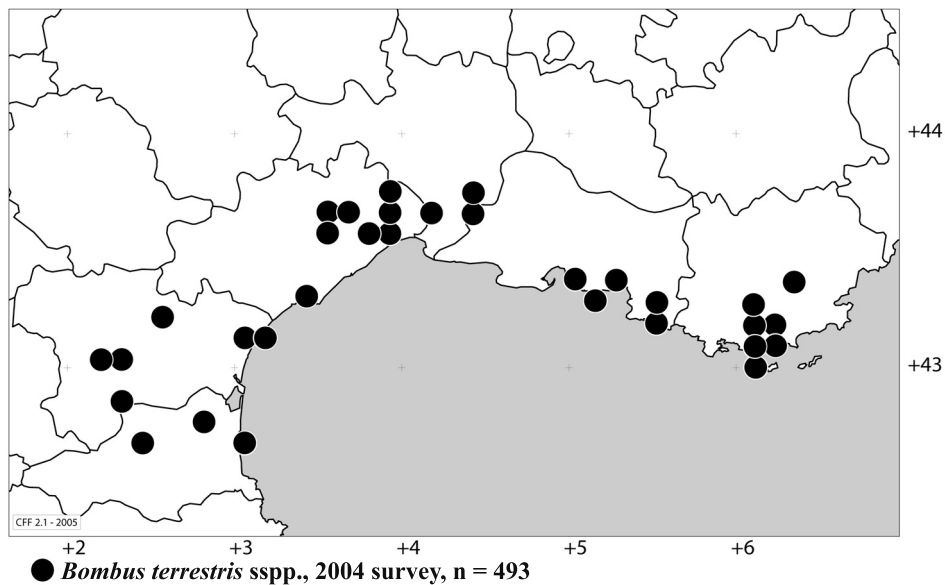
Figure 4. Records of *B. terrestris* subspecies collected during 2004. NB. no *B. t. sassaricus* were found.
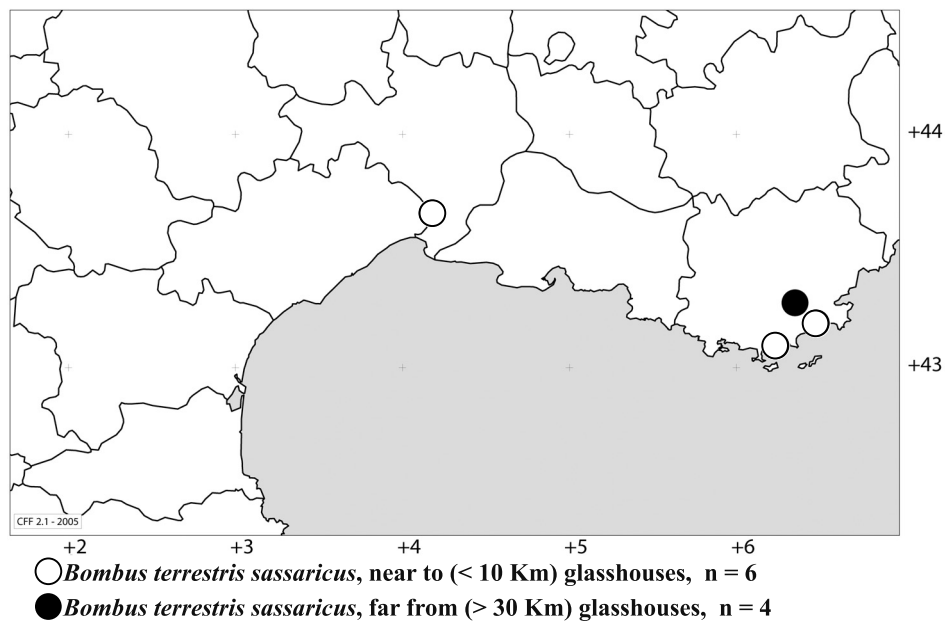

Figure 5. Location of *B. t. sassaricus* records collected between 1993 and 1998.

terrestris in continental France (Rasmont, 1985; Duhayon and Rasmont, 1993).

2.3. Data collection

2.3.1. 1988-2002

Since 1988, PR made ad hoc visits of 1–2 months every year in the Mediterranean region of France (Fig. 3), typically in October, November, December, April, May, July and August. Most of these visits (April, May) involved intensive insect collection by students from the Université de Mons-Hainaut, as part of a Zoology and Ecology field course. The October-November trips were devoted to collecting queens for bumblebee breeding and the December and July observations were part of short collecting excursions during holidays. *Bombus terrestris* is in aestivation during August in the Mediterranean basin. During this time a total of 7 946 *B. terrestris* specimens were examined.

2.3.2. Survey of 2004

To follow up previous observations, and determine whether *B. t. sassaricus* had indeed become established in southern France, extensive searches were carried out in 2004 along the length of the French Mediterranean coastline (Fig. 4), from near Hyères (43°08' N 6°07' E) in the east to near Perpignan (42°42' N 2°53' E) in the west. Three visits were made to encompass different generations of *B. terrestris.* The first visit occurred in May (9th to 20th) to coincide with peak worker activity of the spring generation. A second survey was carried out near Montpellier and Perpignan in October (18th to 21st) to coincide with peak activity of nest founding queens after the first autumn rains. Finally, a return visit to the Montpellier region was made in December (19th to 23rd) to coincide with peak worker activity of colonies founded by the generation of queens observed in October.

During these periods over 100 flower rich sites at 32 locations were monitored by two observers for the presence of bumblebees. A total of 478 *B. terrestris* specimens were examined. We used either standard bee walks (e.g. Pollard, 1977; Banaszak, 1980) or fixed observations, depending on the habitat type. Bee walks entailed walking slowly (~ 1 m s^{-1}) along a linear habitat (e.g. roadside verge or flowering hedge) identifying and recording all visible bumblebees (typically within 2 m either side of the transect). For habitats where flowers were in discrete patches (e.g. flowering shrubs), individual patches (typically 4 by 4 m) were observed (10–20 minutes combined observation time per patch – up to 1 hour if bumblebees were detected). All sites were monitored during dry weather. During October and December, all bees were captured and marked, by placing a dot of white correction fluid (Tippex®) on the thorax, to avoid re-recording the same individuals.

When a bumblebee was observed it was scored as a queen, worker or male and identified as nonnative *B. t. sassaricus* (all black thorax and red legs) or native French *B. terrestris* sl. (yellow banded thorax and black legs). Queens and workers of the native French *B. terrestris* showing distinct characteristics were further split into subspecies: *B. t. terrestris* (narrow yellow band on the thorax), *B. t. dalmatinus* (wide yellow band on its thorax) and *B. t. lusitanicus* (distinctive reddish-brown hairs on its legs).

3. RESULTS

3.1. Extensive surveys 1988 to 2002

3.1.1. Before importation of B. t. sassaricus (pre 1989)

The original survey by Rasmont (1988), which occurred largely before the mass import of *B. t. sassaricus*, revealed the co-occurrence of three native subspecies of *B. terrestris* (*B. t. terrestris, B. t. dalmatinus* and *B. t. lusitanicus*) in the Mediterranean coastal regions of France (Fig. 2). However, although 1 848 individuals (mainly those cited by Rasmont, 1985) were observed (Fig. 2) across all departments (66, 34, 30, 13, 84 and 83), no specimens of *B. t. sassaricus* were found (mean proportion in population = 0, upper 95% Confidence Interval (Wilson score interval: Newcombe 1998) = 0.0021).

3.1.2. During importation of B. t. sassaricus (1989–1996)

During the second survey between 1988 and 2002, a further 7 946 *B. terrestris* were

recorded across all surveyed departments (Fig. 3). The majority of these records (5 626 bees) were from the autumn/winter generation (recorded between September 21 and January 31) and were observed visiting *Salpichroa origanifolia* (Lam.) Baillon and *Arbutus unedo* L. A small number of *B. t. sassaricus* (6 in total between 1991 and 1994) were observed for the first time at three different locations in areas close (< 10 km) to commercial greenhouses (Tab. I, Fig. 5). One of the males observed in 1994 showed characteristics of both *B. t. terrestris* and *B. t. sassaricus*.

3.1.3. *After importation of* **B. t. sassaricus** *ceased (1998)*

In 1998, two years after the last colonies of *B. t. sassaricus* were imported into France, several *B. t. sassaricus* workers were observed foraging alongside native subspecies in an isolated garden surrounded by forest close to Gonfaron, Var (Tab. I, Fig. 5) more than 30 km from the nearest commercial greenhouses (which typically occur along the coastal plains). However, despite frequent return visits in all seasons, no more *B. t. sassaricus* have been recorded at this location.

3.2. Survey of 2004

3.2.1. *May*

Bumblebee abundance was low in May 2004, with less than 200 *B. terrestris* being recorded, despite extensive searches being carried out at 75 flower rich patches during good weather. Furthermore, *B. terrestris* was only recorded at just over half (39 out of 75) of the flower rich patches surveyed (Fig. 4). Most records of *B. terrestris* were workers (152), although some queens (12) and a few males (7) were seen. All three native subspecies (*B. t. terrestris, B. t. lusitanicus, B. t. dalmatinus* and various intermediate forms (putative hybrids)) were recorded. However, no *B. terrestris sassaricus*, or F1 hybrids, were found in a total sample of 171 bees (mean proportion = 0, upper 95% Confidence Interval = 0.022).

3.2.2. *October*

A large number of queens (135) and a few males (20) of the three native subspecies were observed at six *S. origanifolia* and two *A. unedo* sites in October (Fig. 4). About 45% of the 60 queens recorded at the largest *S. origanifolia* location (Mas de St-Michel, near Aimargue) were *B. t. lusitanicus*, 33.3% *B. t. terrestris* and 16.7% *B. t. dalmatinus.* However, no *B. terrestris sassaricus*, or F1 hybrids, were found in a total sample of 155 bees (mean proportion = 0, upper 95% Confidence Interval = 0.024).

3.2.3. *December*

During the final survey in December, *B. terrestris* was recorded at all of the six locations near Montpellier. Mostly workers (135), a few males (16) and one queen were observed foraging on *A. unedo, Erica multiflora* L. and *Rosmarinus officinalis* L. About two thirds of bees recorded were either *B. t. terrestris* or *B. t. dalmatinus* (they were not separated on this occasion) with the remaining third being *B. t. lusitanicus*. However, no *B. terrestris sassaricus*, or F1 hybrids, were found in a total sample of 152 bees (mean proportion = 0, upper 95% Confidence Interval = 0.025).

4. DISCUSSION

This study is one of the first to document the escape, temporary establishment and apparently failed invasion of an imported subspecies. Extensive surveys of southern France carried out during the 1990's revealed that males and queens (i.e. reproductively active castes) of the commercially imported, non-native subspecies *B. t. sassaricus* were escaping into the wild. More importantly, by 1998 *B. t. sassaricus* appeared to have become naturalised in at least one wild area of southern France far from greenhouses. However, in subsequent surveys we were unable to detect the presence of *B. t. sassaricus*, indicating that it has been unable to persist, possibly through competitive exclusion by the three native subspecies. Alternatively, *B. t. sassaricus* may be

Table I. Detailed records of all sightings of *B. t. sassaricus* workers (W), queens (F) and males (M) observed during the 1988–2002 survey period which yielded 7946 sightings of *B. terrestris*.

Date	Location (with European data coordinates)	Habitat	Flower	Subspecies	
22.VII.1991	43° 13′46″N 6° 31′04″E Var, Cogolin, Les Faisses	Fallow land in cultivated plain (vineyards, greenhouses)	*Echium plantagineum* L.	*B. t. terrestris*	4W
				B. t. sassaricus	1W
4.X.1993	43° 07′05″N 6° 11′53″E Var, Hyères, Les Salins d'Hyères	Salty grassland with *Salicornia* and some rubble on the verge	*Salpichroa origanifolia* (Lam.) Baillon	*B. t. lusitanicus*	6F
				B. t. terrestris	25M
				B. t. sassaricus	1F
				B. t. terrestris	2W
25.VII.1994	43° 41′26″N 4° 10′46″E Gard, Aimargues, Mas de St-Michel	Fallow land in cultivated plain (vineyards, orchards, greenhouses), ruderal vegetation with *S. origanifolia*	*S. origanifolia*	*B. t. terrestris*	1F
				B. t. terrestris	20W
				B. t. terrestris	10M
				B. t. sassaricus	1W
				B. t. sassaricus	2M
				B. t. terrestris x sassaricus	1M
16.IV.1998	43° 18′28″N 6° 18′33″E Var, Gonfaron, Notre-Dame du Figuier	Small garden in Mediterranean Forest *Quercus pubescens, Q. suber, Erica arborea, Arbutus unedo*	*Wisteria floribunda* (Willd.) DC. (ornemental)	*B. t. lusitanicus*	10W
				B. t. lusitanicus	20M
				B. t. terrestris	40W
				B. t. terrestris	3F
				B. t. terrestris	20M
				B. t. sassaricus	4W

present in very low numbers or its appearance may have become indistinguishable from the other native subspecies as a result of frequent hybridisation.

The structure of *B. terrestris* populations is complex: insular forms (including *B. t. sassaricus* and *B. t. xanthopus* from the Tyrrhenian Islands and *B. t. canariensis* from the Canary Islands) are significantly genetically differentiated from mainland forms (Estoup et al., 1996; Widmer et al., 1998; Rasmont et al., 2008). Several of the subspecies are able to hybridise, both under laboratory (Ings et al. 2005b) and natural conditions (Rasmont and Adamski, 1996; Rasmont and Quaranta, 1997). Therefore, moving subspecies, especially insular ones, into regions where they are not native could have important implications for the genetic diversity of *B. terrestris*.

Discovery of both male and queen *B. t. sassaricus* close to commercial greenhouses in the 1990's showed that they were escaping in to the wild. *B. t. sassaricus* will hybridise with *B. t. xanthopus* in southern Corsica, although hybrids are very rare (Rasmont and Adamski, 1996), so it is conceivable that hybridisation would be a problem in southern France. However, only one male showing mixed characters, i.e. a putative hybrid, was discovered near to greenhouses during this study (Tab. I).

Although low numbers of *B. t. sassaricus* were observed outside greenhouses, large quantities (thousands) of *B. t. sassaricus* colonies were used in southern France over 8 years (1989–1996). Release of a few individuals from each colony every year (possibly several times a year) would represent a high propagule pressure, which is known to increase the probability of establishment by alien species (Kolar and Lodge, 2001). Furthermore, *B. terrestris* appears to be able to establish viable populations from a very small pool of foundress queens (Buttermore et al., 1998). Southern France also provides *B. t. sassaricus* with suitable habitats containing important biota necessary to sustain its autumn/winter generation. Notably, extensive *A. unedo* populations, a common food plant for *B. t. sassaricus* in northern Sardinia (Krausse, 1910), are present in the Massif des Maures to the north-west of Saint Tropez and the Massif

de l'Arboussas to the north-west of Montpellier. We therefore expected that *B. t. sassaricus* should readily become established in southern France.

Our expectations were met to some extent in 1998 when workers of *B. t. sassaricus* were observed foraging in an isolated area of the Massif des Maures. This observation occurred nearly two years after the importation of *B. t. sassaricus* ceased, and was more than 30 kilometres from the nearest commercial greenhouses. Clearly *B. t. sassaricus* had established feral colonies in the region and had persisted for at least 2 years. However, no further observations of *B. t. sassaricus*, or visible F1 hybrids, have been made since, despite continued visits to the same area and extensive surveys along the south coast of France (between Hyères in the east and Perpignan in the west: Fig. 4). This leads us to ask why no more *B. t. sassaricus* were seen again.

A problem with surveys is that it is easier to show presence than it is to conclusively show absence. Survey effort, i.e. area covered, observation hours and number of observations is important. In our study, the surveys undertaken between 1988 and 2002, when a few specimens of *B. t. sassaricus* were observed, covered a larger area and involved many more observations (7 946 compared to 493) than the 2004 survey. It is therefore possible that *B. t. sassaricus* were missed in the 2004 surveys. Furthermore, low bumblebee densities occurred during the surveys in May 2004: *B. terrestris* was only recorded at 39 out of 75 suitable habitat patches. This scarcity, which may have been a consequence of the extreme dryness in 2003, might have affected our ability to detect *B. t. sassaricus.* However, our surveys incorporated areas close to commercial greenhouses, where feral colonies are most likely to be found (Inari et al., 2005), and areas where *B. t. sassaricus* had previously been recorded (e.g. near Aimargue). The surveys also targeted areas of habitat containing favoured food plants of *B. t. sassaricus* (e.g. *A. unedo* in the Massif des Maures and near Montpellier). The surveys in October and December also increased the total area covered and the number of bees identified. Yet, no *B. t. sassaricus* or its F1 hybrids were seen,

even amongst the large number of queens that were recorded near Aimargue. More importantly, the upper estimate for the proportion of *B. t. sassaricus* present in the population of *B. terrestris*, i.e. those potentially missed was only 0.8% for the combined 2004 survey.

It is possible that no *B. t. sassaricus* were found because hybridisation with other subspecies during the last decade has led to loss of the distinctive colouration of *B. t. sassaricus*. Coat colouration seems to be controlled by a single locus (Velthuis and van Doorn, 2006), so continued mixing with other native subspecies over at least 16 generations (two generations per year) could remove colour variation from the resident population. Yet, the three native subspecies recorded in this study still maintained their natural colour forms despite low levels of hybridisation among subspecies. Therefore, although southern France appears to be a *B. terrestris* hybrid zone (only *B. t. terrestris* is present in central and northern France), a reasonably large degree of reproductive isolation must be occurring, for example through non-random mating (Ings et al., 2005b; Coppée et al., 2008). Clearly the only way to fully resolve this issue would be to sample the population of *B. terrestris* close to historical importation sites and to use molecular techniques to determine subspecies membership and/or presence of hybrids beyond the F1 generation, if it is still possible.

If we conclude, as our data suggest, that *B. t. sassaricus* was briefly established in the wild in France but was not able to persist as a pure subspecies, we are prompted to ask: why not? *B. terrestris* has readily become established in several countries outside its native range as result of intentional or accidental introductions (e.g. in New Zealand: Hopkins, 1914; Chile: Ruz, 2002; and Japan: Inari et al., 2005). However, the key difference in these countries is that *B. terrestris* is a non-native *species* that may be able to utilise a slightly different niche to native species, whereas in France it is a non-native *subspecies* which shares a very similar niche to the native subspecies already present. Furthermore, in Tasmania, *B. terrestris* is able to utilise both native and introduced plants (Hingston, 2005). Thus, niche availability, which is believed to be im-

portant in invasion success (Shea and Chesson, 2002; Le Breton et al., 2005), is perhaps a limiting factor in France.

B. t. xanthopus seems to have been able to cross the 33 km distance between the Capraia and the Elba Islands, where it hybridizes with *B. t. terrestris* (Rasmont and Quaranta, 1997). *B. t. sassaricus* is easily able to cross the 12 km from Sardinia to Corsica where it hybridises, albeit rarely, with the native Corsican subspecies *B. t. xanthopus.* However, *B. t. sassaricus* has not been able to gain a foothold in Corsica, and hybrids are restricted to the southern coast (Rasmont and Adamski, 1996). This suggests that vagrant *B. t. sassaricus* and hybrid offspring are competitively excluded by the native *B. t. xanthopus.* Niche overlap between *B. t. sassaricus* and the three subspecies native to the French mainland is likely to be the same. In contrast, in New Zealand and Tasmania there are no native species of bumblebee, although *B. terrestris* may have to compete with other native bees for floral resources (Hingston and McQuillan, 1999). Furthermore, it has been suggested that introduced bumblebees in these countries rely heavily on plants introduced from Europe that are not utilised by the native bee fauna (Stout et al., 2002; Goulson and Hanley, 2004).

Our long-term study has documented the brief establishment and apparently failed invasion of a non-native bumblebee subspecies in France. *B. t. sassaricus* is no longer present, or its population density is negligible in comparison to native subspecies. We conclude that the inability of imported *B. t. sassaricus* to become properly established in France reflects competitive exclusion by the three native subspecies. However, a number of questions regarding the impact of the release of non-native subspecies into the wild remain open and need to be addressed in the future. In particular, it is necessary to use molecular techniques (e.g. Murray et al., 2008) to confirm that *B. t. sassaricus* has not disrupted the native subspecies gene pool.

ACKNOWLEDGEMENTS

Échec d'une invasion ? Celle des pollinisateurs *Bombus* introduits commercialement dans le Sud de la France.

***Bombus terrestris sassaricus* / commercialisation de *Bombus* / installation de populations / sous-espèce introduite / pollinisateurs / compétition intraspécifique/niche écologique**

Zusammenfassung – Eine fehlgeschlagene Invasion? Kommerziell eingeführte Bestäuber in Südfrankreich. Obwohl die Kommerzialisierung der Hummelbestäubung ökonomisch wichtig ist, gibt es Befürchtungen, dass sich dieser Handel negativ auf einheimische Hummelpopulationen auswirkt (Velthuis und van Doorn, 2006). Innerhalb Europas werden einige Rassen von *B. terrestris* in großer Zahl in Gebiete eingeführt, in denen sie nicht heimisch sind. Es ist daher wichtig festzustellen, ob eingeführte Rassen sich im Freiland etablieren können und eventuell invasiv werden. Das Ziel unserer Arbeit war es, eine mögliche Ansiedlung der eingeführten sardischen Hummelrasse *B. t. sassaricus* in Südfrankreich zu dokumentieren.

Wir führten eine Langzeitstudie durch, die kurz vor der Einfuhr von *B. t. sassaricus* begann (zwischen 1989 und 1996) und 8 Jahre nach dem Ende des Imports abgeschlossen wurde. Während dieser Zeit untersuchten wir alle ans Mittelmeer angrenzende Departemente des französischen Festlandes (Abb. 2–5).

Männchen und Königinnen von *B. t. sassaricus* entkamen ins Freiland und wurden in den Jahren 1991, 1993 und 1994 beim Sammeln außerhalb der Gewächshäuser beobachtet (Abb. 5). Wir fanden auch einige Arbeiterinnen in einer verwilderten Gegend nahe Gonfaron, Var, viele Kilometer vom nächsten Gewächshaus entfernt und fast zwei Jahre nachdem die Einfuhr von *B. t. sassaricus* beendet worden war. Allerdings wurden trotz fortlaufender Suche in der Nähe von Gonfaron und an 32 anderen Orten zwischen Hyères im Osten und Perpignan im Westen (Abb. 4) keine weiteren *B. t. sassaricus* mehr gefunden.

Unsere Ergebnisse zeigen eindeutig, dass kommerziell eingeführte Hummeln ins Freiland entkommen sind und in der Lage waren, sich einzubürgern.

Allerdings scheinen verwilderte Populationen von *B. t. sassaricus* nach Beendigung des Imports nicht länger als zwei Jahre zu bestehen. Diese Ergebnisse sind überraschend wenn man berücksichtigt, dass *B. t. sassaricus* in Südfrankreich ein vertrautes Habitat vorfindet und dass *B. terrestris* in Ländern weit außerhalb des natürlichen Verbreitungsgebietes zur invasiven Art geworden ist (z.B. Japan). Wir vermuten, dass die Konkurrenz durch drei einheimische Rassen verhindert hat, dass *B. t. sassaricus* in Frankreich Fuß fassen konnte, im Gegensatz zur Situation in Japan, wo *B. terrestris* sich als neue Art etabliert hat. Bevor wir aber abschließend feststellen, dass die Auswirkungen durch den Import von *B. t. sassaricus* vernachlässigbar sind, müssen wir noch überprüfen, ob die Populationsstruktur von *B. terrestris* in Frankreich durch Hybridisierungen von *B. t. sassaricus* mit einheimischen Rassen verändert wurde.

***Bombus terrestris sassaricus* / Hummelimport / Ansiedlung / eingeführte Rassen / Nischenverfügbarkeit**

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