

***Bombus terrestris*, pollinator, invasive and pest: An assessment of problems associated with its widespread introductions for commercial purposes**

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Abstract

Bombus terrestris L. (Apidae) is a native of temperate Eurasia and has been moved around the world since the 1800s. Dispersal of *B. terrestris* gained momentum in the 1980s when bees were reared artificially in Europe and supplied commercially for greenhouse pollination services. Very early after its commercial introduction, it was recognized that this species is invasive, can island hop to new locations and may disturb local ecosystems. The invasive characteristics of *B. terrestris* are: high migration ability, early seasonal emergence, high adaptability under adverse climatic conditions in various habitats, generalist or polylectic foraging strategies, enabling it to work a wide variety of flowers for resources, foraging over wide distances, a thermoregulatory metabolism that enables it to withstand low temperatures, no natural enemies to check population growth in areas outside its natural range, and it may develop two reproductive cycles in a year (bivoltine) in a newly colonized area. In addition, commercial bees produce more gynes and are better competitors than the local conspecific populations and may replace them in the likely event of an escape. The documented evidence on invasive impact of *B. terrestris* on natural ecosystems includes: negative interactions with local bee fauna, competition for nest sites with, and genetic contamination of, local *Bombus* spp., spread of parasites and pathogens and negative interactions with plant reproductive capacity. We discuss the possible measures that must be taken to minimize the *B. terrestris* invasion on local as well as on global levels.

Key words: *Bombus terrestris* L.; invasive species

WHAT IS *BOMBUS TERRESTRIS* AND WHY IT IS USED IN AGRICULTURE?

Bombus terrestris is a large (10–28 mm long), short-tongued (4.5–6.5 mm long) social bee of temperate Eurasia. Its general biology is well known (Sladen, 1912; Free and Butler, 1959; Alford, 1975; Goulson, 2003a). It can withstand adverse climatic conditions and, by its thermoregulatory abilities, can be active even on cloudy days when air temperatures are below 10°C (Heinrich, 1979) and when European honeybees (*Apis mellifera*) are unable to leave their hives.

B. terrestris has a great capacity for learning and is able to manipulate various types of flowers, including those with intricate systems (Stout et al.,

1998). It visits flowers rapidly and may visit 20 to 50 small and simple flowers per minute and on red clover between 20 and 35 flowers per minute (Free, 1993). It is an efficient pollinator of a wide variety of native plants and of crops (Velthuis and Cobb, 1991; Free, 1993; Proctor et al., 1996; Velthuis and van Doorn, 2006) and is now important as a managed pollinator in greenhouses (Table 1). Even so, its short proboscis restricts the types of flowers that it can access legitimately and so, to extract deeply hidden nectar in tubular flowers, it often resorts to nectar robbing (Inouye, 1980) by piercing the corolla tube. Hasselrot (1952) pioneered techniques for rearing bumblebees, including *B. terrestris* and by the early 1980s methods for artificially rearing this species were developed in the

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Table 1. Advantages of *B. terrestris* as a commercial pollinator

Character	Reference
Highly efficient in open air crops	Velthuis and van Doorn (2006) Calzoni and Speranza (1998), Italy, open plum orchard Meynie and Bernard (1997), France, sunflowers in cages Porporato et al. (1995), Italy, green peppers, greenhouse Willmer et al. (1994), Scotland, raspberries, open field Chen and Hsieh (1996), Taiwan, tomatoes, greenhouse Free (1993), Europe and New Zealand, red clover, open fields Porporato et al. (1993), Italy, tomatoes, greenhouse
Available active all around greenhouse conditions	Ravestijn and van der Sande (1991); van Heemert et al. (1990); van der Eijnde and de Ruijter (1991); van der Eijnde et al. (1991); Abak et al. (1997)
More economic than hand-pollination	Tomatoes, Banda and Paxton (1991); Abak et al. (1995) Raspberries, Willmer et al. (1994) Eggplants, Abak et al. (1995) Peppers, Abak et al. (1997)
Highly efficient in open air crops	Almonds, avocados, Ish Am et al. (1998) Red clover, Europe, New Zealand, Free (1993)

Netherlands (Röseler, 1985) to the extent that today *B. terrestris*' colonies are a "ready made shelf product", easily suitable for marketing and transport to any given greenhouse or habitat (van der Eijnde et al., 1991; Free, 1993; de Ruijter, 1997; Velthuis and van Doorn, 2006; Winter et al., 2006, Kwon, 2008).

The primary crop of interest for pollination by bumblebees world-wide is greenhouse tomato (*Solanum lycopersicum*, Kevan et al., 1991; Dogterom et al., 1998; Morandin et al., 2001a, b, c; Velthuis and van Doorn, 2006; Winter et al., 2006 and references given to *B. terrestris* below). As for many plants in the Solanaceae, pollination is effected through buzz-pollination by pollen collecting bees (Buchmann, 1983). Tomato flowers do not secrete nectar. The bees, foraging from commercially provided hives, visit the flowers and gather pollen. They hang upside-down from the flowers by gripping the poricidal anthers with their mandibles and in that position they vibrate their flight muscles, which makes an audible buzz and releases the pollen through the pores of the anthers onto their venters. The bees groom the pollen into their corbiculae for transport back to the hive. It is important to note that in North America *B. terrestris*' imports are not allowed and native species of *Bombus* are used commercially with equal success (Kevan et al., 1991; Meisels and Chaisson, 1997; Dogterom et al., 1998; Morandin et al., 2001a, b, c;

Winter et al., 2006).

The combination of the adaptability of *B. terrestris* and the available technology to mass-produce colonies cheaply, has made this species a commercially valuable pollinator and, in some situations, a substitute for the less flexible honeybee (de Ruijter, 1997; Velthuis and van Doorn, 2006). *B. terrestris* is an efficient as well as economic pollinator of various crops under greenhouse and open-field conditions (Table 1). There is also evidence that product quality is improved by pollination with *B. terrestris* (Table 1).

This behavior may detract from its value as a pollinator of some crops (Free, 1993). *B. terrestris* was imported into New Zealand in the 1880s to service seed production of red clover. It has since become naturalized (Montgomery, 1951; Donovan and Weir, 1978; Dunning, 1986). The characteristics of this bee, both natural and manageable, contribute to its recent and rapid distribution internationally (van der Eijnde and de Ruijter, 1991; de Ruijter, 1997; Griffiths, 2004; Velthuis and van Doorn, 2006; Winter et al., 2006). The proven value of *B. terrestris* for pollination seems to have resulted in little consideration to the development of parallel technologies for pollinators indigenous to places where *B. terrestris* is not native, except in Canada and the USA (see references above). In Australia native blue-banded bees (*Amegilla* spp.) are being developed for glasshouse pollination

(Bell et al., 2006; Hogendoorn et al., 2006, 2007) although horticulturists have been pressing to introduce *B. terrestris* to Australia for some time (Goodwin and Steiner, 1997; Cooke, 2001; Caruthers, 2003, 2004; Griffiths, 2004). The bans against import of *B. terrestris* into Canada and the USA recognize the well-known risks associated with imports of exotic species, their escape, invasive and pest potentials (Winter et al., 2006). Calls have been made by the international scientific community for all nations to extend the Canadian, American, and Malaysian approaches to imports of pollinators (e.g. Kang and Karim, 1982; Resolution at Apimondia 1997).

THE BIOTIC POTENTIAL FOR *BOMBUS TERRESTRIS* TO SPREAD?

Human beings have changed the world by purposely or accidentally introducing animals and plants far beyond their natural ranges. Even so, many human attempts to introduce species to parts of the world where they do not occur naturally have failed. In other instances, human care is required for species to persist outside their ranges. Those species that have become naturalized may be beneficial, especially to agroecosystems (e.g. various biocontrol agents and some pollinators (Batra, 1984), but more often they are notorious as pests. For example, there are many examples of the long term damage caused to Australian ecosystems from the introduction of exotic species that were initially promoted as essential and beneficial for the economy (Low, 1999). Many such species were introduced without adequate research into their potential impacts and subsequently they became serious pests (e.g. rabbits, foxes, cane toads, prickly pear, Low, 1999). It is usually impossible to eradicate established populations of introduced species, and difficult and costly to control their populations, thus it is important that thorough impact assessments are carried out in relation to proposals to introduce exotic species. For pollinators, the Malaysian example of the careful importation of the oil palm pollinating weevil from West Africa serves as exemplary (Kang and Karim, 1982). There are various international protocols, rules, treaties, and the like that are intended to prevent repetition of past mistakes of intentional, but ill-considered, even illegal, introductions (includ-

ing of pollinators and their diseases and unintentional introductions through carelessness).

There have been various cautions voiced from the scientific community about moving pollinators beyond their native ranges (Crane, 1982; Kevan, 1986, 1999, 2003; Goulson, 2003b; Thorp, 2003). Organisms that can become naturalized share some characteristics. Those that become pests variously compete with other native organisms, consume or otherwise cause destruction of native or farmed organisms, become threats to human well-being, or are nuisances.

Does *B. terrestris* have characteristics that allow it to become naturalized easily outside its natural range? Can *B. terrestris* become a pest, as Dafni (1998) has suggested?

B. terrestris has various characteristics that prove its capacity to be a successful invasive species following its introduction, namely:

A high dispersal ability is characteristic of invasive and pestiferous species

This trait, when accompanied with highly invasive abilities even from very few founders (Allen et al., 2007; Schmid-Hempel et al., 2007), means that there is a high potential for rapid spread (Hergstrom et al., 2005 and references therein but see MacFarlane and Gurr (1995) that in New Zealand large numbers of queens are required to successfully colonize an area). *B. terrestris* can spread rapidly; 90 km/year in New Zealand (Hopkins, 1914), 25 km/year (Hingston et al., 2002) in Tasmania. Buttermore (1997) warned, in reference to Tasmania, that “of course, external influences such as predatory habits by birds, availability of food, competition from other insects, and deliberate introduction by people into these areas, make the rate of spread unpredictable”. Hingston et al. (2002) showed that in the nine years since its introduction, the range of *B. terrestris* now includes all of Tasmania’s major vegetation types and an area of c. 30,000 km².

Early seasonal emergence

Early seasonal emergence, particularly of queens (Sladen, 1912; Prys-Jones and Corbet, 1991; Matsuura et al., 2004; Ings et al., 2005; Inoue et al., 2008) and long activity periods (Inari et al., 2005; Japan) could deplete spring resources before local species of *Bombus* (and other bees) are able to es-

establish nests. In Israel, *B. terrestris* queens were seen at Mt. Carmel throughout the year except January (A.D., personal observations) and in Tasmania queens were seen throughout the year, except in June, and workers and males were also found in all months except July and August (Goulson et al., 2002). *B. terrestris* is active throughout the day beginning before and ending after most of the foraging bouts of native bees (Goulson, 2003a).

High adaptability provides an invasive or pest species the capacity to become widespread and problematic

B. terrestris is highly adaptable as shown by its generalist foraging habits and broad environmental tolerances. Thus, it can establish under adverse climatic conditions in various habitats (Semmens et al., 1993; Hingston and McQuillan, 1998b; Hingston et al., 2002; Ruz, 2002 (Chile); Hergstrom, et al., 2005 (Tasmania); Hingston, 2006a; Torretta, et al., 2006 (Argentina).

Generalist foraging preference

B. terrestris is a generalist or polylectic forager that can utilize a wide variety of flowers for resources (nectar and pollen) within (Müller, 1883; Sladen, 1912; Free and Butler, 1959; MacFarlane, 1976; Proctor et al., 1996) and outside its natural range (Dafni and Shmida, 1996; Semmens, 1996a, b, 1998; Hingston and McQuillan, 1998a; Ne'eman et al., 2000; Matsumura et al., 2004; Goulson and Hanley, 2004). It may use simple flowers but can learn to manipulate and exploit complex flowers (Stout et al., 1998). Moreover, it can take advantage of deep tubular flowers by piercing corollas to illegitimately obtain nectar that (Free, 1993; Stout et al., 2000; Matsumura et al., 2004; Dohzono et al., 2008).

Broad ecological tolerances

B. terrestris (like all members of the genus *Bombus*) has a thermoregulatory metabolism which enables it to withstand low temperatures (Heinrich, 1979; Goulson, 2003a) and to be active in winter in countries that are warmer than its native region, which is established, such as Chile (Ruz, 2002), Tasmania (Semmens, 1996a) and New Zealand (Donovan and Weir, 1978).

Pathogen, parasite and predator release

Species that become invasive outside their natural ranges are often not held in check by local biotic agents. In areas outside its natural range, *B. terrestris* has few or perhaps no natural enemies to check population growth (Buttermore, 1997; Hingston and McQuillan, 1998a; Goka, 2010).

High reproductive capacity

In its native range *B. terrestris* is univoltine (Alford, 1975; Prys-Jones and Corbet, 1991), but it may develop two reproductive cycles in a year (bivoltine) in a newly colonized area (Donovan and Weir, 1978 for New Zealand; Buttermore, 1997; Hingston et al., 2002 for Tasmania). This adaptation may enhance *B. terrestris*' reproductivity and invasiveness. Commercially produced colonies of *B. terrestris* produce more gynes than do the local conspecific populations which could be swamped upon contact (Ings et al., 2006 for Great Britain).

Large home ranges

Because *B. terrestris* forages widely, its effects on the landscape are thought to be great (with respect to competitive interactions with other pollinators, and for pollen flow and population effects on plants). Workers may travel 1,500 m (Osborne et al., 2007); 1,750 m (Walther-Hellvig and Frankl, 2000) to 4 km (Goulson and Stout, 2001; Inari et al., 2005) from their nests and in Israel pollen of cultivated plants have been found on *B. terrestris* at a distance of 5 km from the nearest garden (Dafni and Shmida, 1996).

Flexible nesting preferences

B. terrestris is adaptable and readily accepts artificial nests (Prys-Jones and Corbet, 1991; Matsumura et al., 2004). Thus, it can be presumed that it is less susceptible to nest-site shortages than other species (Matsumura et al., 2004). *B. terrestris* queens may also be a social parasite and invade nests of other *Bombus* species (Sladen, 1912; Matsumura et al., 2004; Inoue et al., 2008).

DOES *BOMBUS TERRESTRIS* HAVE THE POTENTIAL TO BE A PEST OUTSIDE OF ITS NATURAL RANGE?

From the foregoing, it is apparent that *B. terrestris* has a number of characteristics that would

dispose it becoming invasive and a pest outside its natural range. Could it become pestiferous? A pest may be defined as an organism that is sufficiently abundant that its activities adversely impact human activities or environmental stability (Peterson, 2003). The major concerns surrounding *B. terrestris* are environmental.

The classical case is the spread of *B. terrestris* in New Zealand. It was introduced in 1881 and after five years, it was found to have spread into natural habitats. The speed of its spread was estimated as 90 km/year (Hopkins, 1914) but its ecological impact has never been assessed.

In Israel, *B. terrestris* was introduced commercially in the early 1990s and ten years later it had become the dominant bee on Mt. Carmel, especially following forest fires (Dafni and Shmida, 1996; Ne’eman et al., 2000; Potts et al., 2001). In Japan, it was introduced in 1991 and was found in the wild five years later (Goka, 1998) and it continues to spread (Matsumura et al., 2004). The rapid spread of *B. terrestris* was observed in Tasmania as early as two years after its introduction in 1990. There, it quickly occupied various habitats and exploited the flowers of several native species (Semmens et al., 1993; Buttermore, 1997; Hingston and McQuillan, 1998a, b; Stout and Goulson, 2000; Hingston et al., 2002; Hergstrom et al., 2005). Table 2, which documents invasions and the growing use of *B. terrestris* in various countries and in different climatic conditions, leads us to predict more escapes and spread of *B. terrestris*.

However, recently its potential to vector novel

parasites and pathogens to other species of *Bombus* (Goka et al., 2008) provides an insidious note to the risks of its anthropogenically expanding range. The danger of pathogen spillover from commercially reared *B. terrestris* to native species of *Bombus* in North America is already proven (Colla et al., 2006; Otterstater and Thompson, 2008). Clearly, with this new information more introductions of *B. terrestris* to regions outside its natural range have to be considered with a great care.

Pollination of weed

Several studies have shown that introduced social bees are effective pollinators of weeds (Simpson et al., 2005 and references therein). Simpson et al. (2005) note that the introduction of novel pollinators could lead to increased seed production of introduced plants that currently lack an efficient pollinator (‘sleeper weeds’) causing proliferation of these weed species. This is likely to be a major threat in Australian ecosystems. Bumblebees could prove the ideal pollinator for several introduced plant species there that currently occur in low densities, and for plants that have not as yet ‘straddled the garden fence’ and become pests. For example, bumblebees are specialized pollinators of foxgloves (*Digitalis purpurea*) in Europe (Faegri and van der Pijl, 1979; Barth, 1991). In Australia foxgloves are naturalized in some parts (e.g. near Bargo, NSW (Harden, 1992)) but as yet are not found in high densities probably because of limited seed production. Foxgloves are however abundant on disturbed soil and roadsides in New Zealand,

Table 2. The spread of *B. terrestris*

Countries with commercial suppliers	Evidence of spontaneous spread after introduction	Countries in which <i>B. terrestris</i> was introduced with no evidence of spontaneous spread
Netherlands	Tunisia	Saudi Arabia
Belgium	Korea	Jordan
Spain	Uruguay	South Africa
Israel	Russia*	Great Britain
Russia		
New Zealand	Mexico	
France	Malta*	
Great Britain	Turkey*	
	Morocco	
	Taiwan	
	Israel*	
	Poland*	

* *B. terrestris* is also native in this country.

where introduced bumblebees have been present since the 1800s. Because of its preference for disturbed areas, foxglove invasions could seriously hamper revegetation by native plants. Other potential weed species that might be boosted include buzz-pollinated species belonging to the Solanaceae, many of which are poisonous- and prickly, noxious-weed species that could cause problems to the dairy and cattle industries (e.g. *Datura* spp.), *Tecoma stans* (Bignoniaceae), *Rhododendron ponticum* (Ericaceae), *Chamaecytisus palmensis* (Fabaceae) and *Polygala myrtifolia* (Polygalaceae). Recently, a correlation was found between bumblebee density and seed production in yellow lupine (*Lupinus arboreus*) (Stout et al., 2002), *Agapanthus praecox* (Hingston, 2006b), *Buddleia davidi* (Hingston, 2007) and maybe also *Rhododendron ponticum* (Hingston, 2007) in Tasmania. *Rhododendron ponticum* forms tall, dense shrubs that shade out native species. Apart from boosting sleeper weed species, pollination by *B. terrestris* could cause an increase of problems with already existing weeds, for example blackberry (*Rubus fruticosus*), gorse (*Ulex europaeus*), broom (*Cytisus scoparius*) and Paterson's Curse (*Echium vulgare*) (Rademaker et al., 1997). These concerns have prompted the successful public nomination of bumblebees as a key threatening process to the New South Wales and Victorian governments.

THE THREAT OF *BOMBUS TERRESTRIS* SPREAD, OR WHY WORRY ABOUT IT?

From the foregoing, it is clear that *B. terrestris* is an invasive species wherever it has been introduced and studies have been made (New Zealand, Israel, Tasmania, Japan, Chile, Argentina). All recent evidence shows negative aspects of *B. terrestris* invasion into natural habitats (Table 3). *B. terrestris* may interfere with the flora as well as with the fauna at both community and population levels, displacing native pollinators and probably changing the capacity of some native plants to reproduce at normal rates. All of this evidence of the negative implications of its massive invasion lead us to consider *B. terrestris* as a pest in Israel, Japan and Tasmania.

We are not familiar with any study which shows any positive or even neutral intervention of *B. ter-*

restris in natural ecosystems, but Goodwin and Steiner (1997) concluded, concerning the possible introduction of *B. terrestris* into mainland Australia for pollination of horticultural crops, that: "Bumblebees are as likely to have a positive impact on Australian ecology as a negative one, but in either case it is a drop in the bucket compared with the effect of habitat destruction created by man... The impact of bumblebees on crop yields, however, will be immediate and substantial... Australia will not be able to sustain the market share in Australia, let alone compete for export market. Bumble pollination is an essential part of the necessary yield increase". Although their suggestion for potentially high proximate gain for the greenhouse tomato industry rings true, the risks associated with cheaper Australian greenhouse tomatoes for local markets (field tomatoes do not require insect pollination) have not been investigated. It is highly unlikely, given the evidence from other introductions and the above, that *B. terrestris* would be beneficial to the natural Australian environment, there appears to be no need of it in mainstream Australian agriculture and alternatives with native species are being developed (e.g. Hogendoorn et al., 2006). The remark about anthropogenic habitat destruction is a "red-herring" and not germane to the discussion regarding the impacts of *B. terrestris* on Australian landscapes. The current available evidence does not support Goodwin and Steiner's views (e.g. see Hingston et al., 2002).

WHAT TO DO?

Most countries have quarantine regulations and legislation and international agreements to control the possible adverse effects of introductions, and most have special regulations concerning the import/export of agricultural insects especially agents considered for release for biocontrol of pests. Many countries are signatories to international phyto- and zoo-sanitary agreements that also pertain to stemming the international flow of pests and diseases. As far as we are aware, many countries have no specific legal restrictions on the import or export of bees as commercial pollinators. Nevertheless, trade in exotic pollinators may be contraventions of international phyto- and zoo-sanitary agreements and similar conventions. Some countries are careful and unwilling to import exotic pol-

Table 3 The environmental threats of *B. terrestris*' spread

Threat	Evidence and references
Negative interactions with local bee fauna	Depletion of floral resources (Dafni and Shmida, 1996, Israel; Hingston, 2007, Tasmania; Matsumura et al., 2004, Japan). Displacement of local bee species (Dafni and Shmida, 1996, Israel; Hingston and McQuillan, 1999; Hingston, 2007, Tasmania; Matsumura et al., 2004, Japan), possible through resource competition (Hingston and McQuillan, 1999; but see Nagamitsu and Kenta, 2007; Nagamitsu et al., 2007).
Competition on nest's sites	<i>B. terrestris</i> competes and also occupies nesting sites of local <i>Bombus</i> species (Matsumura et al., 2004).
Genetic contamination of local <i>Bombus</i> species	<i>B. terrestris</i> has the capacity to copulate with local <i>Bombus</i> species (Goka, 1998, 2010; Kanbe et al., 2008, Japan). <i>B. terrestris</i> may cause genetic contamination of local subspecies (Ornosa, 1996, Spain). <i>B. terrestris</i> mate with the local endemic <i>B. canariensis</i> , a threat to biodiversity (van der Eijnde and de Ruijter, 2000). <i>B. terrestris</i> in Mediterranean islands are, significantly, genetically differentiated from continental populations. "DNA data from Canary islands calls for protection against importation of <i>B. terrestris</i> of foreign origin for pollination" (Estoup et al., 1996).
Invasion and spread of parasites and pathogens	Parasitic protozoans and endoparasitic mites were already found in <i>B. terrestris</i> introduced colonies (Goka, 1998, 2010; Goka et al., 2000, 2001, 2006; Okada et al., 2000; Schmid-Hempel et al., 2007; Yoneda et al., 2008). Recent epizootic of protozoa (<i>Nosema</i> spp.) in cultured <i>B. occidentalis</i> colonies in western North America may have come about through transfer from other <i>Bombus</i> species in commercial rearing facilities (Winter et al., 2006).
Disturbances with the reproduction of the local flora	Less effective pollination and reduction of seed set when <i>B. terrestris</i> is a main visitor (Ne'eman and Dafni, 1999; Ne'eman et al., 2000; Hingston et al., 2004; Kenta et al., 2007) as well as fruit quality (Kenta et al., 2007). Reducing pollination, piercing and robbing flowers, possibility to interfere with the plants' reproductive success (Hingston and McQuillan, 1998a; Hingston, 2007). Disruption of native plant-pollinator systems may precipitate reduced seed set in native plants. In Australia, several native plant species have co-evolved with, and are dependent on, one or two species of bird or insect pollinators (e.g. Hopper and Burbidge, 1986; Gross, 1992, 1993a, b; Houston, 1993). The presence of bumblebees could decrease the density of these natural pollinators, through competition for nectar and direct displacement. In the long term, this could jeopardize fruit and seed availability (Gross and Mackay, 1998). A decrease in seed production through direct displacement of native bees by honeybees has been demonstrated to occur in <i>Melastoma affine</i> (Gross and Mackay, 1998).
Rapid invasion rate	Spread rate 90 km/year in New Zealand (Hopkins, 1914), 12.5 km/year in Tasmania (Buttermore, 1997).

linators without proper and scientific consideration. In Canada and the USA the introduction of foreign bumblebees is prohibited and only local species are reared (de Ruijter, 1997; Winter et al., 2006). Malaysia was extremely careful in its scientific as-

essment of the risks of importing the oil palm pollinating weevil (*Elaeidobius kamerunicus*) from West Africa (Kang and Karim, 1982), and like many countries has strict regulations about the movement of honeybees (*Apis* spp.) because of the

risk of transmission of diseases and affecting other indigenous insects and plants.

The warnings and precedents are clear, yet the pressure to export *B. terrestris* to more and more exotic destinations continues. Several measures need to be considered before such exports and imports are allowed. These measures apply to all pollinators considered for import (Ings et al., 2006)

1) National benefits resulting from pollinator import should be evaluated through environmental, social and economic analysis with particular attention to the precautionary principle and intergenerational equity.

2) Environmental risk assessment of such an import should be undertaken (Ings et al., 2005). The Malaysian example of import of the oil palm pollinating weevils serves well (Kang and Karim, 1982). One condition of any pollinator import (including that of *B. terrestris*) should be a survey on the potential impact of the introduction (see Ings et al., 2006). This is especially important in regions with high numbers of unique and endemic flora and bee fauna (e.g., South Africa, Australia, Madagascar, Canary Islands) and where there are sleeper weeds. In Japan, an ecological risk assessment of *B. terrestris* has recently and legally restricted their importation through the new statute the *Invasive Alien Species Act* (2007) Japan.

3) The lack of indigenous pollinators with potential for practical application must be proven. The potential for domestication or encouragement of indigenous pollinators has been proven for *Bombus* spp. (Dogterom et al., 1998; Morandin et al., 2001a, b in Canada; Asada and Ono, 1996; Goka, 1998 in Japan), *Xylocopa* (Hogendoorn et al., 2000 in Australia) and *Amegilla* (Bell et al., 2006; Hogendoorn et al., 2006, 2007 in Australia). It is also strongly suggested to domesticate local subspecies of *B. terrestris* (when available) to avoid genetic contamination with imported subspecies (Ings et al., 2006). The known successes of the use of leaf-cutting bees, *Megachile rotundata* (accidentally introduced into North America), various orchard bees, *Osmia* spp., and other species in crop pollination, serve as other examples (Bohart, 1972; Parker et al., 1987; Torchio, 1987, 1994; Kevan et al., 1990; Richards, 1993).

4) If, after steps 1, 2, and 3, the importation of an exotic pollinator is recommended, then legislation should be applied (enacted, modified, or speci-

fied) to control the zoo-sanitary quality of the pollinator. The health certification should be a precondition to any commercial export and/or distribution of commercial colonies as is the case for shipments of honeybees (*Apis mellifera*) in many countries. Quarantine and inspection services should be established by the importing and exporting country. The responsibility and onus for the eradication of escaped bumblebees should lie with the industry that is using this species and not with the public. The costs of a 'clean-up' for escaped *B. terrestris* could be phenomenal given their likely facilitation of weed pollination. For example, weeds already cost Australia \$3,554–4,532 billion per annum in control and lost production (Sinden et al., 2004), and an Australian government report conservatively estimated that if nine current sleeper weeds were not eradicated they could eventually cost \$100 million dollars annually in lost agricultural production (Brinkley and Bomford, 2002). Bumblebees have the potential to exacerbate the eradication program for many weed species, e.g. gorse.

5) Specifically with respect to pollination services in enclosed spaces, e.g. greenhouses, pollinator domiciles should be designed specifically to minimize the likelihood of escape (e.g. for *Bombus* queens mechanical restriction in the beehive entrance which may reduce the in out traffic (Thompson, 1997; Thorp, 2003; Griffiths, 2004; Ings et al., 2006; Hingston, 2007; Yoneda et al., 2007) and perhaps hormonal treatment and thorough containment, destruction and disposal of the pollinators after they have served their purpose. Control measures for dealing with escapees must be formulated and should include control measures/protocols, responsible authorities and penalties for misuse or deliberate release of the bees.

In summary, we have collated and evaluated much of the considerable information on the ecology and impacts of *B. terrestris* on native ecosystems. In concert with many scientists worldwide we urge governments to exercise extreme caution and to implement the precautionary principle in any requests for live importations of *B. terrestris*. However, in some parts of the world, for example Australia, Canary Islands, South Africa and South America the risks to the native biota are assessed here as too great to warrant the risk of live importations.

REFERENCES

- Abak, K., N. Sari, M. Kaftanoglu, O. Yeninar, H. Fernandez-Manoz, R. Cuartero and M. L. Gomez-Guillamon (1995) Efficacy of bumblebees on the yield and quality of eggplant and tomato grown in unheated greenhouses. *Acta Hort.* 412: 268–274.
- Abak, K., O. Kaftanoglu, O. Dasgan, H. Y. Ikiz, O. Sayalan, M. Uygun and H. Yeninar (1997) Pollen production and quality of pepper grown in unheated greenhouses during winter and the effects of bumble bees (*Bombus terrestris*) pollination on fruit yield and quality. *Acta Hort.* 437: 303–308.
- Alford, D. V. (1975) *Bumblebees*. Davis-Poynter, London. 352 pp.
- Allen, G. R., D. Seeman, P. Schmid-Hempel and R. E. Buttermore (2007) Low parasite load accompany the invading populations of bumblebee, *Bombus terrestris* in Tasmania. *Insect. Soc.* 54: 56–63.
- Asada, S. and M. Ono (1996) Crop pollination by Japanese bumblebees, *Bombus* spp. (Hymenoptera: Apidae): Tomato foraging behavior and pollination efficiency. *Appl. Entomol. Zool.* 31: 581–586.
- Banda, H. J. and R. J. Paxton (1991) Pollination of greenhouse tomatoes by bees. *Acta Hort.* 288: 194–198.
- Barth, F. G. (1991) *Insects and Flowers: The Biology of a Partnership*. Princeton Scientific Library, Princeton, NJ. 297 pp.
- Batra, S. W. T. (1984) *Anthopora pilipes villosula* Sm. (Hymenoptera: Anthophoridae). A manageable Japanese bee that visits blueberries and apples during cool, rainy, spring weather. *Proc. Entomol. Soc. Wash.* 96: 98–119.
- Bell, M. C., R. N. Spooner-Hart and A. M. Haigh (2006) Pollination of greenhouse tomatoes by the Australian blue banded bee *Amegilla (Zonamegilla) holmesi* (Hymenoptera: Apidae). *J. Econ. Entomol.* 99: 437–442.
- Bohart, G. E. (1972) Management of wild bees for pollination of crops. *Annu. Rev. Entomol.* 17: 287–312.
- Brinkley, T. R. and M. Bomford (2002) Agricultural sleeper weeds in Australia. What is the potential threat. http://www.weeds.crc.org.au/documents/mr_investment.pdf
- Buchmann, S. L. (1983) Buzz pollination in angiosperms. In *Handbook of Experimental Pollination Biology* (C. E. Jones and R. J. Little, eds.). Van Nostrand Reinhold, New York, pp. 73–113.
- Buttermore, R. E. (1997) Observations of successful *Bombus terrestris* (L.) (Hymenoptera: Apidae) colonies in southern Tasmania. *Austral. J. Entomol.* 36: 251–254.
- Calzoni, G. L. and A. Speranza (1998) Insect controlled pollination in Japanese plum (*Prunus salicina* Lindl.). *Sci. Hort. (Amsterdam)* 72: 227–237.
- Carruthers, S. L. (2003) Plight of the bumblebee. *Pract. Hydrop. Green.* 69: 24–30.
- Carruthers, S. L. (2004) A bee's eye view. The cases for and against the importation of bumblebees onto mainland Australia to pollinate crops. *Pract. Hydrop. Green.* 77: 24–28.
- Chen, C. T. and F. K. Hsieh (1996) Evaluation of pollination efficiency of the bumblebee *Bombus terrestris* (L.) on greenhouse tomatoes. *Zhonghua Kunchong* 16: 167–175 (Biosis no. 99473431).
- Colla, R. S., M. C. Otterstatter, R. J. Gegeer and J. D. Thompson (2006) Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biol. Conserv.* 129: 461–467.
- Cooke, A. (2001) Bumblebees under study. *Pract. Hydrop. Green.* 59: 20–24.
- Crane, E. (1982) Introduction of non-native bees into new areas. *Bee World* 63: 28–30.
- Dafni, A. (1998) The threat of *Bombus terrestris* spread. *Bee World* 79: 113–114.
- Dafni, A. and A. Shmida (1996) The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt. Carmel, Israel. In *The Conservation of Bees* (A. C. Matheson, ed.). The Linnean Society of London, London, pp. 183–200.
- Dogteron, M. H., J. A. Matteoni and R. C. Plowright (1998) Pollination of greenhouse tomatoes by the North American *Bombus cosnesenskii* (Hymenoptera: Apidae). *J. Econ. Entomol.* 91: 71–75.
- Dohzono, I., K. Y. Kunitake, J. Yokoyama and K. Goka (2008) Alien bumble bee effects native plant reproduction through interactions with native bumble bees. *Ecology* 89: 3082–3092.
- Donovan, B. J. and S. S. Weir (1978) Development of hives for field population increase and studies on the life cycle of the four species of introduced bumblebees in New Zealand. *N. Z. J. Agr. Res.* 21: 733–756.
- Dunning, J. W. (1886) The importation of humble bees into New Zealand. *T. Roy. Ent. Soc. London* 6: 32–34.
- Eijnde van der, J. and A. de Ruijter (1991) The use of bumblebee colonies (*Bombus terrestris*) for pollination of glasshouse tomatoes. *Proc. Appl. Entomol. Nether. Entomol. Soc.* 2: 129–130.
- Eijnde van der, J. and A. de Ruijter (2000) Bumblebees from the Canary Islands: Mating experiments with *Bombus terrestris* L. from Netherlands. *Proc. Experimen. Appl. Entomol. Netherlands Entomol. Soc.* 11: 159–162.
- Eijnde van der, J., A. de Ruijter and J. van der Steen (1991) Method for rearing *Bombus terrestris* continuously and the production of bumblebee colonies for pollination purposes. *Acta Hort.* 288: 154–158.
- Estoup, A., M. Solognac, J. M. Cornuet, J. Goudet and A. Scholl (1996) Genetic differentiation of continental and inland populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Mol. Ecol.* 5: 19–31.
- Faegri, K. and L. van der Pijl (1979) *The Principles of Pollination Ecology*. 3rd ed. Pergamon Press, Oxford. 244 pp.
- Free, J. B. (1993) *Insect Pollination of Crops*. 2nd ed. Academic Press, London. 768 pp.
- Free, J. B. and C. G. Butler (1959) *Bumblebees*. Collins, London. 208 pp.
- Goka, K. (1998) Influences of invasive species on native species—will the European bumblebee, *Bombus terrestris*, bring genetic pollution into Japanese native species? *Bull. Biograph. Soc. Jpn.* 53: 91–101 (in Japanese with English summary).

- Goka, K. (2010) Introduction to the Special Feature for Ecological Risk Assessment of Introduced Bumblebees: Status of the European bumblebee, *Bombus terrestris*, in Japan as a beneficial pollinator and an invasive alien species. *Appl. Entomol. Zool.* 45: 1–6.
- Goka, K., K. Okabe, S. Niwa and M. Yoneda (2000) Parasitic mite infestation in introduced colonies of European bumblebees. *Bombus terrestris*. *Jpn. J. Appl. Entomol. Zool.* 44: 47–50 (in Japanese with English summary).
- Goka, K., K. Okabe, M. Yoneda and S. Niwa (2001) Bumblebee commercialization will cause world wide migration of parasitic mites. *Mol. Ecol.* 10: 2095–2099.
- Goka, K., K. Okabe and M. Yoneda (2006) Worldwide migration of parasitic mites as a result of bumblebee commercialization. *Popul. Ecol.* 48: 285–291.
- Goka, K., K. Okabe and M. Yoneda (2008) Bumblebee commercialization has caused worldwide migration of parasitic mites. In *Acarology XI: Proceedings of the International Congress* (J. B. Morales-Malacara, V. Behan-Pelletier, T. M. Ferez, C. Gispert and M. Badii, eds.). Sociedad Latinoamericana de Acarologia, Mexico, pp. 25–32.
- Goodwin, S. and M. Steiner (1997) Introduction of *Bombus terrestris* for biological pollination of horticultural crops in Australia. A submission to AQIS and Environment Australia, Gosford IPM Services, Gosford.
- Goulson, D. (2003a) *Bumblebees—Their Behaviour and Ecology*. Oxford University Press, Oxford. 246 pp.
- Goulson, D. (2003b) Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. S.* 34: 1–26.
- Goulson, D. and M. E. Hanley (2004) Distribution and forage use of exotic bumblebees in South Island, New Zealand. *N. Z. J. Ecol.* 28: 225–232.
- Goulson, D. and J. C. Stout (2001) Homing ability of bumblebees: evidence for a large foraging range? *Apidologie* 32: 105–112.
- Goulson, D., J. C. Stout and A. R. Kells (2002) Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania? *J. Insect Conserv.* 6: 179–189.
- Griffiths, D. (2004) A critical study of the introduction onto mainland Australia of the bumblebee *Bombus terrestris* for the commercial pollination of protected tomato and other crops. *Pract. Hydrom. Green.* 77: 42–59.
- Gross, C. L. (1992) Floral traits and pollinator constancy: foraging by native bees among three sympatric legumes. *Austral. J. Ecol.* 17: 67–74.
- Gross, C. L. (1993a) The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a pioneer shrub in tropical Australia. *Biotropica* 25: 468–474.
- Gross, C. L. (1993b) The reproductive ecology of *Canavalia rosea* on Anak karakatua, Indonesia. *Austral. J. Bot.* 41: 591–599.
- Gross, C. L. and D. Mackay (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biol. Conserv.* 86: 169–178.
- Harden, G. J. (1992) *Flora of New South Wales*. Vol. 3. University of New South Wales Press, Kensington, NSW. 717 pp.
- Hasselrot, T. B. (1952) A new method for starting bumble bee colonies. *Agronomy* 44: 218–219.
- Heemert van, C., A. de Ruijter, J. van der Eijnde and J. der Steenvan (1990) Year-round production of bumble bee colonies for crop pollination. *Bee World* 71: 54–56.
- Heinrich, B. (1979) *Bumblebee Economics*. Harvard University Press, Harvard. 296 pp.
- Hergstrom, K., R. Buttermore, A. Hopkins and V. Brown (2005) The distribution and spread of the bumblebee *Bombus terrestris* (L.) in Tasmania since introduction in 1991, with notes on food plants. *Kanunnah* 1: 103–125.
- Hingston, A. B. (2006a) Is the exotic bumblebee *Bombus terrestris* really invading Tasmanian natural vegetation? *J. Insect Conserv.* 10: 289–293.
- Hingston, A. B. (2006b) Is the exotic bumblebee (*Bombus terrestris*) assisting the naturalization of *Agapanthus praecox* ssp. *Orientalis* in Tasmania? *Ecol. Manag. Restor.* 7: 236–238.
- Hingston, A. B. (2007) The potential impact of the large earth bumblebee *Bombus terrestris* (Apidae) on the Australian mainland: lessons from Tasmania. *Vic. Nat.* 124: 110–116.
- Hingston, A. B. and P. B. McQuillan (1998a) Nectar robbing in *Epacris impressa* (Epacridaceae) by the recently introduced bumblebee *Bombus terrestris* (Apidae) in Tasmania. *Vic. Nat.* 115: 116–119.
- Hingston, A. B. and P. B. McQuillan (1998b) Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Austral. J. Ecol.* 23: 539–549.
- Hingston, A. B. and P. B. McQuillan (1999) Displacement of Tasmanian megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae) threaten Australian ecosystems? *Austral. J. Zool.* 47: 59–65.
- Hingston, A. B. et al. (2002) The extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral. Ecol.* 27: 162–172.
- Hingston, A. B., B. M. Potts and P. B. McQuillan (2004) Pollination services provided by various size classes of flower visitors to *Eucalyptus globulus* ssp. *globulus* (Myrtaceae). *Austral. J. Bot.* 52: 317–379.
- Hogendoorn, K., Z. Steen and M. P. Schwarz (2000) Native Australian carpenter bees as a potential alternative to introducing bumblebees for tomato pollination in greenhouses. *J. Apicult. Res.* 39: 67–74.
- Hogendoorn, K., C. L. Gross, M. Sedgley and M. A. Keller (2006) Increased tomato yield through pollination by native Australian blue-banded bees. *J. Econ. Entomol.* 99: 828–833.
- Hogendoorn, K., S. Coventry and M. A. Keller (2007) Foraging behaviour of a blue banded bee, *Amegilla chlorocyanea* in greenhouses: implications for use as tomato pollinators. *Apidologie* 38: 86–92.
- Hopkins, I. (1914) History of the bumble bee in New Zealand: its introduction and results. *New Zealand Department of Agriculture, Industries and Commerce* 46: 1–29.

- Hopper, S. D. and A. H. Burbidge (1986) Speciation of bird-pollinated plants in south-western Australia, In *The Dynamic Partnership: Birds and Plants in Southern Australia* (H. A. Ford and D. C. Paton, eds.). Govt. Printer, Adelaide, pp. 20–31.
- Houston, T. F. (1993) Apparent mutualism between *Vertericordia nitens* and *V. aurea* (Myrtaceae) and their oil-ingesting bee pollinators (Hymenoptera: Colletidae). *Austral. J. Bot.* 41: 369–380.
- Inari, N., T. Nagamitsu, T. Kenta, K. Goka and T. Hiura (2005) Spatial and temporal pattern of introduced *Bombus terrestris* abundance in Hokkaido, Japan, and its potential impact on native bumblebees. *Popul. Ecol.* 44: 77–82.
- Ings, T. C., J. Schikorka and L. Chittka (2005) Bumblebees, humble pollinator or assiduous invader? A population comparison of foraging performance in *Bombus terrestris*. *Oecologia* 144: 508–516.
- Ings, T. C., N. L. Ward and L. Chittka (2006) Can commercially bumblebee out-compete their native conspecific. *J. Appl. Ecol.* 43: 940–948.
- Inoue, M. N., J. Yokoyama and I. Washitani (2008) Displacement of Japanese bumblebees by a recently introduced *Bombus terrestris* L. (Hymenoptera: Apidae). *J. Insect Conserv.* 12: 135–146.
- Inouye, D. (1980) The terminology of floral larceny. *Ecol.ogy* 61: 1251–1253.
- Ish Am, G., Y. Regev, Y. Peterman, E. Lahav, C. Degani, R. Elbatzri and S. Gazit (1998) Improving avocado pollination with bumblebees: 3 seasons summary. *California Avocado Society Yearbook* 82: 119–135.
- Kanbe, Y., I. Okada, M. Yoneda, K. Goka and K. Tsuchida (2008) Interspecific mating of the introduced bumblebee *Bombus terrestris* and the native Japanese bumblebee *Bombus hypocrita sapporoensis* results in inviable hybrids. *Naturwissenschaften* 95: 1003–1008.
- Kang, S. M. and Z. A. Karim (1982) Quarantine aspects of the introduction into Malaysia of an oil palm insect pollinator. In *Proceedings of the First International Conference on Plant Protection in the Tropics*. pp. 615–626.
- Kenta, T., N. Inari, T. Nagamitsu, K. Goka and T. Hiura (2007) Commercialized European bumblebee can cause pollination disturbance: an experiment on seven native plant species in Japan. *Biol. Conserv.* 134: 98–309.
- Kevan, P. G. (1986) Pollinating and flower visiting insects and the management of beneficial and harmful insects and plants. In *Biological Control in the Tropics: Proceedings of the First Regional Symposium on Biological Control* (M. Y. Hussein and A. G. Ibrahim, eds.). Pernebit Universit Pertanian Malaysia, Serdang, Malaysia, pp. 439–452.
- Kevan, P. G. (1999) Pollinators as bioindicators of the state of the environment: Species, activity and diversity. *Agr. Ecosyst. Environ.* 74: 373–394.
- Kevan, P. G. (2003) Pollination for the 21st century: pollinator and plant interdependencies. In *For Non-native Crops, "Whence Pollinators of the Future?"* (J. H. Cane and K. E. Strickler, eds.). Proceedings of Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD, pp. 181–204.
- Kevan, P. G., E. A. Clark and V. G. Thomas (1990) Insect pollinators and sustainable agriculture. *Am. J. Sust. Agric.* 5: 13–22.
- Kevan, P. G., W. A. Straver, M. Offer and T. M. Lavery (1991) Pollination of greenhouse tomatoes by bumble bees in Ontario. *Proc. Entomol. Soc. Ont.* 122: 15–19.
- Kwon, Y. J. (2008) Bombiculture: a fascinating insect industry for crop pollination in Korea. *Entomol. Res.* 38: 66–70.
- Low, T. (1999) *Feral Future*. Viking Press, Ringwood, Victoria, Australia. 380 pp.
- MacFarlane, R. P. (1976) Bees and pollination. In *New Zealand Insects Pests* (D. N. Ferro, ed.). N. Z. Lincoln University, College of Agriculture, Christchurch, pp. 221–229.
- MacFarlane, R. P. and L. Gurr (1995) Distribution of bumblebees in New Zealand. *N. Z. Etomol.* 18: 29–36.
- Matsumura, C., J. Yokoyama and I. Washitani (2004) Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokaido, Japan. *Global Environ. Res.* 8: 51–66.
- Meisels, S. and H. Chaisson (1997) Effectiveness of *Bombus impatiens* Cr. as pollinators of greenhouse sweet peppers (*Capsicum annum* L.). *Acta Hortic.* 437: 425–429.
- Meynie, S. and R. Bernard (1997) Pollinator efficiency of some insects in relation to wild species populations of *Helianthus* L. *Agronomie (Paris)* 17: 43–51 (in French).
- Montgomery, B. E. (1951) Bumble bee and red clover in New Zealand. *N. Z. Sci. Rev.* 10: 47–55.
- Morandin, L. A., T. M. Lavery, P. G. Kevan, S. Khosla and L. Shipp (2001a) Bumblebee (Hymenoptera: Apidae) activity and loss in commercial tomato greenhouses. *Can. Entomol.* 133: 883–893.
- Morandin, L. A., T. M. Lavery and P. G. Kevan (2001b) Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. *J. Econ. Entomol.* 94: 462–467.
- Morandin, L. A., T. M. Lavery and P. G. Kevan (2001c) Effect of bumblebee (Hymenoptera) pollination intensity on the quality of green house tomatoes. *J. Econ. Entomol.* 94: 172–179.
- Müller, H. (1883) *The Fertilization of Flowers* (D. A. W. Thompson, ed.). Macmillan, London. 669 pp.
- Nagamitsu, T. and T. Kenta (2007) Abundance, body size, and morphology of bumblebees in an area where an exotic species, *Bombus terrestris*, has colonized in Japan. *Ecol. Res.* 22: 331–341.
- Nagamitsu, T., T. Kenta, N. Inari, H. Horita, K. Goka and S. Hiura (2007) Foraging interactions between native and exotic bumblebee's enclosure experiments using native flowering plants. *J. Insect Conserv.* 11: 123–130.
- Ne'eman, G. and A. Dafni (1999) Fire, bees and seed production in Mediterranean key species *Salvia fruticosa* Miller (Lamiaceae). *Isr. J. Plant Sci.* 47: 157–163.
- Ne'eman, G., A. Dafni and S. G. Potts (2000) The effect of fire on flower visitation and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecol.* 146: 97–104.

- Okada, K., S. Kusakari, M. Kawaratani, J. Negoro and S. Tahki (2000) Tobacco mosaic virus is transmissible from tomato to tomato by pollinating bumblebees. *J. Gen. Plant Pathol.* 66: 71–74.
- Ornosa, C. (1996) A note on admonition on the artificial introduction of foreign subspecies of pollinating bumble bees in Iberian Peninsula (Hymenoptera: Apidae, Bombinae). *Bol. Asoc. española Entomol.* 20: 259–260 (in Spanish).
- Osborne, J. L., A. P. Martin, N. L. Carreck, J. L. Swain, M. E. Knight, R. J. Hale and R. A. Sanderson (2007) Bumblebee flight distance in relation to the forage landscape. *J. Anim. Ecol.* 77: 406–415.
- Otterstater, M. C. and J. D. Thompson (2008) Does pathogen spill-over from commercially reared bumble bee threaten wild populations? *PLoS 3* (7). <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2464710>
- Parker, F. D., S. W. T. Batra and V. Tepedino (1987) New pollinators for our crops. *Agric. Zool. Rev.* 2: 279–304.
- Peterson, A. T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78: 419–433.
- Porporato, M., A. Patetta, F. Marletto, A. Manino and L. Allais (1993) Use of bumblebees for the pollination of tomatoes grown under cover. *Apic. Moder.* 84: 135–140 (in Italian, Biosis No. 97087831).
- Porporato, M., M. Pinna, A. Manino and F. Marletto (1995) Pollination of sweet pepper in greenhouse by *Bombus terrestris* (L.) and *Apis mellifera* L. *Apic. Moder.* 86: 99–112 (in Italian, Biological abstracts No. 199698646881).
- Potts, S. G., P. G. Willmer, A. Dafni and G. Ne'eman (2001) The utility of fundamental ecological research of plant-pollinator interactions as the basis for the landscape management practices. *Acta Hortic.* 561: 141–152.
- Proctor, M., P. Yeo and A. Lack (1996) *The Natural History of Pollination*. Harper Collins, London. 479 pp.
- Prys-Jones, O. E. and S. A. Corbet (1991) *Bumblebees*. The Richmond Publishing, Slough, UK. 92 pp.
- Rademaker, M. C. J., T. J. De-Jong and P. G. L. Klinkhamer (1997) Pollen dynamics of bumblebee visitation on *Echium vulgare*. *Funct. Ecol.* 11: 554–563.
- Ravestijn van, W. J. and L. van der Sande (1991) Use of bumblebees for the pollination of glass house tomatoes. *Acta Hortic.* 288: 204–212.
- Richards, K. W. (1993) Non-*Apis* bees as crop pollinators. *Rev. Suisse Zool.* 100: 807–822.
- Röseler, P. F. (1985) A technique for year-round rearing of *Bombus terrestris* (Apidae, Bombini) colonies in captivity. *Apidologie* 16: 165–170.
- Ruijter, de A. (1997) Commercial bumblebee rearing and its implications. *Acta Hortic.* 437: 261–269.
- Ruz, L. (2002) Bee pollinators introduced to Chile a review. In *Pollinating Bees. 2002: The Conservation Link between Agriculture and Nature, with Emphasis on Bees* (P. G. Kevan and V. L. Imperatriz-Fonseca, eds.). Brazilian Ministry of Environment, Sao Paulo, Brazil, pp. 155–167.
- Schmid-Hempel, P., R. Schmid-Hempel, P. C. Brunner, O. D. Seeman and G. R. Allen (2007) Invasion success of the bumblebee, *Bombus terrestris*, despite a drastic genetic bottleneck. *Heredity* 99: 414–422.
- Semmens, T. D. (1996a) Flower visitation by the bumble bee *Bombus terrestris* (L.) (Hymenoptera: Apidae) now established in Tasmania. *J. Austral. Entomol. Soc.* 32: 346–357.
- Semmens, T. D. (1996b) Flower visitation by the bumble bee *Bombus terrestris* (L.) (Hymenoptera: Apidae) in Tasmania. *Austral. Entomol.* 23: 33–35.
- Semmens, T. D. (1998) New flowers visited by bumble bees. *Invertebrata* 12: 9. Queen Victoria Museum and Art Gallery, Launceston, Australia (cited by R. E. Buttermore, 2000).
- Semmens, T. D., E. Turner and R. E. Buttermore (1993) *Bombus terrestris* (L.) (Hymenoptera: Apidae) how established in Tasmania. *J. Austral. Entomol. Soc.* 32: 346–356.
- Simpson, S. R., C. L. Gross and L. X. Silberbauer (2005) Broom and honeybees: an alien liaison. *Plant Biol.* 7: 541–548.
- Sinden, J., R. Jones, S. Hester, D. Odom, C. Kalisch, R. James and O. Cacho (2004) *The Economic Impact of Weeds in Australia*. Australian Weed Management Technical Series no. 8. CRC, Adelaide. 84 pp.
- Sladen, F.W. L. (1912) *The Humble-Bee: Its Life History and How to Domesticate It*. Macmillan, London. 283 pp.
- Stout, J. C. and D. Goulson (2000) Bumble bees in Tasmania: their distribution and potential impact on Australian flora and fauna. *Bee World* 81: 80–86.
- Stout, J. C., J. A. Allen and D. Goulson (1998) The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees. *Oecologia* 112: 543–550.
- Stout, J. C., J. A. Allen and D. Goulson (2000) Nectar robbing, foragers efficiency and seed set: bumblebees foraging on the self incompatible plant *Linaria vulgaris* (Scrophulariaceae). *Acta Oecol.* 21: 277–283.
- Stout, J. C., A. R. Kells and D. Goulson (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biol. Conserv.* 106: 426–434.
- Thompson, J. D. (1997) Comments on the naturalization of *Bombus terrestris* in Japan. *Jpn. J. Conserv. Biol.* 2: 28–35.
- Thorp, R. W. (2003) Bumble bees (Hymenoptera: Apidae): commercial use and environmental concern. In *For Non-native Crops, "Whence Pollinators of the Future?"* (J. H. Cane and K. Strickler, eds.). Proceedings of Thomas Say Publications in Entomology. Entomological Society of America, Lanham, Md., pp. 21–40.
- Torchio, P. F. (1987) Use on non-honey bee species as pollinators of crops. *Proc. Entomol. Soc. Ont.* 118: 111–124.
- Torchio, P. F. (1994) The present status and future prospects of non-social bees as crop pollinators. *Bee World* 75: 49–53.
- Torretta, J. P., D. Medan and A. Abrahamovich (2006) First record of the invasive bumblebee *Bombus terrestris* (L.) (Hymenoptera, Apidae) in Argentina. *Trans. Am. Entomol.*

- mol. Soc.* 131: 285–289.
- Velthuis, H. H. W. and L. Cobb (1991) Pollination of *Primula* in a greenhouse using bumblebees. *Acta Hort.* 288: 199–203.
- Velthuis, H. H. W. and A. van Doorn (2006) A century of advances in bumblebee domestication and the economic and environmental aspect of its commercialization for pollination. *Apidologie* 37: 421–451.
- Walther-Hellvig, K. and R. Frankl (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Entomol.* 124: 299–306.
- Willmer, P. G., A. A. M. Bataw and J. P. Hughes (1994) The superiority of bumblebees to honey bees as pollinators: insect visits to raspberry flowers. *Ecol. Entomol.* 19: 271–284.
- Winter, K., L. Adams, R. Thorp, D. Inouye, L. Day, J. Ascher and S. Buchmann (2006) *Importation of Non-native Bumble Bees into North America: Potential Consequences of Using Bombus terrestris and Other Non-native Bumble Bees for Greenhouse Crop Pollination in Canada, Mexico, and the United States*. A White Paper of North American Pollinator Protection Campaign (NAPPC). San Francisco, California. 33 pp.
- Yoneda, M., J. Yokoyama, K. Tsuchida, T. Osaki, S. Itoya and K. Goka (2007) Preventing *Bombus terrestris* from escaping with a net covering over a tomato greenhouse in Hokkaido. *Jpn. J. Appl. Entomol. Zool.* 51: 39–44 (in Japanese with English summary).
- Yoneda, M., H. Furuta, K. Tsuchida, K. Okabe and K. Goka (2008) Commercial colonies of *Bombus terrestris* (Hymenoptera: Apidae) are reservoirs of the tracheal mite *Locustacarus buchneri* (Acari: Podapolipidae). *Appl. Entomol. Zool.* 43: 73–76.