

EXECUTIVE SUMMARY

PROPOSAL TO IMPORT *BOMBUS TERRESTRIS* INTO MAINLAND AUSTRALIA FOR CROP POLLINATION PURPOSES

PROPONENTS –

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1. The purpose and scope of the document

This document is the culmination of over 10 years investigation into the proposed importation of a European bumblebee, *Bombus terrestris*, into Australia in managed hives for pollination purposes. While originally use in a wide range of field and greenhouse crops was envisaged, the proposal has been narrowed down to pollination of greenhouse crops, particularly tomatoes, in fully enclosed structures. This final document sets out detailed information on all the Terms of Reference agreed to with the DEH, now DEWHA, and addresses all comments received during a public and government consultation process in 2006. In addressing the many issues that were raised, a further extensive literature search was undertaken and several key researchers were contacted on the biology and ecology of this bumblebee. While a strong and prolonged lobbying campaign against importation has prejudged this application, the AHGA believes,

through thoroughly reviewing all the evidence available pertinent to the arguments received, that there is a strong case to be made for managed importation, with negligible risk of any of the environmental consequences predicted.

2. The proponents of the request

The AHGA represents the Australian greenhouse industry nationally. The original application to import bumblebees was made by Goodwin and Steiner in 1997, to encourage uptake of biological pest management and thus reduce pesticide use, while greatly increasing yields in targeted crops. The AHGA took over responsibility for the application in 1999. The Australian greenhouse vegetable industry is the fastest growing food producing sector in Australia, with a \$600 million farm gate value per annum, currently expanding at 4-6% per annum, yet currently has only an estimated 350-400 ha in tomato production, very small by world standards. It employs over 10,000 people throughout Australia. As an industry that makes use of advanced greenhouse and environmental systems technology, it has the highest capital cost of any agricultural sector, with state-of-the-art glasshouse/greenhouse structures, hydronic heating, and computer-controlled environmental and hydroponic systems, costing on average \$2 million per hectare. This represents a considerable and unprecedented investment into the industry, yet the potential growth remains a long way from being realised, and lags far behind other countries with a greenhouse industry. For a country where water is a precious commodity, perhaps the major benefit of this industry is its water use efficiency. Its environmental footprint is very small compared with other food producing industries, with considerably higher yields per unit area.

3. The need for a biological pollinator

Bumblebees have been reared commercially since the late 1980's. There are over 30 production companies in 19 countries, servicing 40 countries in Europe, North America, South America, New Zealand, and Asia. Bumblebees greatly improve pollination of greenhouse crops (e.g. tomato, capsicum, eggplant, berry fruit), in field crops (e.g. strawberry, blueberry, cranberry, kiwifruit, zucchini, bean, eggplant) and in tree fruit (e.g. almond, apple, stone fruit, avocado). Ninety five percent of use is in greenhouse tomato crops, because not only are bumblebees excellent buzz pollinators, but tomatoes are a high value crop, needed to justify the cost of bumblebee production. Their use not only saves on manual pollination costs, but results in greatly increased yields of better quality fruit. Overall in Australia, it is estimated that the economic benefit of bumblebee pollination would be A\$40 million per year. There has been very rapid uptake of bumblebee technology by growers where they are available. Australia is one of the few countries in the world without access, and this puts us at an increasingly severe disadvantage in a free market economy. It has delayed the expansion of the industry in Australia by several years, and inhibited foreign and local investment. This technology is sophisticated and proven, and is used by all of Australia's major competitors, including New Zealand. This is a major concern to the Australian greenhouse industry.

4. The proposal for importation of *Bombus terrestris*

The AHGA proposes to import bumblebees within secured hives on a weekly basis for distribution to growers. The hives are placed within the crop and worker bees allowed to leave to effect pollination. Several measures will be put in place to mitigate against possible escapes. Bees can only leave the hive through a single exit hole which can be closed, of a size which is too small to allow the larger queen to escape. Thus only worker bees are in the crop, and further breeding is not possible. Greenhouses will be netted over all openings, and hives will be replaced and destroyed after no longer than 8 weeks. Greenhouse operations will be pre-approved, will have to undergo training of staff, and if required by DEWHA, will be monitored regularly by AQIS to ensure compliance with agreed protocols for use and containment. The commercial rearing operation will be sited probably in northern Tasmania, so that quarantine, rearing, packing and shipping operations are conducted where there are no environmental concerns should any breaches in containment occur. The facilities will be regularly inspected to ensure disease-free status.

The rearing stock will most likely be derived from Tasmanian bees, which are proven disease-free, although of limited genetic diversity. The subspecies will most likely be *B. t. audax*, which was derived from English and thence New Zealand stock. It is thus unlikely to adapt to non-temperate climates.

5. Concerns expressed by opponents of importation

The concerns expressed have been wide ranging. They include the following:

- Increased rates of pollination, gene flow and seed set among agricultural and environmental weeds
- Impacts on seed set of native plants caused by nectar and pollen removal by *B. terrestris* and by potential failure of *B. terrestris* to correctly contact the anthers or stigmas
- Impacts on native bee and native insect pollinators from competition for nectar and pollen
- Impacts on native vertebrates, especially threatened species, that utilize nectar and pollen resources from competition with *B. terrestris*
- Impacts on native animals or bees from competition for nest sites
- The potential impacts on the lifestyle and health of humans should *B. terrestris* establish in or near human settlements.

There have also been claims that bumblebees will not be restricted by climate or to one generation a year on mainland Australia, so that they will spread extensively. Their likely impact has been likened to that of cane toads, European wasps, rabbits and foxes. There have also been claims that the native blue-banded bee is an alternative commercial pollinator, so there is no need of bumblebees.

6. Research for and against the proposal

Most local research has been conducted in Tasmania:

- A three-year Environmental Impact Study (EIS) was conducted by the Tasmanian Museum 1999-2002, following an industry workshop in Hobart in 1999 that brought together representatives of the greenhouse industry and other interested parties, including conservationists and apiarists. It was funded by a \$275,000 grant from the former Horticultural Research & Development Corporation, now Horticulture Australia Ltd. The EIS report presented in 2002 found little cause for concern.
- Dr Andrew Hingston, University of Tasmania, who is very much opposed to importation and who, with several co-authors, published several papers claiming substantial negative impacts, which were not verified by many of the EIS studies of Hergstrom *et al.* (2002).
- UK researchers Prof. D. Goulson and Dr J. Stout conducted limited studies on distribution of *B. terrestris*, competition with native bees and seed set of weeds in Tasmania.

Worldwide, as a result of interest in bumblebees as pollinators, and alarm over the widespread decline of bumblebee species around the world, a great deal of research has been conducted on the biology and ecology of bumblebees, *B. terrestris* in particular. Over 500 references have been accumulated and referenced in this report, but many others more peripheral to this issue have been published. This bee is very well researched, and much about its biology and ecology are known. Within this wealth of material, only very few authors point to potential problems with bumblebees rather than regarding them as a critical asset, and all have to do with transport of bumblebees to areas outside their natural range.

A great deal of credence has been given to these few papers by environmentalists opposed to importation. While there are valid concerns, these are context-dependent, and almost exclusively relate to countries where native bumblebees already exist. Negative publicity has emanated primarily from establishment of feral populations of *B. terrestris* in Hokkaido, Japan, with concerns being transfer of pathogens and parasites to native bumblebees, usurpation of their nest sites, competition for resources, interference with pollination mechanisms, and hybridisation with native bumblebees. Of these, only pathogen and parasite transfer (manageable) and possible competition for nest sites (not yet proven) appear to have any substance there. Other strong opposition has come from Prof. Amos Dafni in Israel, who became concerned about displacement of native bees in fire-burnt areas after a temporary range expansion of *B. terrestris* in the early 1980's. In New Zealand, where *B. terrestris* and three other bumblebee species were introduced over 130 years ago, there have been no negative impacts, despite the much more suitable climate than in mainland Australia, and many positive impacts recorded.

The opposition to importation led the AHGA to secure the services of a wide range of experts on bumblebees and related technologies to examine claims of negative impact. These include the following initiatives:

- ‘A Critical Study on the Introduction onto Mainland Australia of the Bumblebee (*Bombus terrestris*) for the Commercial Pollination of Protected Tomato and Other Crops’, authored by Dr Don Griffiths. Dr Griffiths is a world-respected authority on bumblebees - one time Director of Research at the Ministry of Agriculture Central Science Laboratory, UK, for 10 years; member of the Board of Directors of the International Bee Research Association, Cardiff, UK; responsible for the trials and initial introduction of commercial pollination management systems into Holland, UK, France, Spain, Italy and Japanese commercial glasshouses. Dr Griffiths also contributed to the submission.
- Funding of two climatology studies using the CLIMEX™ model, (Dr K. Hergstrom, 2003 and Dr A. McClay, 2005) to predict where *B. terrestris* is likely to establish should it arrive by any mechanism on the mainland. The more definitive study by McClay is appended to the submission, with extensive discussion on its implications.
- Analysis of three Tasmanian studies by McClay to assess the validity of the scientific methodology and statistics.
- Biocontrol Solutions (M. Steiner & Dr S. Goodwin) were retained in 2007 to undertake an extensive review of information and literature relating to *B. terrestris* and to complete the final report and respond to public and government comments. The AHGA secured a grant of \$100,000 from HAL to complete this undertaking.

7. Examination of claims

Both the EIS and CLIMEX studies indicate bumblebees will not dramatically change the status of native and agricultural eco-systems should bumblebees succeed in establishing in the wild. The McClay CLIMEX study indicates the likelihood of only limited distribution of *B. terrestris* (subspecies *audax*) on mainland Australia should it arrive either by accident or design. The study predicts these areas will be restricted to the wetter areas of Victoria, the southwest corner of Western Australia, and a limited area of NSW across the northeastern border of Victoria, most likely in irrigated areas and urban gardens where there is an abundance of year-round nectar from preferred introduced plant species. The pertinent questions answered by the EIS and by other published studies are as follows:

7.1. Claims of negative effect

Bumblebees will compete with native bees and animals for nectar and pollen?

Bumblebees have a strong preference for exotic (introduced) plant species over native species. Only Hingston in Tasmania claims otherwise, but has no data to support this contention. This does not preclude favouring some native Myrtaceae offering high nectar rewards, such as some Eucalypts, Banksias and Grevilleas. While bumblebees may access a range of native plants, and have been shown to have a presence in native bush, they have not been shown to be abundant there. Native bees prefer to forage on native

plants in native bush at times when these resources are abundant. There is thus little likelihood of any significant competition for floral resources.

Bumblebees are highly invasive pests?

Bumblebees are not regarded as pests anywhere in the world where they are native, nor in New Zealand where they were introduced and have been established for 130 years. Many heavily funded and researched schemes to preserve their diversity and increase their abundance have been established in recent years across Europe and North America. Broad establishment is only possible where the climate and vegetation is suitable. This includes areas of known establishment such as New Zealand, Tasmania and northern Japan, but would include only the coastal south of the Australian mainland. Spurious claims that bumblebees are another cane toad, fox, European wasp, etc., are based on a lack of familiarity with bumblebees and an attempt to distort the truth. New Zealand has imported seven species of exotic bees over the years, and Australia has imported exotic honeybees and carpenter bees, with overall beneficial impacts. Honeybees will in any case always have a much greater presence than other bees, because of their perennial and very large colonies, broad foraging range and subspecies adapted to a range of climates.

Bumblebees will spread sleeper weeds?

Conjecture and suppositions abound alluding to the potential of *B. terrestris* to awaken so-called 'sleeper weeds'. This claim has not been substantiated for any of the weed species named by the CRC and by Hingston as being most likely to be sleeper weeds. The EIS found, in a limited, short term study, that there was only some increase in the seed set of two minor weeds, however, a decrease in the seed set of a major weed (Scotch thistle). Where pollinators are needed for weed spread, honeybees are already ubiquitous and performing that service. The limited potential distribution of bumblebees on the mainland will also limit any potential for weed spread.

Bumblebees will carry parasites and pathogens, including Varroa?

There is *no possibility* of transmission of Varroa to honeybees. They do not live on bumblebees. Most pests, parasites or pathogens associated with *B. terrestris* are unique to bumblebees. Very few parasites and pathogens are shared with honeybees, and these can be screened for. There is no known or likely risk to native bees. Therefore, no deleterious health effects on honeybees or Australian native bees are expected. Two studies have confirmed that Tasmanian bumblebees are parasite- and pathogen-free. Nevertheless, as a matter of routine, bumblebees will be quarantined and screened prior to addition to breeding stock.

Bumblebees will escape and populate the entire Australian mainland?

Not so. Agreed protocols that will be put in place will minimise the possibility of escapes from imported hives. Even should this occur, successful establishment in the environment is unlikely. Previous deliberate releases in the late 1800's and early 1900's failed, and no establishment has occurred from periodic accidental arrivals via ships and planes, a few recently documented by AQIS. *Bombus terrestris s. l.* would be at the latitudinal limit (30°) of its known range in southern Australia. A commissioned CLIMEX study indicates a restricted distribution for the subspecies *B. t. audax* in the cooler, wetter areas of the

mainland, limited to Victoria, just over the NSW border, and the southwest corner of WA. Temperatures over 30°C are detrimental. Other subspecies will also be limited to more coastal temperate areas with good floral resources during colony development. An extensive review of information available on diapause has been undertaken and concludes that a long resting period (diapause) is innate in *B. terrestris*. It will limit the species to one or two generations a year, and a primarily spring- or summer-active population, as is evident in Tasmania and New Zealand.

Bumblebees will compete with the swift parrot and other endangered birds?

Not so. The threat to the survival of the swift parrot, helmeted honeyeater and regent honeyeater has everything to do with land clearing, wood chipping and habitat destruction, and absolutely nothing to do with bumblebees. EIS studies show bumblebees represent only 2% of visitors to Tasmanian blue gum, the preferred nectar source of swift parrots, compared with visits by honeybees (56%) and birds (25%).

Bumblebees will affect seed set of native plants?

No impact has been shown or is expected, given the limited potential distribution on the mainland, and the low visitation rate to native plants except to those well serviced by other pollinators. A positive effect is just as likely as a negative one.

Bumblebees will competitively displace native bees?

There is no evidence for this. Hingston's single, two-day study purporting to show this has several flaws and does not support this contention. Similarly, Dafni's prognosis of dire effects in Israel has not been realised and pertained to habitat alteration by fires and not to temporary presence of indigenous *B. terrestris*. Most plants are visited by a broad range of pollinators, not limited to bees and birds. Resource partitioning normally ensues so that overlap is minimised in time and space. Bumblebees are blenders, not usurpers.

Bumblebees will displace native animals from nest sites?

Quite the contrary. Bumblebees utilise *abandoned* rodent nests. In fact, rodents, ants, lizards and other animals are known to destroy bumblebee nests. Lack of suitable nest sites may well limit both abundance and area of establishment of bumblebees.

Bumblebees are aggressive and sting repeatedly, leading to severe reactions and possible death?

Bumblebees are not aggressive, but will defend a nest if disturbed. However, nests are seldom encountered as they are sited below ground and away from domiciles. While bumblebees are capable of stinging, and in rare cases inducing anaphylactic shock, the public is very rarely affected. As with honeybees, this is an occupational hazard for those working closely with bees in closed environments. Incidence of stings is much lower than for honeybees, and treatment is similarly available.

Bumblebees are a Key Threatening Process?

State Governments of NSW and Victoria have declared bumblebees a "Key Threatening Process" due to intense lobbying over a 10 year period by a small segment of the conservation lobby. Conclusions of the Committees were premature and based on

speculation emanating from a single source in Tasmania. It is a disappointment that a decision was reached in advance of evidence and contrary to known biology and ecology of this species. Conversely, the Federal Government in 2001 declined to support this unfair claim due to 'insufficient evidence to support the claim.' Good science must be allowed to prevail and not suppositions. Frequent use of words such as 'could, possibly, might and maybe' infers a lack of substantiating evidence.

7.2. Claims of positive effect

Bumblebees are very efficient and cost-effective pollinators

Studies show that the cost of pollinating a tomato crop is approximately \$25,000/ha for manual pollination compared with \$7,000/ha for bumblebees. Manual pollination is achieved through mechanical hand-held vibrators touching each plant three times per week (a huge impost on manual labour). Bumblebees also achieve a higher % of pollination success (approximately 95% vs. 85%).

Bumblebees deliver potentially up to 28% crop yield increase

Bumblebees work over a wide range of conditions found in typical greenhouse installations and select flowers at the optimum time for good pollination, resulting in high yields of quality fruit. Several overseas studies have shown that this optimum pollination can deliver a crop yield increase of up to 28% at the low cost of 1% of production. Even with a conservative 10% increase in yield, it is projected that the greenhouse tomato industry would benefit by \$40 million/year on 250 ha.

Bumblebees will deliver much improved fruit set

Good fruit set is always important, even more so given the move towards truss production. This system also provides an increase in tomato fruit size (around 5%), improves quality and extends shelf life.

Bumblebee pollination is proven technology, is hassle-free and is available year round on demand

The technology has been improving over the last 15 years and is now very advanced. All growers need to do is place the hive in the crop and change it within a set time frame or when it is no longer productive. Usage is well established in many countries under varying conditions, and is not limited seasonally. Three companies have been producing bumblebees in New Zealand for more than 10 years, with usage in both greenhouse and field crops.

Bumblebee technology is available to almost every country on the planet, except Australia

Over one million colonies were produced globally in 2004 for pollination purposes, demonstrating that this technology is very much in demand and is very reliable. With current pressure from New Zealand imports (with recent approval for importation of Dutch produce), access to this technology is mandatory if Australian growers hope to match production standards with our international competitors.

Consumers can be assured of pesticide-free produce

Due to the low tolerance of bumblebees to pesticides, Australian greenhouse growers would be required to adopt IPM strategies involving the usage of arthropod biocontrol agents, as is strongly practiced overseas by the protected cropping industry. The availability of bumblebees would ensure a 100% compliance rate. Bumblebee images on produce tags overseas are used to signify ‘clean, green, pesticide-free’ produce.

8. Alternative pollinator proposals

Claims have been made that native bees able to buzz pollinate tomatoes can replace bumblebees. Research has focused for several years on blue-banded bees, *Amegilla* spp. Native bee research is encouraged; however, growers must be practical. So far no commercial outcome is on the horizon, and the level of difficulty in commercialising a solitary bee such as this is prohibitive. Can this be accomplished in a reasonable time frame (5, 10, 20 years), if at all? Can they adapt to artificial enclosed rearing systems and transportation systems? Are they reliable and obtainable year round? Can enough be produced to sustain a viable commercial enterprise? Is the biology well-known, and can diapause be controlled? Can pathogens and parasites be managed? Can a species indigenous to all Australian growing areas be found? How much research money will be spent with the possible result of no suitable alternatives at the end of it all? Ultimately, many years of study and substantial financial input may yield a negative result that will further delay the competitiveness of Australian growers, whereas growers could be using bumblebees within two years of approval to import being granted.

9. Conclusions

The AHGA is entirely satisfied that certified clean stock can safely be brought to the Australian mainland for pollination of greenhouse crops, while presenting negligible risk to the environment, even should escapes occur. Only two of the 40 countries currently enjoying bumblebee technology, Japan and Israel, claim deleterious effects on their local flora or fauna, and none of these claims has been substantiated. Importation of bumblebees into Japan has been permitted to continue, and concerns in Israel have abated while use of its native bumblebee species continues. New Zealand has been successfully rearing and using bumblebees for many years, with no negative effects identified. These facts are entirely at odds with claims by Australian opposition groups that “all hell will break loose” if bumblebees are allowed to leave Tasmania for the mainland, and that their impact has been “devastating” in Tasmania. There is no evidence to substantiate this doom and gloom scenario. Bumblebees will not change their benign character when they reach the mainland.

Each area of the TOR has been carefully addressed to ensure that no environmental issue was missed. This definitive study confirms that importation, particularly with the safeguards outlined, should be approved as representing no risk to the Australian environment while conferring substantial benefits to the greenhouse

domestic and export sector and to the health of the general public through reduced pesticide use.

10. Recommendation

That the Australian Department of Environment, Water, Heritage and the Arts approves the live import of the European bumblebee *Bombus terrestris* onto the Australian mainland for the purposes of greenhouse crop pollination, on the basis that it is satisfied with reasonable certainty that the risk of environmental impact will be negligible.

Graeme Smith

A handwritten signature in black ink, appearing to read 'G. Smith', with a large, stylized initial 'G'.

President - Australian Hydroponic & Greenhouse Association
March 2008

**FINAL REPORT ON THE
TERMS OF REFERENCE FOR ASSESSING THE
SUITABILITY FOR LIVE IMPORT INTO MAINLAND
AUSTRALIA OF THE LARGE
EARTH BUMBLEBEE (*BOMBUS TERRESTRIS*, L. 1758)**



Submitted by

**THE AUSTRALIAN HYDROPONIC AND GREENHOUSE
ASSOCIATION INC.**

March 2008



AGREED TERMS OF REFERENCE

Australian Department of Environment and Heritage¹

8 February 2005

¹ now Department of Environment, Water, Heritage and the Arts

1. Provide a summary of the proposed activity, including:
 - The intended use of the specimens (e.g. commercial, scientific) and whether breeding populations are to be established.
 - The number of individuals to be imported. If any imports are to be queens, provide the number of queens to be imported.
 - The origin of *B. terrestris* populations from which the specimens will be sourced.
 - Detail on how the specimens will be kept, transported and managed (including breeding and disposal of nests and specimens) during and after import in accordance with the proposed activity and to preclude the escape of *B. terrestris* into the Australian environment.
2. Provide information on the taxonomy of the species.
3. Describe the current conservation status of the species in its natural range including:
 - Its natural distribution, whether it's currently expanding or contracting.
 - Its abundance within its natural distribution range and whether it's increasing or decreasing.
4. Identify countries where the species has become naturalised subsequent to its importation, and describe the status of the species and its impact on native species and ecosystems and the broader environment in those countries, with particular reference to New Zealand, Japan and Israel.
5. Describe the history of the species in Tasmania, including its current status and the known impact on the environment of any feral populations established there.
6. Assess the likelihood of the species becoming established in the Australian mainland environment, including:
 - The range of habitats the species could inhabit, and how abundant could it become in these habitats.
 - The ability of the species to compete with native insects and animals for nectar.

- The probable effect of Australia’s climatic conditions on hive number, size and ability of new queens to survive.

7. Using inference and extrapolation from studies of other species (e.g. *Apis mellifera*) where appropriate, assess the probable consequences of the species becoming established including the potential impacts that could arise from:

- Increased rates of pollination, gene flow and seed set among agricultural and environmental weeds, including those identified by The Cooperative Research Centre for Australian Weed Management (Weeds CRC) as ‘sleeper’ environmental weeds.
- Impacts on seed set in native plants caused by nectar and pollen removal by *B. terrestris* and by potential failure of *B. terrestris* to correctly contact the anthers or stigmas
- Impacts on native bee and native insect pollinators from competition from *B. terrestris*.
- Impacts on native vertebrates that utilize nectar and pollen resources from competition with *B. terrestris* especially threatened species.
- The potential impacts on the lifestyle and health of humans should *B. terrestris* establish in or near human settlements.

8. Provide information on and results of any other similar risk assessments undertaken on the species (including the results of assessments conducted as part of nominations for or listings as a key, or potentially, threatening process by Commonwealth, State or Territory Governments).

9. Provide information on all other relevant Commonwealth, State and Territory legislative controls on the species.

10. Assess what conditions or restrictions, if any, could be applied to the import of the species to reduce any potential for negative environmental impacts.

11. Provide an overall analysis of the potential impacts of importing the species. Include both the potential impacts of the particular import that is proposed, and the potential impacts of the species on the environment should the specimens ever be released or escape from effective human control.

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For truss tomatoes, bumblebee pollination of all flowers on the truss is essential to avoid gaps.

Bombus terrestris
buzz-pollinating a
tomato flower.
Photo courtesy of
Agrobio,
Almeria, Spain.





Greenhouse tomato operations in Australia are moving into a new, technologically advanced phase. Above, Freshpak, Tatura, VIC, and below, Top of the Range Tomatoes, Guyra, NSW.

BACKGROUND TO THE PROPOSAL TO IMPORT *BOMBUS TERRESTRIS* INTO MAINLAND AUSTRALIA FOR CROP POLLINATION PURPOSES

i) **Historical background** The European bumblebee *Bombus terrestris* (L.) was discovered in Tasmania in a Hobart garden in 1993 (Semmens *et al.* 1993). When it became apparent that the bees were well established and spreading, interest was generated in the commercial potential of the species as a crop pollinator. The genetic base was found to be very narrow (Pomeroy *et al.* 1997; Buttermore 1998), so in 1995 the Tasmanian Greenhouse Vegetable Growers Association applied to the Australian Quarantine Inspection Service (AQIS) for permission to import new genetic material (Carruthers 2003). Permission was refused on the basis that there were possible environmental concerns which had to be addressed before this could be considered. A request to permit importation of bumblebees from New Zealand into Australia was also made to AQIS in February 1996 by Dr S. Goodwin, on behalf of the Australian horticultural industry. A copy of the application was forwarded for consideration to the Australian Nature Conservation Agency (ANCA, subsequently Department of Environment and Heritage (DEH), now Department of Environment, Water, Heritage and Arts (DEWHA), in August 1996. ANCA responded to AQIS on 9 September 1996 with a request for additional information.

The reason for the original request was to make available in Australia, through managed hives, a supply of bumblebees for pollination of a range of horticultural crops (Goodwin & Steiner 1997, Carruthers 2004). Bumblebees are reared commercially by over 30 companies in 19 countries, covering Europe, North America, South America, New Zealand, and Asia (Velthuis & van Doorn 2006) to improve pollination in greenhouse crops (e.g. tomato, capsicum, eggplant, berry fruit), in field crops (e.g. strawberry, blueberry, cranberry, kiwifruit, zucchini, bean, eggplant) and in tree fruit (e.g. almond, apple, stone fruit, avocado) (Griffiths & Robberts 1996; Velthuis 2002; Velthuis & van Doorn 2004a, b; 2006).

Since bumblebees first became available through commercial insectaries in the late 1980's, there has been very rapid uptake of the technology by growers, for the simple reason that they work extremely well. Over one million colonies were sold in 2004, 95% to greenhouse tomato growers (Velthuis & van Doorn 2004a, 2006), and 40,000 ha of tomatoes were pollinated. The value of these bumblebee-pollinated tomato crops is estimated to be €12,000 million per year (AU\$20,000 million) (Velthuis & van Doorn 2006). From Iceland to New Zealand, in every continent except Australia, there has been almost complete uptake of bumblebee pollination technology. This is not a novel, experimental system. Australia is one of the few countries in the world not able to access it, and this puts us at an increasingly severe disadvantage in a free market economy (Carruthers 2003, 2004).

The earlier request to AQIS proposed to import the most commonly reared species, *Bombus terrestris*, from established commercial rearing facilities in New Zealand. This would be on a regular basis as ready-to-use hives. Weekly importation of

hives from mass production facilities is the norm in most other countries. Because of concerns expressed about possible transfer of pathogens and parasites, this was amended to request establishment of a commercial rearing unit in Australia. A full submission was then made to AQIS and Environment Australia in October 1999 (Goodwin & Steiner 1997 URL: <http://www.tmag.tas.gov.au/workshop/append2.html>). This document was sent to various stakeholders, and it was recommended that an Environmental Impact Study (EIS) be carried out addressing concerns raised by ecologists about the potential impact on native flora and fauna.

The Tasmanian Museum in Hobart, through Dr Roger Buttermore, who had expertise in rearing and studying bumblebees, volunteered to carry out the EIS, as an unbiased, independent agency. The study was funded for a three-year period (1999-2002) through the Horticultural Research and Development Corporation (HRDC), now Horticulture Australia Ltd. (HAL), with support from grower levies. Prior to the study commencing, a workshop was held in Hobart in November 1999, to which all the stakeholders were invited. The 36 participants agreed on priorities and study methods for the EIS (<http://www.tmag.tas.gov.au/workshop/proceedings.html>). In 1999, the Australian Hydroponic and Greenhouse Association (AHGA) took over responsibility for the submission to import bumblebees.

Following a satisfactory report from the EIS indicating minimal potential for any negative impact (Hergstrom *et al.* 2002, Carruthers 2003), the AHGA progressed to the next stage. In 2004, it lodged an application with the then DEH to amend the list of specimens suitable for live import under the *Environment Protection and Biodiversity Conservation Act 1999*. Draft Terms of Reference for a decision on this request were posted for public comment by DEH, and this closed in April 2004. The final Terms of Reference were agreed to on 28 February 2005. A draft report on the Terms of Reference was submitted to the DEH in December 2005, finally accepted in March 2006, and subsequently posted on its website for public and Government comment from 19 April-16 June 2006. The DEH then collated public and Government comments and provided them to the AHGA for a response. This document is an amended version of the submission, and includes many additional references and updated information. It is submitted as a Final Report on the Terms of Reference for consideration by the Minister. Detailed responses to the public and Government comments are provided by the AHGA under separate cover. It should be noted that the proposal is now restricted to a request to import commercial hives of *B. terrestris* for the sole purpose of pollination in secure greenhouses.

ii) Economic and social value of bumblebees The AHGA represents the Australian greenhouse vegetable industry nationally. This industry is the fastest growing food producing sector in Australia, with a \$600 million farm gate value per annum, currently expanding at 4-6% per annum. It employs over 10,000 people throughout Australia. As an industry that makes use of advanced greenhouse and environmental systems technology, it has the highest capital cost of any agricultural sector, with state-of-the-art glasshouse/greenhouse structures, hydronic heating, and computer-controlled environmental and hydroponic systems, costing on average \$2 million per hectare. This represents a considerable and unprecedented investment into the industry, often involving large areas. For example, in Victoria, Freshpak recently constructed 5 ha of glasshouses

at Tatura, and Flavorite has completed 14 ha of greenhouses at Warragul, and will add another 18 ha of glasshouses; in NSW, Costas has erected 10 ha of glasshouses at Guyra, and are building another 10 ha; and in SA, Timbercorp have erected 8 ha of glasshouses. This area is all for hydroponic tomatoes. The high technology greenhouse and hydroponic industry will assume even greater significance in the future with diversification into other crops. Approval was recently granted for a 21 ha glasshouse development in the Sydney Basin for cucumber and capsicum production. This is 86 ha of new, high technology greenhouses in a short time period.

In environmentally-controlled conditions, grown under expert systems, crops grow faster and have far higher yields than when grown under field conditions (e.g. tomatoes 76 kg/m² per annum vs. 18 kg/m² in the field; capsicum 30 kg/m² vs. 12 kg/m²; cucumber 100 kg/m² vs. 20 kg/m²; lettuce 70 kg/m² vs. 21 kg/m²) (pers. comm. Graeme Smith, G. Smith Consulting, January 2008). Greenhouse production offers better product quality, out-of-season production, and more effective management of nutrients, run-off and pests and diseases. For a country where water is a precious commodity, perhaps the major benefit of this industry is its water use efficiency. For example, the value of production per megalitre for various crops is \$613 for cotton, \$189 for rice, \$418 for sugar, \$1,460 for fruit, and \$1,760 for field vegetables (ABS 2003) (http://www.lwa.gov.au/downloads/final_reports/VPI4_ResPotential_0312.pdf). Hydroponic crops can return a staggering \$167,000 per megalitre (600L per \$100 of output) (G. Smith, pers. comm. 2005).

What will bumblebees add to this already considerable yield advantage over field-produced crops? The first is a very substantial saving in labour. Instead of manual pollination with an electric vibrator three times a week, bumblebees will do the job: from dawn to dusk, every day, seven days a week, no overtime rates, no vacation down-time. Secondly, bumblebees are very efficient buzz-pollinators, a necessary attribute to effectively pollinate tomatoes. Fruit set, uniformity and quality are greatly improved over hand pollination methods, with estimated 10-20% increases in marketable yields (D. Griffiths, pers. comm. 2004; Banda & Paxton 1991; van den Eijnde *et al.* 1991; van Ravestijn & van der Sande 1991; Asada & Ono 1996; Vecchio *et al.* 1996; Dogterom *et al.* 1998; Pressman *et al.* 1999; Morandin *et al.* 2001a, b, c). With the demand for truss tomatoes of both round and cherry types, it becomes critical to have even-sized fruit and complete pollination of the truss so that there are no gaps. Only bumblebees can provide surety of complete pollination (Velthuis & van Doorn 2004a). Hydroponic tomatoes sold as an intact truss are an expanding market.

The Australian greenhouse tomato industry has been seriously disadvantaged through not having access to the biological pollination technology provided by *B. terrestris*. It has delayed the expansion of the industry by several years, and inhibited foreign and local investment (Carruthers 2004; NZ Hothouse, pers. comm. 2004; G. Smith, pers. comm. 2005). There is now a sense of urgency in having this application approved at the earliest convenience. Bumblebee technology is available and used by all of Australia's major competitors. In an era of unbridled open trade opportunities, Australia is now open to imports of greenhouse tomatoes from New Zealand and The Netherlands, and a free trade agreement with China is pending. China has in excess of 1.6 million ha of greenhouses, easily the largest greenhouse industry in the world, and it is both rearing and using bumblebees (Velthuis & van Doorn 2006). This is a major concern

to the Australian greenhouse industry.

Common practice in Australia is to grow either one or two tomato crops per year, which is 42 and 38 weeks of pollination, respectively. An estimate was obtained of the cost of hand pollinating a one-hectare greenhouse tomato crop using an electric vibrator, compared with that using biological pollination with *B. terrestris* (Table 1). A regular hive is presumed to have an effective life of 8 weeks. The savings per hectare in pollination costs alone are clearly substantial. Added to this can be the savings from freeing up labour and trolleys for other greenhouse duties, the cost of hand pollinators, and the value gained from a 10-20% increase in marketable yield and better quality. At a conservative estimate, if just 250 ha of Australia's tomato producers (400-450 ha total) could use bumblebees, and assuming a conservative 10% increase in yield, 45 kg/m² production and \$3/kg return, the industry would benefit from an annual cash bonus of over \$40 million.

Bumblebee technology could benefit the greenhouse tomato industry in Australia by over A\$40 million per annum in savings and increased

Table 1. Estimated relative costs of manual and bumblebee pollination for a crop of tomatoes (D. Griffiths 2005).

	One crop/year	Two crops/year
Pollination period	42 weeks	38 weeks
Hand pollination costs	1730h @ \$16/hr = \$27,680	1300h @ \$16/hr = \$20,800
Bumblebee hive costs	50 hives @ A\$140/hive = \$7,000	45 hives @ A\$140/hive = \$6,300
Savings/ha	\$20,680	\$14,500
Savings/250 ha	\$5.2 million	\$3.63 million

The main crop for which bumblebees are used is greenhouse tomato (Velthuis & van Doorn 2006). In Europe, growers buy a 'pollination service', which means that, for a set price, they are supplied with as many colonies as are needed to achieve full pollination. Because of the strong inter-relationship between bumblebee pollination and biocontrol, all bumblebee producers also sell biocontrol agents and microbials for crop protection. Globally, the total turnover of this industry (producers and distributors) is estimated at €100 million annually, with approximately €55 million attributed to bumblebee sales. The value of bumblebee-pollinated greenhouse tomato crops is estimated at €12 billion annually (Velthuis & van Doorn 2006).

Another very good reason to employ bumblebees is that they are susceptible to most pesticides, precluding the use of toxic pesticides. This will place strong positive pressure on the adoption of biological pest management strategies to replace the present frequent use of synthetic chemicals and concerns over residues. Modern greenhouse production technology has complete control of the growing environment, enabling both biological pest management and pollination techniques to be routinely used. Overseas, the adoption rate of biocontrol methods and bumblebees has been very high. The near elimination of synthetic chemicals from within greenhouse vegetable crops will considerably enhance the safety of produce for Australian consumers, and the reputation of this industry as a supplier of such produce.

Use of bumblebees will greatly reduce pesticide use and encourage uptake of IPM

iii) Alternative pollinator proposals There has been a strong lobby in support of using a native Australian bee to pollinate tomatoes. A disturbing misconception exists among some researchers in the field that there is no urgency to do this as the greenhouse industry is too small and too reliant on chemicals to effectively use a pollinator. This is incorrect. To date, Australian research into alternative pollinators is limited to a few trials on a very few species (Rees 2003) with little progress towards a commercial outcome. It has even been suggested that there are 1500 native bees to look at before bumblebees are considered, clearly not a viable proposition. Of the native bees, the green carpenter bee, *Xylocopa* spp. and the blue banded bee, *Amegilla* spp., are considered the best contenders as it has been shown that they will 'buzz' pollinate tomatoes (Hogendoorn *et al.* 2000; Hogendoorn 2004; Sedgley *et al.* 2004). Stingless bees, *Trigona* spp., have been mooted, but they do not 'buzz' pollinate and therefore are not suitable for tomatoes (<http://www.agnet.org/library/tb/167/>). Although an initial contender, *Xylocopa* spp. are no longer considered to have practical application as a commercial pollinator because the life-cycle is complicated and rearing not easily resolved (Hogendoorn 2004). Besides this, they are rare and becoming more so, therefore collecting them would be a problem. Attention then shifted to *Amegilla*.

Research on *Amegilla* spp. as a potential pollinator has now been conducted for several years, through the University of Western Sydney and the University of Adelaide. There have been three publications (Bell *et al.* 2006; Hogendoorn *et al.* 2006, 2007). An analysis of Bell *et al.* (2006) was published in Practical Hydroponics and Greenhouses, Issue 89, July/August 2006 (Carruthers 2006). While confirming that blue-banded bees are able to potentially increase yields of tomato through buzz pollination, the authors claim a pollination efficiency equivalent to that of bumblebees, which cannot be shown from their data. All their research was carried out in a 22.58m² chamber heavily overstocked with blue-banded bees. There were several reporting errors and the methodology was inadequately described.

Hogendoorn *et al.* (2006), reporting on increased tomato yield by *Amegilla chlorocyanea*, claimed increased yield of 24% greater than wand pollination through multiple buzz pollination of cherry tomatoes by *Amegilla*. They also equate this to bumblebee pollination efficiency, a conclusion which cannot be reached with the methodology employed. All experiments were performed in a small greenhouse compartment of 28m² with only a single trial for each set of variables. The set-up for each of the three experiments differed, so must be considered separately. Experiment 1 (single buzz) was conducted on a larger tomato variety, cv Izabella, with two bees assigned per flower. Experiments 2 (1-2 or 3-6 buzzes) and 3 (unknown number of buzzes) had an unknown number of bees assigned to each flower, and the cultivar was a cherry tomato. Results at a range of temperatures should be considered, particularly when attempting to compare two bees with different temperature requirements for activity.

Hogendoorn *et al.* (2007) further reported on foraging behaviour of *A. chlorocyanea* in three greenhouse facilities of 37m², 750m² and 1000m², one semi-commercial. Data collected from these sites were used to estimate the number of bees needed per hectare, based on number of flowers buzzed/minute x number of trips/day x duration of trip, and then to compare this with estimates for bumblebees taken from commercial greenhouse trials overseas. There was a great deal of variation between data

collection methods among the three greenhouses and number of bees observed, which makes it difficult to unravel how the eventual figures were reached. The methodology would benefit greatly from being standardised; there appears not to have been any established research protocol. Female blue-banded bees reportedly buzzed 9.3 flowers per minute, and this estimate included multiple buzzes of the same flower. The data for this estimate were collected only in the 37m² research greenhouse, where there were 10-20 bees in the greenhouse throughout the observation period. Thus the stocking rate per area was very high, perhaps leading to a shortage of pollen (indicated by double the time spent on a foraging bout). The plants were short, the cultivar was 'Conchita', a cherry tomato carrying less pollen than a round tomato, and the area to be traversed had no relationship to that in a commercial crop. The estimated foraging rate of 9.3 flowers per minute is therefore probably greatly overestimated when applied to round tomatoes and to a commercial crop. The number of trips/day was estimated as 9.1, similar in the two semi-commercial greenhouses of 750 and 1000m² (cv Conchita in one, six different unnamed varieties in the other), but it is unclear how this was calculated when 53 of the 59 bees were only observed for 1-2 hour periods. The duration of a flight averaged 13.4 minutes in the larger greenhouses. If a female returned to her nest or if sight of the bee was lost, a new bee was selected, potentially biasing results towards longer flights. There is no information on the distance into the crop travelled by the bees, nor of pollination success. Most of the crop in the 1000m² greenhouse was wand pollinated (J. Altmann, Biological Services, pers. comm., 2006), so little pollen would have been available in anthers of these flowers, necessitating a longer flight period and more trips/day. The monitoring period for flight duration was also of only one or two hours, at a time and temperature not specified. The final figure calculated of 282 blue-banded bees needed per ha is therefore extremely questionable. A great deal more work needs to be carried out, in particular in commercial situations, before any real estimate of the numbers needed can be made, or any comparison with bumblebee performance is warranted.

Amegilla is a solitary species, which means it does not produce a colony, but females prefer to nest in aggregations in sandstone and mud brick. In nature, females have a short lifespan of 4-5 weeks, with brood development taking approximately 6 weeks. The brood then diapauses as prepupae (Hogendoorn 2004). Discovering how to break diapause without negative effects will be essential for all-year round use in greenhouses. However, no information on conditions for inducing or terminating diapause has been published, only that it seems to occur in response to low temperatures. Information gleaned from 'The Buzz', a newsletter put out by the researchers, from an article in *Practical Hydroponics & Greenhouses* (Sedgley *et al.* 2004), and from ongoing discussions with James Altmann, Biological Services, Loxton SA (the primary commercial partner), suggests that a practical solution is not on the horizon. Only very small numbers of bees have been available for trial in commercial greenhouses. Further difficulties stem from the fact that screening of vents is necessary to keep them within the greenhouse, they become trapped and die above thermal screening, and the nesting blocks must be removed from the greenhouse and broken up to extract pupae to put through diapause for the next generation (J. Altmann, pers. comm. 2007). Chalkbrood disease, *Ascosphaera* sp., is another major potential problem.

Hogendoorn (2004) originally envisaged growers rearing brood on the greenhouse site, as it is difficult to provide pollen artificially. It is not easy to see how a do-it-yourself

Blue-banded bees have a long way to go before they can present a viable commercial alternative to bumblebees, if ever

approach can ever provide a practical solution to the needs of a technologically advanced industry that is moving into operations of several hectares in size. Blue-banded bees will not accept honey-bee collected pollen, so they must rely on a plant-based production system for a pollen supply. An off-plant rearing system is essential for progress towards commercialisation. Hogendoorn has suggested enough bees for the Australian industry could be reared in a 1 ha commercial tomato greenhouse recovering costs through sale of tomatoes. The bees would still require a source of nectar. Apart from the unreliability of such a system, the cost of a modern greenhouse structure with environmental controls would be prohibitive, so this is not a viable proposition.

A further major difficulty is that whereas *Bombus* species leave a mark on tomato flowers during buzz pollination, providing growers with a means for determining whether a flower has been visited, *Amegilla* does not. There is thus no mechanism for determining whether bees need replenishing or what level of pollination is likely to have occurred. At least three buzzes are reported as necessary, even for cherry tomatoes, to ensure full pollination. How will this be assessed? The producer cannot rely on guesswork to know whether pollination has been achieved. Bumblebees also leave repellent-scent marks on the flower which alerts other bumblebees to the fact that it has been visited recently (Goulson *et al.* 1998, 2000, 2001; Stout *et al.* 1998a; Stout & Goulson 2001), so time is not lost visiting empty flowers. Honeybees and stingless bees also do this (Stout & Goulson 2001; Jarau *et al.* 2004).

The AHGA supports research into native bees in principle; however, practical application is purportedly at least five years away, if ever, and progress has been slow and not very encouraging, despite claims to the contrary by some of the researchers involved. The greenhouse tomato industry is in a major expansion phase (G. Smith, Graeme Smith Consulting, pers. comm. 2007), and it cannot afford to wait for a result that may not eventuate. Commercial bumblebee experts who understand the difficulties and economics of mass production are sceptical about the prospects of success. Because a bee buzz-pollinates successfully does not guarantee a successful commercial outcome. A candidate for commercial pollination of tomatoes must conform to the following requirements:

- Able to buzz pollinate flowers.
- Tolerates the physical conditions within the greenhouse.
- Adapts to an artificial, enclosed, rearing system, in order to supply bees on demand.
- Must be readily replaceable in the event of insectary production losses.
- Exists and multiplies within a safe hive suitable for delivery to the grower.
- Accepts an artificial supply of nectar, in which the tomato flower is deficient.
- While in the greenhouse, must be able to breed in sufficient numbers to provide the correct ratio of bees to open flowers (~240,000 flowers/ha/week).
- Is economical when compared with manual methods of pollination, requiring minimum handling and maintenance.
- Is available 12 months of the year, on demand, and is able to cope with seasonal highs and lows in demand.
- Will work at the temperatures optimal for tomato production.
- Requirements for diapause are known and can be controlled.
- Pathogens, predators and parasites are known and can be controlled.
- Is a sustainable operation able to return an attractive profit on investment.

These bees will need to be sourced from the wild in large numbers to start a substantial breeding colony or to replace stock. Proponents of developing a native bee such as *Amegilla* as a commercial pollinator should bear in mind that shipping a single species around Australia, without regard to whether it is native in all those regions, or whether there are strain differences within the same species, raises the same issues as whether *Bombus impatiens* should be used in western North America when it is native only to the east of the continent, or *B. terrestris* should be moved around Europe without regard to its several subspecies.

It is an immense step from showing that a species can 'buzz' pollinate and live in a greenhouse to realising and implementing a viable commercial enterprise capable of servicing, year after year, the whole of the mainland protected tomato crop. Currently, the research work being conducted on the mainland appears to be seriously under-funded, lacks expertise in the development of commercial pollination systems, and requires a more coordinated approach if it is ever to have a viable outcome. Such an enterprise, starting from minimal knowledge about the species, and dependent on funding bodies and finite periods for support, is a long shot at best. Ultimately, many years of study and research dollars may still result in failure with the capacity of Australian greenhouse tomato growers to compete in the marketplace further compromised.

iv) Preparation of the document The AHGA is a national body representing the hydroponic and greenhouse industry. It takes seriously its responsibility to its industry members and to the Australian community on this matter of such fundamental importance to both parties. The TOR was prepared after exhaustive study to identify all of the relevant information and to provide an objective basis for its request. To this end, Dr Don Griffiths, Dr Alec McClay and Biocontrol Solutions were retained as consultants to assist the AHGA in providing a detailed, scientifically credible report.

Dr Griffiths is a former senior government scientist in the UK, until 1995 a Technical Director of Bunting Brinkman Bees, and a member of the board of directors of the International Bee Research Association (IBRA), publishers of the scientific journal *Apidologie*. Prior to joining Bunting Biological Control in 1987, he spent many years in scientific research, eventually becoming Director of Research of a Government Scientific Institute employing up to 90 scientific staff. He is now an internationally recognised private consultant in the field of horticultural biological control, including pollination practices. His credentials include an intimate knowledge of bumblebees, including their biology and commercial use. He was prominent in the development of *Bombus terrestris* for commercial use by the greenhouse industry in Europe and overseas. Dr Griffiths assisted in researching and compiling the data.

Dr Alec McClay is a former senior research scientist and weed biocontrol specialist at the Alberta Research Council in Canada, now a private consultant in ecology with considerable knowledge in statistical methodology and modeling. Dr McClay provided unbiased expert opinion on the scientific validity of three published and one unpublished Australian studies on *B. terrestris* in Tasmania, and applied the CSIRO CLIMEX weather modeling software to *B. terrestris* to determine its potential for establishment on mainland Australia.

Following posting of this document by the DEH in April 2006, the AHGA

secured a Horticulture Australia Limited grant in 2007 to enable it to fully respond to public and government comments and criticisms, and to prepare the final document. Biocontrol Solutions, Mangrove Mountain, NSW (Marilyn Steiner and Dr Stephen Goodwin), with the assistance of Dr Don Griffiths, were retained for this purpose. A further 300 references were sourced and information updated.

Having reviewed available literature and relevant data on this issue, the AHGA stands by its application to import *B. terrestris* for pollinating greenhouse crops as being necessary technology for the Australian greenhouse vegetable industry, particularly tomatoes, while representing no risk to the Australian environment. This ambition has not excluded interest in the development of a native bee species for pollination purposes, despite some of the comments made to the contrary by others in the media.

With regard to opposition to import *B. terrestris* for this purpose, and the promotion of native bee species as a viable alternative, a number of facts need to be established. Firstly, much of what has been written and said about bumblebees in Australia has been alarmist and not based on fact (Griffiths 2004; Carruthers 2004). The AHGA has criticised the standard of scientific study conducted, which for the most part is based upon poor methodology, and that has been used to reach conclusions the data cannot substantiate (Griffiths 2004). The AHGA has amended the submission where respondents have pointed out errors, but stands by its assertions regarding the poor quality of much of the research conducted in Tasmania and rejects the premature conclusions of negative impact that have been made.



Top of the Range Tomatoes greenhouse operation, Guyra, NSW, 2007 (Phases 1 and 2, 10ha)

1. SUMMARY OF PROPOSED ACTIVITY

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1.1. The intended use of the specimens

The intended use of *B. terrestris* is as a pollinator for greenhouse crops on mainland Australia, primarily tomatoes. Use in field situations was initially envisioned but is no longer seen as a realistic proposition at this time due to concerns surrounding feral establishment, whether these are justified or not.

1.2. The number of queens to be imported

A minimum of 200 queens will be used to start breeding colonies which will form the nucleus of commercial production. Such material will undergo rigorous quarantine procedures before introduction to the production unit. Approximately 50 hives/ha/year will be required to provide pollination services to an estimated 100-200 ha of production. If the rearing facility is sited in Tasmania, the importation unit will be a sealed hive containing one queen and about 50 workers. These would be shipped weekly as required direct to distributors on the mainland. If approval were to be given for the rearing unit to be sited on the mainland, further sourcing from the wild would only occur to prevent inbreeding or re-establish a nuclear stock.

1.3. The origin of *B. terrestris* populations from which the specimens will be sourced

The source of the initial material is open for discussion (see Section 10). The likely source is *B. t. audax* from Tasmania, as the stock is free of any major pathogens and parasites (Pomeroy *et al.* 1997; Schmid-Hempel *et al.* 2007), and also does not constitute importation into Australia in the strict sense. There is no commercial production of *B. terrestris* in Tasmania, so initially queens would have to be collected from the wild. However, another option might be starter colonies from the queen rearing unit of a commercial producer in countries able to provide an approved certificate of health with each consignment of queens. Health certificates are issued by a Government Department or a recognized bee research institute. There are regular inspections of commercial facilities during the production cycle to ensure freedom from pests such as nematodes, *Locustacarus acarus*, *Kuzinia laevis* and *Nosema bombi*. This is the current arrangement for importing countries such as the UK where the European Commission has legislation governing importation of bumblebees (http://www.defra.gov.uk/animalh/int-trde/imports/iins/livebalai/bal_live_4.htm). Listed pests and diseases include those of honeybees. Commercial producers of *B. terrestris* include Syngenta Bioline Bees BV (The Netherlands), Zonda Bees and BioBees (New Zealand), Biobest (Belgium), Bio-Bee (Israel) and Koppert (Holland) (Velthuis & van Doorn 2006). Websites of these suppliers

are: <http://www.biobest.be/> or <http://www.beesorbugs.com/pollination.htm> (Biobest), <http://www.bio-bee.com/site/> (Bio-Bee), <http://www.koppert.nl/e005.shtml> (Koppert), <http://www.syngentabiolinebees.nl> (Syngenta) and <http://www.zonda.net.nz/library.asp> (Zonda). Importation will depend on approval by DEWHA and Australian Quarantine and Inspection Service (AQIS).

1.4. Detail on how the specimens will be kept, transported and managed during and after import

The AHGA would develop a protocol for containment of live bumblebees from commercial production to the end of their use as a greenhouse crop pollinator on the farm. The protocol would be developed in collaboration with the Departments of the Environment, Water, Heritage and the Arts (DEWHA) and Agriculture, Fisheries and Forestry (DAFF), hereafter referred to as 'the Departments'. The Departments would be expected to have a role in ensuring compliance. In order to prevent queen escape from the unit or ingress of feral bees, the following procedures would operate (*see also* Section 10):

The commercial production unit would be sited in Australia, probably in northern Tasmania where the species is established and any escapes would have no impact on the environment. Notwithstanding, it will be built as a secure system, comprising a queen-rearing facility, a commercial production facility and a packing room (*see* Velthuis & van Doorn (2004b) (<http://www.webbee.org.br/bpi/solitary/velthuis.pdf>) for a view inside a commercial rearing system in Europe). A separate quarantine facility for processing any new material will also be provided. Note that the production facility is an indoor unit, with no plant material or greenhouse necessary. A second option, if acceptable, would be to site the secure system on the mainland in an area where establishment would be highly unlikely if escape were to occur.

Colonies ready for delivery to growers will, within the confines of the production unit, be packed into what is termed a 'total system hive'. This is a strong, double-layered cardboard container in which there is either one or two self-contained plastic inserts, the inner one securing the bumblebee colony and food supply. The supply of both 'nectar' and pollen is sufficient for colony survival over five or more days of transportation (*Figures 1 and 2 and Appendix IV*). The size of each unit is approximately H 20cm x W 25cm x L 35cm. Each hive is fitted with a 'queen excluder' device, which permits exit and entry of workers but prevents the exit of queens, which are larger (*Figure 1*).

In the United States, APHIS quarantine authorities have accepted hives fitted with 'queen excluder' devices as a safe means for importation into western States of *Bombus impatiens*, naturally confined to the east of the Rocky Mountains. *Bombus impatiens* is now the sole commercial pollinator across Canada and the United States, as the indigenous western species, *B. occidentalis*, was unsuitable for mass rearing because of susceptibility to *Nosema bombi*. The entrance in which the queen excluder is situated, will be sealed within the packing unit before being put into a delivery truck. There are usually four units to a strong outer cardboard box, with a number of boxes secured to a wooden delivery pallet. The whole may be secured with netting.

Transportation between production unit and farms Hives will be transported from northern Tasmania to the greenhouse in one of two ways: either air freight from

Launceston to the mainland, then overnight courier or truck transport to users' properties, or sea freight from Devonport to Melbourne, then overnight courier or truck transport. Hive security during transport will be assured by agreement on a handling protocol signed by the AHGA and the transport company with the knowledge and approval of the Departments.

On-farm escape mitigation A protocol describing the greenhouse and handling conditions to be met by growers who wish to use bumblebees will be developed by the AHGA, in collaboration with the Departments. Prior to any grower obtaining their first consignment of bumblebee hives, a site inspection will be made to ensure compliance and an understanding of the requirements for the destruction of spent bumblebee colonies and hive disposal. Each potential grower client will sign an agreement to this effect. Greenhouse security will involve requirements such as bumblebee-proof screening (4mm x 4mm hole size) of all vents including roof vents and sidewall vents, similar to Japanese requirements (Yoneda *et al.* 2007a). In a stand-alone greenhouse/glasshouse i.e. one not attached to a packing shed or any other adjacent annex used for any purpose other than entry to the greenhouse, a double-entry annex will be required to be constructed at the entry doorway.

Hive use Since the hive requires no attention from the grower, other than placement in the crop, the lid will be sealed with a metal band to prevent interference. The program of hive replacement during the growing season is such that a hive does not normally remain within the greenhouse long enough for colony development to produce young queens before it is removed and destroyed. It should be noted that the 'mother' queen rarely, if ever, exits the hive, dying *in situ* after egg-laying has been completed. In a large, one hectare greenhouse, the number of hives to be disposed of each week should be no more than three. Hive life varies depending on size and other factors, but the replacement program will be such that no hive will remain in the greenhouse for more than eight weeks. Growers will be instructed on how to humanely destroy spent hives, usually by placing them in a deep freeze, or a box filled with carbon dioxide gas, or in hot water. Hives so treated may then be incinerated. None of the materials will be reused. The exit hole has a 'closed' position also, which will ensure that no bees escape should no additional action be taken to dispose of them. Spot inspections will be instituted, along with regular visits to advise growers on pollination requirements.

Penalties While demand is expected to be high, only facilities which fully comply with requirements will be serviced. A penalty of immediate suspension of service for breaching protocols is a very strong incentive for compliance.

Summary of Section 1

It is proposed that a commercial rearing unit be set up to provide hives of the bumblebee *Bombus terrestris* for pollination of tomato crops in greenhouses in Australia. The mass rearing unit will be a secure system most likely sited in Tasmania. A second option, if approved, is to site the unit on the Australian mainland. It will be stocked with 'clean bees' from certified pathogen and parasite-free material. Each hive sent to growers will

consist of a single queen and sufficient worker bees to support pollination. The hive is destroyed after no more than eight weeks. Construction of the hive is such that should any new queens be produced, they are unable to exit, making it a secure system. Using such a ‘total system hive’, the risk of queens escaping into the outside environment and then any subsequent establishment of feral colonies is minimal. A precedent has already been set in North America with *Bombus impatiens*. Netting over greenhouse openings, as practiced in Japan, will also contain any escapes. A government–approved protocol will be developed to manage the secure disposal of commercially-produced bumblebee hives. Periodic inspections will be conducted to ensure compliance.



Figure 1. Example of a ‘total system hive’ used for providing *B. terrestris* pollination services. Photo courtesy D. Griffiths.



Figure 2. Example of a cardboard outer unit (centre) with plastic insert, and further plastic insert with bumblebee colony and sugar unit (right). Photo courtesy S. Goodwin.

2. INFORMATION ON THE TAXONOMY OF THE SPECIES

Kingdom	Animalia
Phylum	Arthropoda
Class	Insecta
Order	Hymenoptera
Family	Apidae
Taxon	<i>Bombus terrestris</i>
Author	Linnaeus, 1758

The taxonomy of the species is relevant to the terms of reference, as it has a bearing on both the source of genetic material for importation, and the life-style traits of the material selected. It is therefore dealt with in some detail in this Section.

The phylogenetic relationships between bumblebees were examined recently using nuclear gene sequences (Kawakita *et al.* 2004). The authors showed that early diversification of bumblebees took place primarily in the Palaearctic, followed by repeated intercontinental faunal exchanges. There are over 300 species of bumblebees, extending across Europe, Asia and North America. They are most abundant in the high altitude and cooler parts of the world, and absent in deserts and tropical areas. There are 78 species in America, 100 species in Asia, 48 species in Turkey and 25 species in England (Kaftanoglu 2000; Goulson & Darvill 2004), for example. Details of species distributions can be found at <http://www.nhm.ac.uk/entomology/bombus/bo.html>.

Bombus terrestris sensu lato (*B. terrestris s. l.*) ('*sensu lato*' = in the broad sense) comprises several subspecies which inhabit separate geographic regions, sometimes overlapping. Together they occupy most of Europe, parts of Asia and the northern fringe of Africa (*Figure 3*, Section 3). While the subspecies can be distinguished on morphological characteristics, they can also hybridise, although some of the data to support this conclusion needs further verification (pers. comm. D. Griffiths 2008). Subspecies are rarely referred to outside taxonomic literature, especially when discussing aspects of the biology of *B. terrestris*, but this should be a firm requirement as the species is not homogenous across its range. Information on the taxonomic status of *B. terrestris* (L) is also provided by the Natural History Museum website <http://www.nhm.ac.uk/entomology/bombus/bo.html>.

Since Linnaeus first described *B. terrestris*, taxonomists have debated the status of the taxa represented by populations confined to the Canary Islands and Madeira, as to whether they are conspecific or actually separate species. Revisers who consider these intra-specific variations insufficient to warrant specific status are Pekkarinen & Kaarnama (1994), Estoup *et al.* (1996), Widmer *et al.* (1998) and Williams (1998).

Early determinations were based on studies of differences in morphology and colour patterns. Estoup *et al.* (1996) published the first genetic study, using 10 microsatellite loci and a partial sequence of the COII mitochondrial gene, followed by Widmer *et al.* (1998), with Estoup now as a co-author. Both of these publications contribute knowledge to the speciation issue. Estoup *et al.* (1996) assessed eight

mainland populations (representing the six subspecies *terrestris*, *ferrugineus*, *calabricus*, *dalmatinus*, *xanthopus* and *sassaricus*), together with a further five from different Mediterranean islands, and one from the Canary Island of Tenerife. Using these 14 populations, they showed that, on the basis of their mitochondrial genes, genetic differentiation among European continental populations (France, Spain, Greece, Italy, Bulgaria, and Poland) was very low, but these were strongly differentiated from the Mediterranean island populations, which also varied one with another. However, the only haplotype found in the Tenerife population differed by just a single substitute from the commonest mainland haplotype. They concluded that this result cast doubt on the specific status of *B. canariensis*.

Widmer *et al.* (1998) attempted to improve ‘the robustness of the scenario’ of the Estoup *et al.* (1996) work. They examined one population from each of four of the seven islands of the Canary Islands group, and one from Madeira Island, both lying off the west coast of Africa. They incorporated the mitochondrial data from all 14 populations used by Estoup *et al.* (1996), together with one population from the UK, as well as a Swiss population of *Bombus lucorum* as the outgroup. Using virtually the same molecular techniques as Estoup *et al.* (1996), their results and conclusions were as follows.

Populations from the Canary Islands are strongly differentiated from both Madeira and continental populations; they may have originated in Africa. Madeira is clustered with the continental and Mediterranean populations, particularly with those of the Iberian peninsula, now 900 km away. Both populations have probably been isolated for some considerable time and show colour differences. Genetic differences have now been shown by these molecular studies. Original colonisation through migration over open water is likely. The climatic conditions prevailing in both the Canary Islands and Madeira are such that it is reasonable to expect some racial differences between them and northern European populations. Six different haplotypes were observed among the 19 populations, each with a clear distribution pattern (Table 2). The most primitive haplotypes were from the Canary Islands. While separate species status for *canariensis* might be suggested by this finding, *B. t. canariensis* and *B. t. terrestris* readily hybridise (van den Eijnde & de Ruijter 2000).

Table 2. Distribution of six haplotypes among 19 *B. terrestris* populations (after Widmer *et al.* 1998).

Haplotype	Source
A	Continent (Italy, France, Greece, Spain, Bulgaria, Madeira) Mediterranean islands (Mallorca, Samos, Cyprus, Crete)
B	Mainland Greece
C	Great Britain
D	Tyrrhenian islands (Elba, Corsica, Sardinia)
E	Canary Islands (Tenerife, La Gomera, El Hierro, Gran Canaria)
F	Canary Island (Tenerife)

Williams (2005) (<http://www.nhm.ac.uk/research-curation/projects/bombus/bo.html>) also has reservations about assigning separate species to the various taxa at this time. There remain some populations still to be tested, notably those from Africa. A recent overview

B. terrestris has a Palaeartic distribution with at least nine distinct subspecies. Island populations such as **B. t. audax** (UK) are genetically and morphologically distinct

by Rasmont *et al.* (in press), combines the subspecies *maderensis* and *ferrugineus* under *lusitanicus*, with *ferrugineus* possibly being a hybrid of *terrestris* and *lusitanicus*.

Genetic differences between bumblebees are part of the scope of the European Union ALARM project (Assessing LARge-scale environmental Risks with tested Methods) (http://www.rdg.ac.uk/caer/project_alarm.html; <http://www.alarm-project.ufz.de/>), which is addressing topics related to the decline in pollinating insects in Europe. This may result in local subspecies being used commercially where substantial genetic or adaptive differences are indicated, for example, in the Canary Islands (Velthuis & van Doorn 2006). Genetic markers can also be used to analyse population relatedness within a species (Roldán Serrano *et al.* 2006; Kokuvo *et al.* 2007). In addition to the taxa involved in these molecular studies, several other subspecies of *B. terrestris* are recognized on the basis of colour variations and differences in their geographic range (Chittka *et al.* 2004). Their geographic boundaries are shown in *Figure 3* and their identities in *Table 3*. Cross breeding of some subspecies has been reported, for example *B. t. canariensis* with *B. t. terrestris* (van den Eijnde & de Ruijter 2000) and *B. t. terrestris* with *B. t. xanthopus* (De Jonghe 1986). Ings *et al.* (2005a) claimed hybridisation of several subspecies in *Table 1* in the paper, but provided no supporting information in the text, reporting only that mating had occurred between males of *B. t. audax* and females of *B. t. dalmatinus*. Intermediate forms, especially on the European mainland, are also reported by Rasmont (P. Rasmont, pers. comm., Jan. 2008).

The New Zealand population is derived from pure British stock, and thus is *B. t. audax*, as is the Tasmanian population (Schmid-Hempel *et al.* 2007). This subspecies has its own unique haplotype (*Table 2*). The Tasmanian population is genetically very reserved and is derived from possibly one but no more than five queens (Pomeroy *et al.* 1997; Buttermore *et al.* 1998; Schmid-Hempel *et al.* 2007). It originates from the South Island of New Zealand.

Table 3. Subspecies of *Bombus terrestris* s. l. with area inhabited.

<i>Bombus terrestris audax</i>	British Isles
<i>Bombus terrestris terrestris</i>	Northwest continental Europe
<i>Bombus terrestris ferrugineus</i>	Spain
<i>Bombus terrestris lusitanicus</i>	Iberian peninsula
<i>Bombus terrestris dalmatinus</i>	Southeast Europe
<i>Bombus terrestris sassaricus</i>	Sardinia
<i>Bombus terrestris xanthopus</i>	Corsica and Elba
<i>Bombus terrestris africanus</i>	North Africa
<i>Bombus terrestris maderensis</i>	Madeira
<i>Bombus terrestris calabricus</i>	Italy
<i>Bombus terrestris canariensis</i>	Canary Islands

Summary of Section 2

Bumblebees originated in the Palaeartic, with *Bombus terrestris* being one of 300 known species. It is comprised of 9-11 known subspecies occupying different geographic and climatic areas in Europe, Asia and northern Africa. These subspecies have traditionally

been separated on the basis of distinct morphological features. In recent years, molecular studies have confirmed the existence of at least six haplotypes, with most of continental Europe sharing the same haplotype. Island populations, including that of Great Britain (the source of New Zealand and thence Tasmanian *B. terrestris* populations), diverged into separate haplotypes, reflecting isolation over substantial periods, and thus possibly differentiations in their physiology and their behaviour patterns, although these have been little studied so far.



Young queen of *B. terrestris audax*. Photo courtesy M. Steiner.

3. THE CURRENT CONSERVATION STATUS OF THE SPECIES IN ITS NATURAL RANGE

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3.2. Abundance of <i>B. terrestris</i> within its natural distribution range.....	21

3.1. Natural distribution of *B. terrestris*

As previously mentioned, *Bombus terrestris s. l.* comprises several subspecies (Section 2, Table 3), the genetics of which are discussed in that Section. Because it is relevant to questions of distribution, abundance and commercial usage, a map of the geographical distribution of the subspecies is shown in Figure 3.

Information on the natural distribution of *B. terrestris s. l.* is detailed in the Natural History Museum website (<http://www.nhm.ac.uk/entomology/bombus/bo.html>), with some measure of comparative abundance. Contributions were made by many authors (Krüger 1954, 1956, 1958; Løken 1973; Erlandsson 1979; Pekkarinen 1979; Pekkarinen *et al.* 1981; Rasmont 1983, 1984, & pers. comm. to D. Griffiths; Williams 1986, 1988, 1989, 1998 & pers. comm. to D. Griffiths; Pekkarinen & Teräs 1993; Özbek 1997; Widmer *et al.* 1998; Kosior *et al.* 2007; Williams *et al.* 2007).

Further bumblebee distribution data is presently being compiled by various agencies in Europe in order to provide a clearer picture of actual distribution of the various species and subspecies, so that any future change can be assessed. The general natural distribution of *B. terrestris* is now known to encompass temperate regions of the Palaearctic. The individual borders of some of the subspecies are for the most part easily defined in that they represent island taxa, namely: Great Britain (*audax*), Sardinia (*sassaricus*), Corsica and Elba (*xanthopus*), Canary Islands (*canariensis*) and Madeira (*maderensis*). Of the remaining mainland subspecies, the two Spanish taxa (*ferrugineus* and *lusitanicus*) are separated from mainland Europe by the Pyrenees and, of course, from the Mediterranean terrain by the sea. The North African subspecies (*africanus*) is limited by the sea to the north and the Sub-Saharan desert to the south. According to Rasmont (pers. comm. to D. Griffiths, 2005), the exact status of this last subgroup is still uncertain.

The two remaining subspecies, *B. t. terrestris* and *B. t. dalmatinus*, share between them the main landmass of Europe. The line of division is somewhat obscure, but it begins with the barrier of the Swiss and Austrian Alps, then possibly along the Tatra mountains, as Rasmont (pers. comm. to D. Griffiths 2005) has recorded *B. t. terrestris* in Slovakia. But then the line is even more uncertain, running somewhere northeast across the Ukraine, where *B. t. dalmatinus* is recorded as far east as the Altaj Mountain Range. Then the distribution line turns north between the Volga and the Urals, until, at latitude 58-60°N, it turns west across northern Europe, along the tip of Sweden and the extreme southern shore of Norway, and so across to encompass western Europe. The southern border for *B. t. dalmatinus* takes in at least northern Italy, then Greece, the Balkans, Turkey, Lebanon, northern Israel, northern Iran, the Caucasus, then up to the Altaj Range on the eastern border of Kazakhstan. According to Rasmont (pers. comm. to D. Griffiths 2005), this taxon has a constant form, with a broad collar and yellow band. The extreme

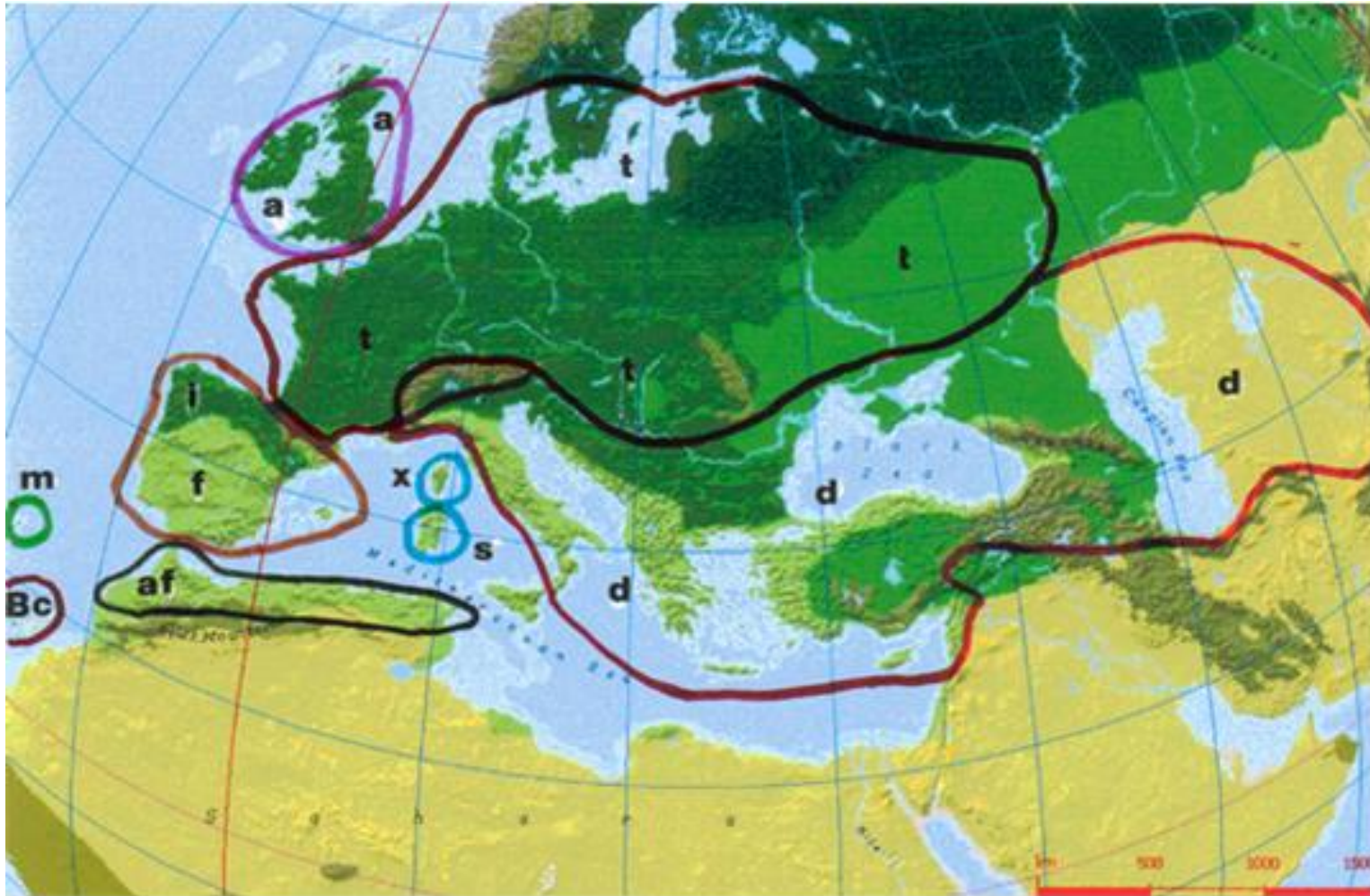


Figure 3. Probable boundaries of 10 of the subspecies of *B. terrestris*. Legend: subspecies of *B. terrestris*; a, *audax*; t, *terrestris*; l, *lusitanicus*; f, *ferrugineus*; d, *dalmatinus*; x, *xanthopus*; s, *sassaricus*; af, *africanus*; m, *maderensis*; Bc, *canariensis* (compiled by D. Griffiths, 2005).

range of *B. terrestris* has boundary limits of 60°N, 30°N, 10°W and 105°E (Figure 3). It is not found in Sub-Saharan nor in other desert regions. It has colonised all major Mediterranean Islands and some Atlantic Islands, including most of the Canary Islands. The Canary Islands are at latitude 28°N, but contain high Mountains and are subject to cold sea currents which provide rain and more temperate conditions than those experienced in other far southern latitudes of the species range. The species does not naturally occur in the Nearctic Region, comprising Canada and United States of America, or South America, or Australasia. *B. t. audax*, can be separated genetically from other subspecies, as is typical of island populations isolated from the mainland. A degree of genetic exchange may have occurred over the centuries because the distance from the Continent is only ~ 40 km, with sea transportation a possibility.

Is *B. terrestris* expanding its natural range? In recent times, limited expansion of *B. t. audax* has occurred into northern areas of Scotland, perhaps a result of global warming or increase in irrigated gardens providing increased floral resources (MacDonald 2001). In the extreme east of Europe, the recent spread of *B. t. dalmatinus* from Turkey down into Israel, reported by Dafni & Shmida (1996), appears to have halted and even retreated, being confined to the northern territories, e.g. upper Galilee, western Galilee and Mount Carmel, just above latitude 33°N (see discussion in Section 4.4). Again, irrigated areas and gardens may have enabled survival. Incursions into new areas would be the expected norm for any species at the edges of their natural range. This has no doubt occurred many times in the history of the species. Persistence in the long term will clearly depend on many controlling factors, including ecoclimatic conditions and availability of food.

3.2. Abundance within its natural distribution range It is generally acknowledged that bumblebees (and other pollinators) are in serious decline in their native ranges, particularly in relation to abundance. The reasons for the decline are numerous and still debated (Williams 1986; Rasmont *et al.* 2000; Kells *et al.* 2001; Cunningham *et al.* 2002; de Ruijter 2002; Goulson *et al.* 2002a; Goulson 2003a; Kells & Goulson 2003; Thorp 2003; Edwards & Williams 2004; Goulson & Darvill 2004; Goulson & Hanley 2004; Goulson *et al.* 2005; Williams 2005; Biesmeijer *et al.* 2006; Goulson 2006; Goulson *et al.* 2006; Carvell *et al.* 2007; Kluser & Peduzzi 2007; Kosior *et al.* 2007; Williams *et al.* 2007). Williams (<http://www.nhm.ac.uk/entomology/bombus/decline.html>) argues that while competition, predation, parasites, pesticides and climate change all potentially contribute to bumblebee decline:

‘the most important factor to have affected the decline of British bumblebees... is the loss of open habitats rich in certain kinds of food plants,’ particularly ‘a decrease in the abundance of the most rewarding food plants.’

This situation appears to be mirrored in continental Europe. While *B. terrestris* is among six species of bumblebees which are still relatively abundant, various pollinator initiatives are aimed at enhancing populations of all bumblebees, without discrimination. Information on their distribution is far more complete than that on abundance. Generally, populations are less abundant and more transitory at the edges of their range (Hengeveld & Haeck 1982; Brown 1984; Williams 1986, 1988, 1989; Guo *et al.* 2005; Williams *et al.* 2007), a factor relevant to the mainland Australian situation (for further discussion on climate-related distribution see Section 6).

Pollinator conservation information is a major target of the European Union ALARM project (http://www.rdg.ac.uk/caer/project_alarm.html), which is addressing topics related

to the decline in pollinating insects in Europe. There are also worldwide Pollinator Initiatives (North American, European, African, Brazilian, and ICIMOD), and the International Pollinators Initiative which have been operational now for several years (Freitas & Pereira 2004) (http://www.webbee.org.br/bpi/solitary/livro_04.pdf) (see also Simon Potts http://www.reading.ac.uk/caer/staff_simon_potts.html; <http://www.fao.org/AG/agp/agps/C-CAB/Castudies/pdf/9-002.pdf>). Syngenta recently launched Operation Bumblebee, the aim of which is to save some of the rare UK bumblebees (<http://www.syngenta.co.uk/about/operation-bumblebee.asp>). Other relevant general pollinator conservation initiatives relevant to sustainable agricultural use are <http://europeanpollinatorinitiative.org/>; <http://www.bumblebeeconservationtrust.co.uk>; Chapman *et al.* (2003), Edwards & Williams (2004), Goulson *et al.* (2005), Goulson (2006), Goulson *et al.* (2006), and Carvell *et al.* (2007). Bumblebee pollination services are considered essential. There is widespread alarm over overall declines in pollinator species and in particular bumblebee populations and species richness. Bumblebees are not a named pest in any country in which they are endemic, and this includes most of the northern Hemisphere, and for the last 130 years, New Zealand.

Because they are highly valued pollinators, bumblebees are the target of extensive conservation measures around the world to enhance their numbers and species diversity

Summary of Section 3

The natural distribution range of *Bombus terrestris s. l.* is in the Palaearctic region between latitude 60°N and 30°N, and longitude 10°W and 105°E. This is a very broad geographic area. Within that range, 9-11 subspecies are recognized, with some overlap on its southern border between the continental *B. t. terrestris* and *B. t. dalmatinus*, whereas island subspecies such as *B. t. audax*, being geographically separated, are probably far more genetically isolated.. While *B. terrestris* is one of the more robust species of *Bombus*, there is agreement among the several agencies studying the decline in pollinator populations in Europe and elsewhere that bumblebee populations should be enhanced. The reasons for the decline in some species are generally related to man-made activities leading to a loss of suitable habitat and food resources, primarily through habitat fragmentation and agricultural activities.

4. COUNTRIES WHERE THE SPECIES HAS BECOME NATURALISED SUBSEQUENT TO ITS IMPORTATION, THE STATUS OF THE SPECIES, AND ITS IMPACT ON NATIVE SPECIES AND ECOSYSTEMS, WITH PARTICULAR REFERENCE TO NEW ZEALAND, JAPAN AND ISRAEL

4.1. Background and experiences in other countries.....	23
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Background At least 40 countries have imported *B. terrestris* for crop pollination purposes since its commercialization in the late 1980s and early 1990s (Velthuis & van Doorn 2004 a, b, 2006). Over a million colonies are now produced annually, some 95% of which are used in tomato greenhouses. Concerns about introductions of non-indigenous *Bombus* species, subspecies and biotypes have gathered momentum in recent years, but it should be noted that such concerns are also pertinent to other beneficial insects used in biological control programs against weeds, pests and diseases. Bumblebee-importing countries fall into three categories:

- A. Those where *B. terrestris* is indigenous, but possibly as a different subspecies or biotype.
- B. Those where other indigenous species of *Bombus* are present, but which may be unsuited to commercial development.
- C. Those very few countries, such as New Zealand, Saudi Arabia, and Oman, where *Bombus* species are not native.

Countries in category A, within the natural distribution area of *B. terrestris s. l.*, particularly those with a commercial greenhouse tomato industry, would almost all have produced or imported commercial hives. Importing countries in category B include Japan, Mexico, Uruguay, Chile, South Korea, China, Finland, Taiwan, Jordan and Iceland (Velthuis & van Doorn 2004b). Details of year of first importation are not known for most countries, but 10-15 years of introduction history is not unusual. Some countries in group B have no greenhouse industry but have imported *B. terrestris* for pollination of field crops. Chile imported *B. ruderatus* from 1982, *B. terrestris* from 1998, and also a limited number of *B. impatiens* (Ruz 2002).

The AHGA is aware only of Australia, South Africa, Argentina and Brazil which have a greenhouse industry but have *not* imported *B. terrestris* or other commercial *Bombus* species.

Commercial colonies initially contained *B. t. terrestris*, but in recent years the preferred subspecies has been *B. t. dalmatinus*, with the exception of *B. t. sassaricus* for southern Europe, and *B. t. canariensis* for the Canary Islands (Table 4) (Velthuis & van Doorn 2006). New Zealand uses its naturalised subspecies *B. t. audax*, which it also exports in small numbers around the world (Global Bees Ltd., http://www.pollinator.com/alt_polvendors.htm). Four additional *Bombus* species (*B. ignitus*, *B.*

Bumblebee technology is used in more than 40 countries with over one million colonies sold annually

Australia is one of the few countries with a greenhouse industry that is not using bumblebee technology

impatiens, *B. lucorum* and *B. occidentalis*) have been commercialized to a lesser degree, with *B. impatiens* the most successful of these (Velthuis & van Doorn 2006). *Bombus pennsylvanicus* was sent from Washington, USA to The Philippines in 1907 (The New York Times, Oct 7, 1907), but did not establish. Only a few bumblebee species appear suitable for mass rearing (Ptáček & Drobna 2006).

Table 4. Bumblebee species commercially cultivated per annum for pollination purposes (adapted from Velthuis & van Doorn (2004a):

(http://www.webbee.org.br/bpi/solitary/livro_04.pdf)

Species	Geographic origin	Where used	Number of colonies
<i>B. t. canariensis</i>	Canary Islands	Canary Islands	30,000
<i>B. ignitus</i>	Japan, Korea	Japan	2,500
<i>B. terrestris</i>	Europe, North Africa, Middle East	Europe, Asia, N. Africa, Chile, New Zealand, Middle East	850,000
<i>B. impatiens</i>	Eastern North America	North America and Mexico	70,000
<i>B. occidentalis</i>	Western North America	Western North America	1,000

Despite the long history of introductions and the numerous importing countries, information on feral establishment following importation is scanty or lacking for most countries. There are reports of establishment of feral colonies in Japan (*see* Section 4.3), Mexico (K. Winter, pers. comm. to M. Steiner, 2006), Chile (Ruz & Herrera 2001; Ruz 2002), Uruguay (Freitas *et al.* 2003) and Argentina (Torretta *et al.* 2006), and incorrect assertions of feral colonies in Israel (*see* Section 4.4).

Nests fitted with queen excluders do not appear to have been used except in the North American context. If ecoclimatic conditions are suitable, then it is possible that local establishment will occur. The North America Pollinators Protection Campaign was reportedly collecting information on the Mexican situation in 2006 (Kimberley Winter, pers. comm. to M. Steiner). As far as we are aware, there are no confirmed sightings. *Bombus terrestris dalmatinus* was initially imported into Mexico in 1995 and 1996 (Winter *et al.* 2006), but it was replaced by *B. impatiens*, which is native to North America. The Republic of Korea has imported *B. terrestris* since 1993 and in November 2002 enacted legislation to continue allowing importation. Both Korea and China are also at suitable latitudes for establishment, but none has been reported. They are also rearing other species; *B. lucorum* in China and *B. ignitus* in Korea (Velthuis & van Doorn 2006).

Establishment of a feral population in Chile was reported by Ruz *et al.* (2001) and Ruz (2002), but it appears to be very limited. First importation of *B. terrestris* colonies was in 1998. A first record of seven *B. terrestris* was reported in Patagonia, Argentina (latitude 40°S, 580 m a.s.l.) (Torretta *et al.* 2006). It was speculated to have arrived from Chile, as Argentina does not permit importation. Southern areas of Chile and Argentina are both at latitudes which are climatically suited to *B. terrestris*, though both have very few native species of bumblebees (<http://nhm.ac.uk/research-curation/projects/bombus/regions.html>; Velthuis & van Doorn 2006).

The situation in New Zealand, Japan, Israel and Australia is discussed in more detail as requested.

4.2. New Zealand

Bombus terrestris, along with three other *Bombus* species, was first introduced into the South Island of New Zealand in a series of releases from 1875, as pollinators of clover crops (Hopkins 1914; Gurr 1957, 1972; Macfarlane & Griffin 1990; Macfarlane & Gurr 1995; Donovan 2007). All bee stocks came from England, and were thus represented by the British subspecies *B. t. audax*, with its characteristic buff tail.

The first recorded successful establishment came from a release in Christchurch in 1885. No further importations have taken place since 1906. Bumblebees were subsequently released also on the North Island. Details on the species composition are meagre, but both natural and deliberate introductions were made of at least four species into farming areas, resulting in the eventual spread of *B. terrestris* over much of New Zealand (Macfarlane & Gurr 1995; Goulson & Hanley 2004). According to Macfarlane & Gurr (1995), *B. t. audax* is now found on all the main islands from 47°S to 35°S. Goulson & Hanley (2004), surveying 70 sites across southern and central South Island, found *B. t. audax* abundance was strongly linked to habitat type:

‘with the highest numbers recorded along river margins, lakes, and in rough pasture. Very few *B. terrestris* were present in native vegetation.’

Abundance was not linked to altitude nor longitude, but to the availability of preferred forage species, particularly red clover, *Trifolium pratense*, and bird’s foot trefoil, *Lotus corniculatus*. As these areas of preferred forage have shrunk, so too has the bumblebee population. This mirrors the general conclusion of Williams (2005) regarding the causes of decline of British bumblebees. Hopkins (1914) reported that there was initial uneasiness about the rapid spread of bumblebees soon after their introduction into New Zealand, in case they should become a pest, but that after some years, there was a check in the population and the numbers rapidly dwindled. Hopkins (1914) notes also that there was a great deal of opposition in the early days from beekeepers, who feared for their livelihood, but because no harm had come to honeybees in other countries, he was able to reassure them, with no further complaints being received. This is a mirror of recent concerns expressed in Tasmania and the mainland.

Donovan (1980) provides a good analysis of the areas of competition between bee pollinators in New Zealand. Further information on pollination systems in New Zealand is provided by Heine (1937), Macfarlane (1976), Norton (1984), Perley *et al.* (2001), Newstrom & Robertson (2005) and Kelly *et al.* (2006). Newstrom & Robertson (2005) in particular give an extensive review of pollination systems as a whole in New Zealand, recognising their complexity and the need for community-level analyses to investigate the positive and negative effects of exotic plants and exotic pollinators on indigenous pollination systems. While indigenous bee species may be depauperate and unspecialised in New Zealand, there is a broad range of non-bee unspecialised pollinators.

Both New Zealand and Australian bees are dominated by the family Colletidae (Armstrong 1979; Donovan 2007). Of the 41 New Zealand bees, 27 are in the family Colletidae, five in Halictidae, one in Megachilidae (introduced), and five in Apidae (introduced). Four Australian Colletid bees have established in New Zealand in recent years, and many New Zealand bees are derived from Australian bees (Donovan 2007). Thomson (1881) reported that many native flowering plants of New Zealand are not dependent on native bees. Flowers at this time tended to be inconspicuous compared with Australian species. Birds, and insects such as flies, beetles and Lepidoptera, were more frequent pollinators than native bees, which Thomson (1881) reported as poorly

New Zealand has imported eight bee species as pollinators, including four bumblebee species. Bumblebees have a 130 year history in New Zealand

represented, with an estimated 10-20 species identified at the time. This perhaps lays the 'ghost of competition past' argument at rest. There was no mention of honeybees, and bumblebees had not yet been established. It would appear that if there is competition for native plants in New Zealand, it is between native pollinators. The introduction of alien plants, both crops and weeds, while providing the resources for survival of non-native Hymenoptera, may have actually increased the number of native bees.

Outside of New Zealand, bumblebees coexist with a great variety of small and large bees, including many other species of bumblebees. Presence of bumblebees, even a common species such as *B. terrestris*, has not precluded establishment of a far more diverse range of bee pollinators than occurs in New Zealand (see Steffan-Dewenter & Tschardt (2000), Roubik & Wolda (2001), Goulson & Darvill (2004), and Potts *et al.* (2006) for information and additional references). In Lithuania, an extraordinary 25,627 native bees were collected from a nature reserve (Monsevičius 2004). Of these, 21 of the 221 bee species were bumblebee species, including *B. terrestris* (no honeybees were recorded).

Most of the *B. terrestris* population in New Zealand hibernates and is active over the summer (Donovan & Wier 1978). Nest founding is reported over an extended period from late August to late January. This results in some winter-active colonies (Hopkins 1914; Cumber 1949, 1954; Donovan & Wier 1978; Macfarlane & Donovan 1976; Donovan 1980), possibly as a result of a second generation. Tree lucerne is an important forage crop that allows survival during late winter/early spring.

Commercial rearing of *B. terrestris* has taken place in New Zealand since 1989, initially for field use (Zonda Resources (<http://www.zonda.net.nz/>); BioForce Ltd and Global Bees Ltd). Queens have also been exported to Europe and Japan (Donovan 1993), and recently other countries including China, Turkey and Korea (<http://www.biosecurity.govt.nz/commercial-exports/animal-exports/export-requirements-omars/omars-list>). The species contributes substantially to pollination of a wide variety of forage, field and fruit crops, including stone and pome fruit, berries, avocado, kiwifruit, and macadamias, and more recently greenhouse crops. Despite the eventual success of introductions of bumblebees into New Zealand, it was reported that deliberate releases to new sites in New Zealand and Chile may require 100-150 queens in a season to guarantee establishment if sites are not particularly favourable (Macfarlane & Gurr 1995, attributed to Macfarlane & Griffin, unpublished).

Macfarlane (1976) recorded visits by *B. t. audax* to 419 plant species, of which only 19 were indigenous to New Zealand. Donovan (1980) considered that the marked specialisation for different flowers shown between many native species and *B. t. audax* indicates that competition between them may be minimal. He also considered that his observation on the ability of some native species to outnumber both honeybees and bumblebees on many native and introduced plants indicates that these native bees are enjoying considerable competitive success.

Further, Macfarlane (pers. comm. to S. Goodwin, 1997) believes that *B. t. audax* will have negligible impact upon Australian solitary bees, relative to competition for food resources, because certain Australian species, which have found their way into New Zealand, have established and spread despite the presence of bumblebees and honeybees (Donovan 2007). *Hyleoides concinna* is a good example.

The main concern about the presence of *B. terrestris* in New Zealand is not the negative effects which may pervade, but how to increase their numbers. Ways of fostering bumblebees on one's property are promoted (Barron *et al.* 2000, <http://www.organicpathways.co.nz/story.cfm?StoryID=129>). Goulson & Hanley (2004), visiting from the United Kingdom, speculated that bumblebees may be contributing to the spread of

Bumblebees prefer exotic plants in New Zealand, with native bees enjoying considerable competitive success because of different flower preferences

New Zealand is looking for ways to increase its bumblebee population

exotic weeds, but this claim is contradicted by the more extensive reviews of causes of weed spread in New Zealand by Butz Huryn & Moller (1995) and Butz Huryn (1997). At a recent meeting with several bumblebee experts in New Zealand, they reiterated that *B. terrestris* is not considered an environmental or public health concern in that country (pers. comm. B. Donovan, R. Read, N. Pomeroy, J. Thompson, T. Marais, Auckland, October 2007).

Conclusion

Four species of bumblebees, including *B. terrestris audax*, were introduced into New Zealand over 130 years ago for pollination of clover. They play an important role in the pollination of a wide variety of field, forage and fruit crops, including greenhouse tomatoes. They are long naturalised, but *B. terrestris* is also produced by three commercial companies for pollination of greenhouse tomatoes, capsicum, eggplant, zucchini and several fruit crops. Visitation records show marked preferences for introduced rather than native plants, and they are rare in native vegetation. They are not considered a pest or of any concern. Populations of native bees are competing successfully and even non-native Australian species have established and spread since their introduction.

New Zealand has been held up by opponents of introduction of bumblebees onto the Australian mainland as an example of the invasive potential of *B. terrestris*, but in fact, it represents an excellent example of successful integration of an exotic pollinator for exotic crops, with no discernible negative effects. This is evidence of ‘no negative effect’ on a grand scale, far more convincing than any number of short-term, artificially manipulated experiments. This is despite an ideal climate across most of the country, which permits broad establishment, and far fewer parasites and pathogens than in its native range. Establishment is still in the ‘settling-in’ stage in Tasmania, but we see no evidence that this situation will not also eventuate there.

4.3. Japan

There are many species of native *Bombus* in Japan, but these do not include *B. terrestris*. Notwithstanding, commercial hives of *B. terrestris* from Europe have been imported annually into most areas of Japan from 1992 onwards for pollination of protected tomatoes because of the enormous commercial benefit (Iwasaki 1995). The number of hives imported into Japan annually now exceeds 70,000 (Velthuis & van Doorn 2006), with the value of shipments of tomatoes grown with the help of bees totalling about 50 billion yen (A\$524 million) (*Japan Today*, January 2005). A conservative estimate is that about 250,000 hives were imported from 1992-2005. Questions have been raised within Japan regarding the possible impact of *B. terrestris* on native *Bombus* species and other bees and pollination of native plants. The native bumblebee species *B. ignitus*, *B. hypocrita* and *B. diversus* were targeted to replace *B. terrestris* as commercial pollinators. *Bombus hypocrita* is quite closely related to *B. terrestris* (Kawakita *et al.* 2004), but *B. ignitus* proved most suitable for mass rearing. Imports of *B. terrestris* are expected to cease if a commercially viable native pollinator becomes available.

Bombus terrestris, along with many other non-native introductions, was listed in 2005 as an alien species in Japan, but importation is permitted on condition that the greenhouse is fully netted and colonies are burned or otherwise destroyed at the end of their useful life (<http://www.env.go.jp/en/nature/as.html>). Economics of production dictated that *B. ignitus* from Japan was mass reared in Europe and then shipped back into Japan to supplement *B. terrestris*. The Japanese species is not popular though because of its much smaller colony size and thus greater cost. In 2004, some 2,500 *B. ignitus* colonies were

used in a total Japanese market of 70,000 colonies Velthuis & van Doorn 2006). Both *B. ignitus* and *B. terrestris* are reared to some extent in Japan, but as far as we are aware, most are still imported from Europe.

The need for better quarantine and inspection procedures was highlighted by evidence of the endoparasitic mite *Locustacarus buchneri* in *B. terrestris* and *B. ignitus* imported into Japan from Holland and Belgium (Asada 2000; Goka *et al.* 2000, 2001) and the microsporidian *Nosema bombi* in imported *B. terrestris* (Niwa *et al.* 2004). These parasites were already present in the native Japanese *Bombus* population, but this was still an unacceptable situation. Goka *et al.* (2001) and Goka (pers. comm. to M. Steiner 2005) found three Japanese haplotypes of *L. buchneri* in *B. hypocrita* and four European ones in *B. terrestris*, with evidence of cross-contamination in commercial colonies of *B. ignitus* and *B. terrestris* imported back into Japan. Whether the foreign haplotype is better or less able to adapt to its new host has not been established, but both *L. buchneri* and *N. bombi* are very rare in properly maintained production facilities (S. Steinberg, pers. comm. to M. Steiner 2005, D. Griffiths, pers. comm. 2005), so this situation should not have arisen. It should be noted that the problems with both *L. buchneri* and *N. bombi* in commercial culture were reportedly resolved several years ago (T. Wada, pers. comm. to M. Steiner 2004) and no further incidences have been reported.

Goka *et al.* (2001), in their investigation of *L. buchneri*, make some questionable allegations outside this field of study. Firstly, that '*B. terrestris* shows great ecological flexibility, yet reference is made only to the data of Dafni & Shmida (1996), which has marginal relevance and whose findings are considered doubtful (Griffiths 2004; Velthuis & van Doorn 2006). They also fail to make any mention of the many subspecies of *B. terrestris* within the ecoclimatic ranges which contribute to this flexibility. Secondly, that 'genetic disturbance [will be] caused by mating between introduced and native species', a claim based on papers by Goka (1998) and Mitsuhata & Ono (1996), on the results of one laboratory cross between a queen of *B. hypocrita* and a male of *B. terrestris* taken from a commercial colony. The authors failed to establish whether hybrid queens developed in the first generation. One cross in the laboratory, without viable offspring, does not constitute the ability to establish a colony. Even should mating occur in the field, the outcome may well not be hybrid, viable eggs. Baer & Schmid-Hempel (2005) found that sperm source in *B. terrestris*, even within that species, strongly influences female hibernation success, survival and fitness, thus in nature insemination with another species is unlikely to result in a viable outcome.

The 'invasion' of Japan by feral *B. terrestris* from commercial hives, probably *B. t. terrestris* or *B. t. dalmatinus*, has been much publicised. Recent papers (Matsumura *et al.* 2004b; Nagamitsu *et al.* 2006) give support to earlier unstructured surveys (Matsumura *et al.* 2003) indicating feral establishment on the more temperate island of Hokkaido, a large island in the northeast of the country, ~ latitude 42-45°N, but there is little data to support establishment in areas south of here. Several Japanese researchers were contacted in 2007 for information on southerly spread, but did not respond. The first feral *B. terrestris* colony in Japan was reported in the vicinity of greenhouses in 1996 in Hokkaido. Japanese structures for protected crops are almost 100% plastic houses, some quite small, and with very poor systems of containment, permitting easy escape, especially for workers and males.

Annual 'sightings' surveys were carried out from 1996-2005 (the majority on the island of Hokkaido). The raw data is published by the Japanese Society of Conservation Biology: http://www003.upp.so-net.ne.jp/consecol/english/maruhana/maruhana_info_eng.html. While the incidence maps published on this website give the impression of widespread

distribution, the 'sighting' figures do not. However, there are now unpublished reports of more than five heavily naturalised regions on Hokkaido and sightings in one quarter of urban communities (Annual Report of the National Institute for Environmental Studies, 2006. URL: <http://www.nies.go.jp/>).

The island of Hokkaido lies along latitude 42 to 45°N and 143°E and, as such, is a mirror-image reflection of Tasmania, which is at 41 to 43°S and 143°E. Both islands enjoy a cool temperate climate, with summer maximum temperatures of 20-25°C, and winter freezing in some areas for periods in January and February. Both enjoy annual rainfalls in excess of 1000 mm. Thus, both islands reflect the natural conditions experienced by *B. terrestris* over a considerable part of its temperate European range.

Below and to the southeast of Hokkaido lies what may be loosely called the Japanese mainland, made up of three tightly knit islands, extending for some 1,500 kilometres, down to the last island Kyushu in the far east of the country. This long thin landmass lies between latitudes 40°N and 30°N. The last 1,000 km are considered to have a tropical climate, both in respect of summer temperatures and annual rainfall, so while the landmass falls between the northern latitudinal limits of *B. terrestris* in Europe, the southern limits have a much wetter climate. Establishment in the southern islands of Japan may thus provide some indication of the potential for establishment in coastal subtropical areas of Australia (see Section 6 and Appendix I and II for discussion on climate-related issues).

Some 75% of the protected tomato production on the Japanese mainland is grown in prefectures in the south and southwest of the mainland (Nishi 1986; Ishi, pers. comm. 2005 to D. Griffiths). This area, which produces many thousands of tonnes of tomatoes throughout the calendar year, has imported up to 30,000 commercial hives each year for the last 12 years, to 2005, totalling well over 250,000 hives. The 'sightings' surveys in this area (2001-2005) have been sporadic and scattered, involving about one-third of the total number of some 40 prefectures. Most of the collecting sites were in close proximity to tomato greenhouses. The semi-tropical to tropical climate of these prefectures is such that winter soil temperatures do not reach the conditions to allow either commercial *B. t. terrestris* sourced from The Netherlands or Belgium, or *B. t. dalmatinus* sourced from mountainous areas of Turkey or Israel, to successfully complete their diapause (temperature data from the 1992 Annual Report of the Japan Meteorological Agency); hence, the low level of feral population establishment which has been recorded on the mainland south of Hokkaido in the Japanese Ecological Surveys.

Other Japanese surveys Further surveys were carried out in 2003 on Hokkaido to search specifically for feral nests. The first, in the spring of 2003, found eight *B. terrestris* nests and 11 nests of native species over 18 person days, principally on the dikes at the edges of paddies and other cultivated fields (Nakajima *et al.* 2004). The second, in the Hadaka region, involving searches from June to September 2003, found 27 *B. terrestris* nests (Matsumura *et al.* 2004a). It is not stated if greenhouses were in the vicinity. Inari *et al.* (2005) (also referenced as Goka *et al.* 2005) surveyed a 270 km² area on Hokkaido Island surrounding a 7 ha greenhouse and several smaller ones with a variable history of 1-11 years of using *B. terrestris* for tomato pollination. They placed 34 traps, from May to September 2003, at distances of 1, 2, 4 and 6 km from the large greenhouse. A total of only 363 *B. terrestris* of all adult stages were trapped. Abundance was positively correlated with the number of commercial hives around the trap sites, and decreased with increasing distance from the large greenhouse. Most bees were trapped within 2 km of the greenhouses and the invasion range appeared limited to less than 6 km from

greenhouses. Early spring appearance of queens (~30 individuals) suggests overwintering outside greenhouses; however, less than 10 queens were trapped during August/September, when new queens would normally be seeking hibernation sites. The distributions of *B. terrestris* and the native *B. ardens* were mutually exclusive, so not surprisingly, the authors could not distinguish any effects of interspecific competition.

None of the three 2003 survey results appears to constitute a massive feral expansion, even after 11 years of use by at least 36 greenhouses.

Recent Japanese studies Several more recent studies have provided information on distribution in Hokkaido, and interaction with native bumblebees and flora (Matsumura *et al.* 2004b; Matsumura *et al.* 2005; Inoue & Yokoyama 2006; Nagamitsu *et al.* 2006, 2007; Inoue *et al.* 2007; Kenta *et al.* 2007).

Matsumura *et al.* (2004b) state that there are 15 native bumblebee species in Japan, with potential for overlap in resource use with *B. terrestris*. The authors claim that bivoltinism is a new trait in invaded areas in New Zealand and Tasmania, which we do not agree with. This trait is rare in those countries, and also known from its natural range (Goulson 2003a), so it is nothing new. It is merely a result of higher temperatures speeding up part of the life cycle (*see* discussion on diapause-related issues, Section 6.3). Nine of 10 *B. terrestris* nests were located in rodent nests, a habitat also favoured by the native *B. hypocrita sapporoensis*. Five of the nests were collected and number of cocoons counted. The output was reported as 4.4 times larger than that of native bumblebees, and thus a concern. This is not a valid claim on the present data, as the output of only four *B. terrestris*, four *B. pseudobaicalensis* and one *B. schrencki albidopleuralis* nests were compared. Apart from the innate variability in bumblebee nest size, and the very small sample size, larger nests have a greater chance of being found than smaller ones, potentially biasing the sample. Claims were also made about potential negative effects of nectar robbing, but it was only occasionally observed. We were unable to find Matsumura *et al.* (2005), perhaps a short report in Japanese.

Inoue & Yokoyama (2006) conducted an excellent study of six Japanese native bumblebees in relation to flower use, demonstrating how resource partitioning occurred on the basis of variation in morphological characters such as head and proboscis measurements, combined with habitat selection and seasonal partitioning. The study demonstrated that caution is needed in claiming competitive exclusion on the basis of apparent overlap in flower use. While *B. terrestris* was not included in those bees studied (the study was conducted on Honshū, south of Hokkaido), the foundation has been laid for some definitive studies on how *B. terrestris* might (or might not) integrate with native species.

Nagamitsu *et al.* (2006) examined abundance, size and morphology of *B. terrestris* and six native bumblebee species in various habitats in southern Hokkaido, noting that 350 commercial colonies were used in 33 greenhouses in the study area in 2003. *Bombus terrestris* was the most common bumblebee caught in water traps, and more frequently trapped in an agricultural area, particularly around paddy fields. The negative association found between *B. terrestris* and *B. ardens* in the earlier study by Inari *et al.* (2005) was shown to be related to differences in habitat preference rather than competition. When land use was taken into consideration, the local abundance of *B. terrestris* was not associated negatively with the number and body size of native bumblebees. The dispersion of *B. terrestris* from greenhouses since 1992 was estimated as an 18.8 km radius by 2004. Tongue length of *B. terrestris* was intermediate between that of *B. ardens* and *B. hypocrita*, suggesting some floral resources would be shared.

Nagamitsu *et al.* (2007) used field cages to measure differences in foraging

Japan has employed bumblebees since 1992 and uses 70,000 colonies a year. Netting of greenhouses is required. It has many native bumblebee species but none has the attributes of *B. terrestris*

efficiency of native bumblebees when *B. terrestris* was included or excluded. The stocking rate was high to increase competition for limited resources. There was no evidence to show that *B. terrestris* showed higher foraging efficiency than the native Japanese species, either when they were alone or when they co-existed. The period of competition was very short, and the authors recommend further study using field experiments in various environments. Importantly, the authors criticize the Hingston & McQuillan (1999) study on competition with *Chalicedoma* (Section 5.3.2) because forager density in the excluded patch was not equal and thus confounded any effect of competitive exclusion.

Kenta *et al.* (2007) conducted enclosure experiments with seven species of native plants of varying corolla lengths and types. Three species of native bumblebees were introduced alone or with *B. terrestris* and pollination efficiency compared with that of *B. terrestris* alone. Fruit set was reduced in some species where *B. terrestris* was used alone and in some cases used along with native bees. The data are an indication of how flower morphology and colour affect resource partitioning between bumblebees, rather than a demonstration that *B. terrestris* will upset pollination of Japanese native plants. It is of relevance only if *B. terrestris* is the only pollinator, is restricted in its access to preferred food plants, or if legitimate pollinators are in insufficient numbers to effect pollination.

Inoue *et al.* (2007) investigated potential niche overlaps between *B. terrestris* and two native bumblebee species in a 7.5 km² area in southern Hokkaido, in terms of morphological characteristics, seasonal flight activity, foraging and nesting habitat, and plant species visited. Exotic flower species were favoured over native species (86.6% of recorded visits). The two native bumblebee species also preferred exotics. There was a large overlap in flower resource use for *B. hypocrita sapporoensis* and *B. pseudobaicalensis*, but this was not believed limiting in this study. Acknowledgement was made of resource partitioning between the different native bumblebee species. Thirty *B. terrestris* nests were found in the 3-year study, most in abandoned rodent nests. The eight nests of the native *B. hypocrita sapporoensis* and one of *B. diversus tersatus* were found in a similar habitat. There was a negative relationship between increasing *B. terrestris* numbers and *B. hypocrita sapporoensis*. The authors concluded that there was no evidence that floral resources were limiting, but that competition for nest sites between *B. hypocrita sapporoensis* and *B. terrestris* was possibly the main reason for the decline. Both species have been observed using the same nesting hole, with *B. terrestris* coming out of hibernation first and possibly occupying most sites. While a logical explanation for the decline, some caution should be placed on this observation. In Europe, *B. terrestris*, *B. lapidarius* and *B. lucorum* compete for nest sites, with *B. terrestris* sometimes taking over a *B. lucorum* nest with workers, yet all are common species. *Bombus terrestris* queens will also compete for favoured locations among themselves, even though other nest sites are available (Sladen 1912; Plowright & Lavery 1984). There is no mention of any study to determine health of *B. hypocrita sapporoensis*, but perhaps this should be ruled out as a reason for their decline, and the study area widened, before conclusions are reached.

Competition for nest sites should not be an issue in Australia, as no other pollinators use these sites. It is more likely that lack of such sites overall will limit establishment of *B. terrestris* itself.

Yoneda *et al.* (2007a) report that net covering of 4 mm x 4 mm hole size over top, sides and entrance of greenhouses in 2004 and 2005 greatly reduced bumblebees foraging in the field compared with the two previous years. This hole size would not impede air flow and would be acceptable to Australian growers.

As elsewhere, *B. terrestris* in Japan visits mostly exotic plants, but an increasing number of native plants (Matsumura & Washitani 2002). These native plants are closely related to many in their European natural habitat, so this is not surprising. They are quite dissimilar to Australian native plants.

There is a recognized pollinator deficit in Japan. *Bombus terrestris* is not the only foreign pollinator imported into this country, but it appears to be the only one attracting attention. Several non-native species of the stingless bee *Trigona* are being trialled for use in greenhouse crops, including, ironically, *Trigona carbonaria* from Australia, with the cooperation of Australian native bee enthusiasts (Kazuhiro Amano, Laboratory of Apiculture, National Institute of Livestock and Grassland Science Tsukuba, Ibaraki, Japan) (<http://www.agnet.org/library/tb/167/>). Japan also exports its native bees to other countries e.g. *Osmia cornifrons* to the United States, suggesting a broadening of investigations might be necessary.

Conclusion

An estimated 350,000 commercial hives of *B. terrestris* have been used in Japan since 1992. Feral establishment appears to have occurred primarily on the more temperate island of Hokkaido, mostly in the vicinity of greenhouses. Some establishment is not surprising given the favourable climate of Hokkaido and open egress into and out of Japanese greenhouse structures until 2005. The climate and latitude is similar to that of Tasmania. Recently, legislated use of netting over greenhouses has greatly reduced escapes. The very limited establishment on the islands south of Hokkaido, with their higher temperatures than Hokkaido, probably reflects the potential situation which may occur in parts of mainland Australia compared with Tasmania.

Japanese studies have concentrated on potential overlap in resources with native *Bombus* species on Hokkaido, hybridization with native species, and transfer of bumblebee-specific pathogens and parasites, which are not an issue in Australia as it has no *Bombus* species. Resource partitioning explains much of the interaction between the native species and the new species. A decline in one species in one area corresponded with an increase in *B. terrestris*. It was surmised that this may have been due to competition for nest sites rather than floral resources, which is a concern for similar-nesting Japanese species, but which may have been due to other causes not examined.

Genetic disturbance from cross breeding was claimed, but only one laboratory experiment was conducted, with no viable offspring. There is evidence that several years ago the parasites *Nosema bombi* and *Locustacarus buchneri* were imported with commercial colonies shipped from Europe, but precautions are now taken and there have been no recent reports of contamination.

4.4. Israel

Two papers by the Israeli ecologist Amos Dafni (Dafni & Shmida 1996; Dafni 1998) form the basis for much of the quoted case against *B. terrestris* with respect to competition with native anthophiles (anthophile = attracted to or feeding on flowers), and the Israeli situation is therefore dealt with in some detail in this Section.

In the first paper, which was a book chapter, Dafni & Shmida (1996) reported that the first *B. terrestris* (*B. t. dalmatinus*) was recorded in the early 1930's at Mt Meron in the Upper Galilee. It was found in the Lower Galilee in about 1960 (Kugler 1962), and at Mt Carmel in 1978. A large fire on Mt Carmel in 1989 drastically changed the composition of the native flora and fauna for several years in the burnt area. In this situation, *B. terrestris* was almost the only bee able to exploit the post-fire plant species. Dafni concluded from this study that *B. terrestris* was a competitively superior

pollinator and a menace to the environment. He warned against commercial production and use, and started a campaign to have the species declared an ecological threat. However, the methodology in the paper was inadequately described throughout and claims were not well supported by the data presented. The authors claimed that *B. terrestris* removed all nectar from *Stachys distans* by 0900h, yet provided no data on activity periods of different bees during the diurnal periods discussed, except in *Table 4* in the paper where at monitoring times prior to 0830h there are relatively high numbers of ‘other bees’. The studies concluded in 1994.

In contrast, Ne’eman & Dafni (1999), in the same area, found no significant differences in visitation frequency to *Salvia fruticosa* between dates and hour of observation for either bumblebees or solitary bees from 0700h to 1500h. The so-called massive increase of *B. terrestris* on *Arbutus andrachne* and *Capparis* (Dafni & Shmida 1996) are from a position of no bumblebees in 1982. The link to a decline in other species is tenuous at best because apart from the 12 year gap in recording for *Capparis* (1982-1994) there have been several fires, one very wet winter in 1991/1992, and changes in human activity, that might well have accounted for the declines. On the other hand, *B. terrestris* was expanding its natural range, perhaps because other pollinators had been decimated by fires and floods.

The Dafni & Shmida (1996) study on *Arbutus andrachne* was performed on a single tree. *Arbutus unedo* is a very important winter flowering, pollen-providing tree for *B. terrestris* in the Mediterranean (Rasmont *et al.* 2005) as is spring flowering *A. andrachne* in Turkey (Gösterit & Gürel 2005), so it may fulfill the same nutritional requirements in Israel and be highly favoured. It is also difficult to see how the authors assume nectar larceny of *Cephalaria* by *B. terrestris* from the presented data. Some plants are favoured for pollen and some for nectar. 14% of the pollen load was of *Cephalaria*, perhaps enough to enable pollination. No study on effectiveness of *B. terrestris* as a pollinator of this plant was conducted.

In a conversation with Dr Roger Buttermore, then of the Tasmanian Museum, at the International Pollination Symposium held in Hungary in 2000, Dafni admitted that *B. terrestris* was no longer in evidence at his study site, and no longer considered a problem at Mt Carmel, but has yet to publish this information.

More recent studies by other authors in Israel do not present *B. terrestris* as a problem. The area around Mt Carmel is elevated and has a Mediterranean climate with cool wet winters and hot dry summers. *Bombus terrestris* is reportedly active from late March to early May in the area (Ne’eman *et al.* 2000). Establishment south of this area would not be expected because it is climatically unsuitable.

The second paper (Dafni 1998) was a short guest editorial, consisting of a series of statements without any accompanying supporting data, such as

‘the conquest of New Zealand by this bee and its triumphal expanding rate ’

‘Each year there are more observations covering, gradually, most of Israel.’

These statements are incorrect. There are an estimated 1500-2000 species of solitary bees in Israel (O’Toole & Raw 1991). Dafni claimed that the so-called ‘invasion’ of *B. terrestris* is a threat to the biodiversity of these solitary bees and also to Israel’s honeybees (Dafni & Shmida 1996; Dafni 1998). Both of the works cited have been criticized (Griffiths 2004; Velthuis & van Doorn 2006). Regrettably, these papers are still quoted as evidence of a major negative impact of an alien species, without reference to several other very thorough studies of pollinator/plant relationships in the area, discussed below, which do not highlight *B. terrestris* as a concern. Dafni himself

Dafni & Shmida spread world-wide alarm about the presence of B. terrestris in northern Israel in the 1990’s but their concerns were ill-founded and short-lived

states that '*B. terrestris* is native to Eurasia (including northern Israel)', and that it spread rapidly after a large forest fire in 1989. Mt Carmel is only 30 km from its 'origin'.

We suggest that Prof Dafni's concerns were premature, not scientifically justified and not in the end supportable in the Israeli context.

Other Israeli studies The focus of several ongoing, long-term studies on pollinators in Israel is not on bumblebees, but in maintaining a diversity of plant-pollinator relationships, by managing fire and other influences such as grazing intensity. Fire and other man-made activities can be expected to cause perturbation, sometimes severe, in plant and pollinator communities. Simon Potts and other authors have published some excellent papers on the subject (Potts *et al.* 2001, 2003a, b, 2006; Ne'eman & Dafni 1999; Ne'eman *et al.* 2000; Vulliamy *et al.* 2006). They are principally interested in the evolving plant-pollinator changes after fire in Israel. They are also examining changes after grazing. These studies are relevant to the Australian situation with regard to the impact of fire management and grazing regimes on pollinator-plant abundance and diversity.

Ne'eman & Dafni (1999) compared a burnt and unburnt area at Mt Carmel in 1995 and suggested six genera of native bees were pollen thieves rather than pollinators on one plant in the area, *Salvia fruticosa*. Seed production in a burnt area, where *B. terrestris* was almost the only visitor, was lower than that in an unburnt area, where a variety of pollinators was present, including a wide range of native bees and *B. terrestris*. This was discussed as a function of the impoverished and changed plant community in the area burnt several years previously. This includes the loss of solitary bee nests due to fire, regrowth and change in the vegetation type, which eliminated available exposed sites for nesting, and reduction in the number of annual nectariferous plants (Dafni & O'Toole 1994). It was not a function of the presence of *B. terrestris*. Visitation by native bees in the burnt area was very low, so seed production would conceivably have been even lower if *B. terrestris* had not been able to exploit the few plants there.

Ne'eman *et al.* (2000) conducted surveys at two sites on Mt Carmel in 1994 and 1995 and found that bumblebees dominated in the burnt site. The numbers of *B. terrestris* greatly declined on one plant species in the second year.

Potts *et al.* (2001) studied two sites on Mt Carmel in May 1997, one unburnt and one burnt eight years previously. A single plant species provided practically the only resource for ~30 species of native bees. *Bombus terrestris* significantly reduced the standing nectar crop very early in the morning and was the most numerous bee present. However, the authors caution that:

'*B. terrestris* is a recent introduction to the area and bee communities in the two habitats may not have reached equilibria; consequently these results should be interpreted with caution.'

Potts *et al.* (2003a) surveyed 21 diverse sites in 1999 and 2000 on Mt Carmel National Reserve and identified 170 species of bees, of which *B. terrestris* comprised <0.1% of all bees surveyed. Similarly, Potts *et al.* (2003b) quantified, in parallel, the response to fire of pollinator communities, floral communities and floral reward structure, demonstrating the changing relationships over time, and not singling out bumblebees for mention.

A study conducted on Mt Carmel by Vulliamy *et al.* (2006) in 1999-2000 on the effect of cattle grazing on plant-pollinator communities found 97 species of bees at 10

**B.
terrestris is
indigenous
to northern
Israel.
Local
production
for
greenhouse
and field
use exceeds
35,000
colonies
per year**

study sites. Sites included post-fire habitats. While *B. terrestris* is briefly mentioned, it was only in the context of being able to identify it on the wing. *Lasioglossum marginatum* and *Apis mellifera* made up 15% and 16% respectively of the total number of bees. This does not suggest that *B. terrestris* is a problem at Mt Carmel.

By comparison, Potts *et al.* (2006) studied bee pollinators in six sites regenerating from fire on the Mediterranean island of Lesvos, Greece, in 2001. *Bombus terrestris* comprised 7.4% and honeybees 65.4% of the 130 species of bee visitors. The greater is the diversity of flowering species, the greater the diversity of bees.

These papers present a far more reasoned position about the long term drastic effects of fire on native bees and plants and the need for a diversity of flowering plant species and nesting habitat. In reviewing these papers, it would appear that the rapid increases in bumblebee numbers were followed by an equally rapid decline after 1997. We wonder why no-one references all the subsequent Israeli studies when debating the 'invasion potential' of *B. terrestris*. Fire is also a constant in the Australian context. It is often deliberately and frequently used as a management tool in our National Parks. These papers are also surely of enormous importance to the debate about preserving the diversity of Australian native bees, perhaps worthy of consideration of fire as a Key Threatening Process way ahead of the dubious listing of bumblebees.

Fire can have devastating and long-term effects on native flora and fauna

The following information on the status of *B. terrestris* in Israel was supplied by Dr Shimon Steinberg, an entomologist and bumblebee expert with Bio-Bee Biological Systems in Kibbutz Sde Eliyahu, Israel, to *Practical Hydroponics & Greenhouses* magazine (Steinberg 2004), and by Dan Weil, Jonathan Cnaani and Amit Einav, Pollination Services, Yad Mordechai, Israel, (pers. comm. to M. Steiner, 1997) and Dan Weil (pers. comm. to M. Steiner 2004). All affirm that *B. terrestris* is naturally distributed in the northern territories of Israel, i.e. the upper Galilee, western Galilee and Mt Carmel. The subspecies is believed to be *B. t. dalmatinus*. The Yad Mordechai authors believed that the first record of *B. terrestris* came from the Galilee region in the 1940's and 1950's, about 50 km to the north, originating from Lebanon. Movement further south into the Mt Carmel area was noted in the early 1980's, perhaps because of the increase in settlements and thus gardens and irrigation. When commercial rearing for tomato pollination started in Israel in 1991, the breeding stock was taken from local populations, considered to be adapted to the climate and also disease-free. Importation of bumblebees into Israel is in any case illegal. Since then, an annual supply of some 35,000 hives has been produced in Israel and distributed throughout the country each year to service over 99% of the protected tomato crop. They are also exported around the world. Honeybees are a serious problem in the field because they invade commercial bumblebee hives and destroy them (Dan Weil, pers. comm. to M. Steiner 2004).

B. terrestris has not established feral colonies in the south of Israel despite use in irrigated field crops

The majority of Israeli tomato greenhouses are in the south in arid and warm regions, outside the expanded natural distribution range for this species in Israel. Despite the large number of bumblebees distributed here, leading to probable escapes from the greenhouses, there is no evidence that any queen has succeeded in establishing a colony in the wild in these areas. Minor use in other greenhouse crops and in field crops also occurs. Avocado is the main crop where *B. terrestris* is used outdoors, on 100 ha situated in Western Galilee (about 25 km northeast of Mt Carmel) and the central-east. Careful inspection each year has failed to find any early spring presence of feral queens or feral nests which could have resulted from commercial escapes. No feral establishment has occurred in six years of open releases, despite irrigation (Steinberg 2004).

Dafni & Shmida's 1996 study of pollination of wild plants in the Mt Carmel area covers the period 1980-1994. As the authors themselves state, this species moved into

this area in the early 1980s. This is many years before commercial hives were used anywhere. Their conclusions about honeybees being driven out by bumblebees are also curious, as no other reports of this activity have been found. Bumblebees do not forage in areas where, or at times when, honeybees are numerous (e.g. Holmes 1961; Thomson 2004, 2006; Forup & Memmott 2005; Walther-Hellwig *et al.* 2006). Bumblebees, honeybees and native bees have coexisted across their natural range for millennia, which is not to say that the balance is not in a constant state of flux.

Conclusion

Bombus terrestris dalmatinus is naturally distributed in the northern territories of Israel, where it may have crossed from Turkey in the 1930's. It does not occur in the south of Israel where there is extensive use of commercial bumblebee hives in greenhouses. Its range expanded southward to Mt Carmel in the 1980's following large fires, but has retracted in the last 10 years, with no acknowledgement of this fact.

Erroneous claims were made, by Dafni in particular, that *B. terrestris* was spreading all over the country, was a menace to the environment and was competitively displacing native bees. These concerns, which have not eventuated, have been given undue credit. Subsequent papers by other pollination scientists in Israel do not support these assertions, but focus on the impact of fire and grazing regimes on pollinator diversity.

Both Dafni's papers are often quoted (e.g. Hingston & McQuillan 1998a; Stout & Goulson 2000; Goulson *et al.* 2002; Thorp 2003; Inari *et al.* 2005) as evidence that the introduction of commercial hives of *B. terrestris* into mainland Australia will lead to an explosion of feral colonies and subsequent general establishment. These assertions are not supported by the 'evidence' presented by these two papers, nor by the present limited distribution of *B. terrestris* in Israel.

4.5. Australian mainland

Attempts to introduce and establish bumblebees on the mainland of Australia for red clover pollination have occurred on several occasions (Cardale 1993). In October 1891, queens from the South Island, New Zealand, were released in the Sydney Botanic Gardens, Centennial Park, Merrylands, Penrith, Valley Heights, Maitland, Kiama, Bodalla, Bathurst, Tenterfield and Richmond (*Agricultural Gazette*, 1891). Survival at Bodalla was reported by the same journal in January 1892. A further shipment was received from Christchurch, New Zealand, later that year. Froggatt (1912) reported that despite several bumblebee introductions from New Zealand, none established (*Agricultural Gazette*, 2 October 1912). No species is stated, but the demand was apparently for long-tongued bees, so possibly they were not *B. terrestris*.

Rayment (1935) states in 'A Cluster of Bees' (p. 492) that bumblebees have been introduced to the Commonwealth on several occasions. This includes queens that he brought into Victoria himself, but which failed to establish. From personal observations, he attributed this failure to predatory birds feeding on the queens. Later in the same book (p. 505), he states that two bumblebee species, *B. terrestris* and *B. ruderatus*, arrived in 1884 and 1885, and later, in 1927 and 1930, further unsuccessful attempts at introduction were made. It appears very likely that these also came from England. Again, there was no establishment. Thus, despite the presence of suitable plant types in release areas, all these earlier attempts to establish bumblebees, including *B. terrestris*, on mainland Australia failed, whereas those in New Zealand succeeded, albeit after multiple attempts.

Several attempts in the 1880's and early 1900's to establish bumblebees on mainland Australia failed. A number of incursions have been intercepted in recent years

Conclusion

Several attempts were made to establish *B. terrestris* in NSW and Victoria approximately a century ago. None was successful. At the time, bird predation was suspected as the main cause.

Summary of Section 4

New Zealand, Japan, and Australia are all countries where *B. terrestris* was introduced where it was previously not native, while Israel was invaded naturally from Turkey via Lebanon on its northern border. These countries present quite different sets of circumstances.

In New Zealand, bumblebees were deliberately introduced, spread and naturalised over a century ago, and no one has considered them other than a great benefit. Consequently, they should not be considered ‘invasive’ in that country.

In Japan, 350,000 bumblebee hives have been deliberately imported since 1992 for uncontrolled greenhouse use. On the island of Hokkaido, feral bees have established outside, mostly near greenhouses, while on the mainland, where the bulk of the greenhouse industry is sited, feral incidents are few. Adverse impacts have been limited to cross-contamination of commercial hives with the protozoan *Nosema bombi* and the mite *Locustacarus buchneri*, which have since been resolved, while research continues on the possible effect of *B. terrestris* on native bumblebees and plants. Imports of *B. terrestris* are permitted to continue into screened greenhouses, despite its listing in 2005 as an Invasive Alien Species.

In mainland Australia, deliberate introductions of *B. terrestris* queens were made in the late 1800’s and early 1900’s, none of which established. The situation in Tasmania is discussed in Section 5.

In Israel, some movement of *B. t. dalmatinus* into northern Israel was recorded by scientists working in the area in the 1980’s, which may or may not persist over the long term depending on climate and food resources, but which presently has retracted. No feral establishment has occurred in southern areas where large-scale use of hives in field crops has occurred for 16 years.

Limited feral establishment of *B. terrestris* is reported in Chile, Uruguay and Argentina, countries with potentially suitable climates, though with very few native bumblebee species.

5. THE HISTORY OF THE SPECIES IN TASMANIA, INCLUDING ITS CURRENT STATUS AND THE KNOWN IMPACT ON THE ENVIRONMENT OF ANY FERAL POPULATIONS ESTABLISHED THERE.

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5.1. Introductions and incursions of bumblebees in Tasmania During 1909, 25 *Bombus* queens from New Zealand were introduced into three sites in Tasmania, including Hobart Botanical Gardens, but no further reference to the outcome appears in the literature (Buttermore 1997). The species involved were not named but were possibly not *B. terrestris*, as long-tongued bees were required. The first confirmed sighting of *B. terrestris* in Tasmania was in 1992. Two individuals were found a few blocks from the Hobart dock area in a Battery Point garden (Semmens *et al.* 1993). There has been much unsubstantiated speculation about the origin of this exotic bee, for example:

‘after being introduced without government approval’
(Hingston *et al.* 2002); but earlier

‘Cargo from New Zealand...may be implicated.’
(Hingston & McQuillan 1998a);

‘they were probably smuggled into the country from New Zealand.’
(Goulson 2003a);

‘was an unauthorized or illegal introduction...of queens smuggled in from NZ.’
(Thorp 2003);

‘A disgruntled tomato farmer may well have smuggled in Tasmania’s bumblebees.’
(Low 1999);

The implication that greenhouse tomato growers were responsible for the incursion(s) is irresponsible and of serious concern to the industry. The only known facts are that the present population in Tasmania is genetically very limited, and may have come from no more than five queens and possibly as few as one (Buttermore *et al.* 1998). A substantial study recently examined the genetic structure with micro-satellites, confirming that the present population most probably originates from a single incursion from South Island, New Zealand in late 1991, which may have consisted of as few as

A recent study indicates that Tasmania's bumblebee population originated in 1991 with a chance incursion from New Zealand, perhaps of only one queen

one or two individuals (Schmid-Hempel *et al.* 2007). The authors suggested that the population in the area south and south west of Hobart is acting as a source-sink for the rest of the island. It was speculated that the female line was 'good', and that success, despite the genetic bottleneck, has been assisted by the absence of major parasites such as *Crithidia*, known to occur in New Zealand. This study effectively dismisses claims that the Tasmanian population is the result of illegal introduction(s). The greenhouse tomato industry in Tasmania is very small and it would appear an unlikely scenario that in 1992, with commercial pollination in greenhouses relatively new, someone would be collecting a few bees in New Zealand and releasing them to an uncertain fate in Hobart. Accidental entry by ship or plane is a much more plausible scenario (Schmid-Hempel *et al.* 2007), and is presumably also the mode of entry of the European and German wasp, *Vespula vulgaris* and *V. germanica*, respectively, which no-one has been accused of importing. This logic might also be extended to the sightings of the occasional *B. terrestris* in the vicinity of mainland Australian ports (May 2003, Appleton Dock, Victoria and Fisherman's Island, Brisbane); even the North American bumblebee *B. vosnesenskii*, which Thorp (2003) and Low (2002) also maintain was deliberately brought in, without naming their source.

Conclusion

The first recorded successful incursion of *B. terrestris* into Tasmania was near the docks in Hobart in 1992. It is not known how the species arrived, but accidental passage from New Zealand by boat or plane of very few individuals appears likely. The population is inbred, but successful because of very low parasite load, favourable resources, and a 'good' genetic line.

5.2. Current status of *B. terrestris* in Tasmania The extent of the colonisation of Tasmania by *B. terrestris* is discussed in Semmens *et al.* (1993), Buttermore (1997), Hingston & McQuillan (1998a), Stout & Goulson (2000), Goulson *et al.* (2002, Hergstrom *et al.* (2002, 2005), Hingston *et al.* (2002), and Hingston (2006a). These papers are discussed in detail as there is some dispute about the extent of the 'invasion' of Tasmania.

Semmens *et al.* (1993) recorded the first collection of *B. terrestris* in Hobart in 1992 and its spread to outlying areas in 1993.

Buttermore (1997) recorded a dispersal rate of 12.5 km per year to October 1996, as far as Kempton (40 km north) and Southport (60 km south of Hobart). Greatest numbers were in urban areas with sightings in the Hartz Mountains and at Mt. Field National Park.

Hingston & McQuillan (1998a) surveyed five locations in various habitats in the vicinity of Hobart in 1996/1997, recording them in all habitats.

Stout & Goulson (2000), in a single season's monitoring, found bumblebees mostly confined to gardens, urban parks and pastures in the south and southeast of Tasmania. They predicted that they would establish in the populated north, be sparse in the dry midland agricultural area, and that they would take longer to establish in the World Heritage Area in central and south-western Tasmania because of the lack of European plant species and the high rainfall ([see http://www.parks.tas.gov.au/publications/tech/state_of_WHA/Chapter4%20p55-122.pdf](http://www.parks.tas.gov.au/publications/tech/state_of_WHA/Chapter4%20p55-122.pdf) (p. 80) for distribution and abundance of introduced plant species in Tasmania).

Goulson *et al.* (2002b) carried out surveys of *B. terrestris*, honeybees and native bees in January, November and December 1999. They found a much narrower distribution of *B. terrestris* than Hingston *et al.* (2002), while acknowledging that fewer

sites were surveyed by fewer people over a shorter time. They did not find bumblebees in the north and west of Tasmania. They were rarely found in native vegetation and were far more abundant in gardens, cultivated areas and where there were substantial numbers of introduced plants. This situation is also mirrored in the UK with respect to greater size of nests and thus population density in suburban areas than agricultural areas (Goulson *et al.* 2002a)

Hergstrom *et al.* (2002) conducted a three-year public survey (2000-2002) on distribution and host plant preference of *B. terrestris* as part of the HRDC study on the environmental impact of *B. terrestris* in Tasmania. The study targeted the general public, but also users and employees of National Parks and World Heritage areas. Approximately 30,000 forms were distributed. There were 613 respondents with 1022 sightings. Sightings information from 1997/98 to 2001/02 was collated and mapped. The maps show a rapid increase in sightings and spread of *B. terrestris*, with concentrations in the southeast and northwest. The general distribution pattern is similar to that of Stout & Goulson (2000) and Hingston *et al.* (2002). Sightings were rare in the northeast, the east coast, and around Launceston. They were more prevalent in wetter areas and in irrigated areas, including gardens. Sightings in bush were rare and often of a single bee.

Researchers also distributed more than 200 hives to various habitats to examine survival. *Vespa germanica* wasps were found in 22 boxes. There was very poor uptake by queens of surface nests, but better of underground ones. Young colonies were found to survive in a variety of habitats, but their number and size fluctuated widely. High altitude sites produced a low number of queens. Only 16% of 43 nests produced new queens, and only 21% more than 50 workers. Sixty percent produced no workers. Nests with high numbers of workers were all in South Hobart and nearby urban bush. A lone bumblebee queen was also seen flying off a boat at Pedra Branca, an island 26 km south of Tasmania, and three over open water (Buttermore & Hergstrom, HRDC Milestone Report No. 3), indicating the reality of travel across wide stretches of water by self propelled migration flights or inadvertent public transport.

Hingston *et al.* (2002) conducted a survey of distribution of *B. terrestris* in native vegetation between December 1999 and April 2001, and included some earlier observations. In the Methodology section the authors state that:

‘comparisons of numbers of *B. terrestris* observed between different climatic conditions, vegetation types, altitudes, distances from gardens, species of plants and months of the year cannot be conducted because search effort levels were not constant across any of these variables.’

but then proceed to attempt just that comparison. This was an observational survey with contributions from many individuals (31) without a standard methodology. Worker bees were recorded in six National Parks in southern and western Tasmania. Data are presented on numbers seen in native vegetation, which are actually very few considering the vast area and effort, but not how many observations (or observers) comprise these numbers, whether the same site was revisited, whether these were observed over one day or several months, whether these were on favoured native plants etc. The study shows only that a range of native plant species were accessed, with a preponderance of bees on a few plant species. This in itself may reflect only the density of the plant species in the environment visited, a particularly attractive flowering period, or the presence of observers during one day or week. Sightings of a single bee also do not prove establishment or persistence or impact. Migration is a key behaviour of queen bumblebees (Mikkola 1984; Vepsäläinen & Savolainen 2000), but has not been considered in sighting incidences. Despite assertions that there is strong evidence of

colonies far from urban areas, the authors appear to confuse sightings with establishment and abundance. A much more thorough and scientific study is required to show either has occurred over the long term. Hingston's data are biased by a wish to show that bumblebees are established in native areas. It would have been far more constructive to conduct a proper survey detailing numbers of bees seen in a specified area or along a known transect length, for a specified time period and during a specific time of day, at set distances apart; also to record both presence and absence of bees, along with details of topography, flora, other pollinators etc. (*see* Teräs (1983), Roubik (2001), Potts *et al.* (2005, 2006) and Thomson (2006) for examples of appropriate methodology). Population density (e.g. number of nests in a given area) can be monitored by described techniques (Teräs 1983; Darvill *et al.* 2004; Knight *et al.* 2005) and should be conducted over several seasons to establish a realistic view of nest density over several years and long-term survival in remote bush (Harder 1986). Such studies will also determine if the population is still in an expansion phase. The Hobart area appears to be acting as a replenishing source for the Tasmanian population (Schmid-Hempel *et al.* 2007). Hingston's methodology is non-repeatable and thus his data are observational only.

Some of the statements in Hingston's papers are both misleading and emotive in nature, for example:

'its extensive invasion of New Zealand'

(where it was deliberately introduced and spread by man over a century ago, and therefore 'established' is the correct terminology (Ricciardi & Cohen 2007)); because of the 'invasion' of New Zealand, Tasmania and Japan,

'it is likely to be invasive in many other regions in which it is introduced.'

(followed by a list of 11 references, none of which relates specifically to *B. terrestris*);

'in view of the proof that *B. terrestris* is highly invasive, and the evidence suggesting it will displace native pollinators, reduce pollination of some native plants, and increase the invasability (sic) of exotic weed species, there are firm grounds for preventing this species from being introduced.'

(when *B. terrestris* has been shown to be 'invasive' only in Tasmania and one island in Japan, proof of displacement of native pollinators has not been shown, nor increased invasiveness of weeds been proved, merely predicted from two instances only of increased seed set). There are many examples of such speculation, not supported by data (Griffiths 2004).

More specific references to invasion biology of Hymenoptera include Moller (1996), Chapman & Bourke (2001), Memmott *et al.* (2004), Traveset & Richardson (2006), Rodriguez (2006) and Ricciardi & Cohen (2007), which demonstrate contrasting views. Moller (1996) recognises that social insects (his examples were wasps, ants and honeybees) have characteristics which promote increased invasiveness, and suggests that they be used to develop better invasion models. He also points out that communities following successful invasion may take a long time to reach equilibrium, and that initial changes in species abundance are often later reversed:

'Since research on invasions is nearly always initiated when the first eruptive wave is noticed and causing alarm, there is a danger that the studies of community responses (or lack of them) are very biased and will not reflect outcomes in the longer term.'

Alarmist sentiment in Tasmania mirrors that in New Zealand in 1914, when introduced bumblebees first began to spread widely. Concerns in New Zealand have long since abated

This is the situation reported by Hopkins (1914) with release of four species of bumblebees into New Zealand 130 years ago, where there was initially concern about the numbers seen. Then the population leveled off and found its niche within the community of pollinators, mostly servicing crops which native pollinators and even honeybees did not. Chapman & Bourke (2001) identify sociality with potential invasion success, again quoting ants and European wasps, but use Hingston's data to infer problems with *B. terrestris* in Tasmania. Memmott *et al.* (2004) claim tolerance of pollination networks to pollinator extinctions, the most-linked pollinators being bumblebees and some solitary bees, and Memmott & Waser (2002) the integration of alien plants into a native flower-pollinator web. Traveset & Richardson (2006) take the opposite view, and claim profound disruptions to plant reproductive mutualisms (papers by Hingston and Dafni are used to support negative impact for bumblebees!). Rodriguez (2006) argues that non-indigenous species may actually facilitate native species through several mechanisms (pollinators are only briefly discussed), and Ricciardi & Cohen (2007) analysed relatedness of invasiveness and impact and found that the mechanisms were not strongly linked, stating that 'invasive' should not be used to connote negative environmental impact. Most alien plants are well served by generalist pollinators (insects and birds), and pollinator limitation does not appear to be a major barrier for the spread of introduced plants (Richardson *et al.* 2000).

Similar criticisms have been directed against Hingston's papers by Carruthers (2004). Certainly, *B. terrestris* has spread (or been spread) through much of southern Tasmania and parts of central Tasmania in a relatively short period. One quarter of Tasmania's land is protected in National Parks, and one fifth has UNESCO World Heritage Area status. These areas are substantial and cover much of the central and southwest of the island. Areas of human habitation are concentrated around Hobart to the southeast and Launceston to the northeast. Sightings (except in Hingston (2006a)), are mostly located along major roads. This is natural because of ease of access, but it also raises the question of whether bumblebees are actually concentrated along roadsides because of floral composition (weeds, pastures or garden plants). This may give quite an erroneous picture of real distribution. Intensive sampling in only one area will also give a biased distribution map. Hingston *et al.* (2002) and Hingston (2006a) show the most forays into National Parks, particularly Southwest National Park, but the surveys of Hergstrom *et al.* (2002, 2005) also covered these areas well and provided a much better context for relative abundance between different areas. Whether or not native plants alone can provide resources to support the population is not crucial to the issue of establishment, only to abundance.

It is not disputed that *B. terrestris* is now distributed over broad areas of Tasmania. Some native vegetation types may well be suitable host plants for pollen and/or nectar, but these must provide a continuous supply for several weeks during nest initiation and breeding to result in long-term viability. *Bombus terrestris* is a large-bodied insect energetically dependent on high rewards from floral resources to sustain its foraging activity and successful colony development (Heinrich 1979a; Eickwort & Ginsberg 1980). The final range of *B. terrestris* will depend on the restrictions of climate, host plant seasonality and local availability, natural enemies and many other factors, and probably not stabilise for a few years, as occurred in New Zealand (Hopkins 1914). Existing natural distribution based on climate is a good indication of *potential* range, but it is not the only factor affecting survival in a particular region. Tasmania has a temperate maritime climate with no point more than 115 km from the sea (Buttermore 1997), so New Zealand is a good comparative indicator of potential distribution within Tasmania. Hingston *et al.* (2002) stated that there were two generations of *B. terrestris*

The climate in Tasmania is temperate, which is ideally suited to bumblebees. They are now broadly distributed there, particularly in habited areas with preferred garden plants

in Tasmania. Buttermore (1997) also concluded that there were two distinct generations in Tasmania, similar to the situation in parts of New Zealand; however, univoltine populations are by far the norm in both countries. The question of viability of a second generation within the same season is discussed in Section 6.

Ants, rodents, birds, lizards, cockroaches and *Vespula* wasps were all recorded invading *B. terrestris* nests in Tasmania. Several respondents have mentioned ants and birds as likely to have a major limiting impact on establishment, abundance and distribution of feral bumblebees in mainland Australia (*see also* Sladen 1912).

Hingston (2006a) reviewed the findings of previous surveys in Tasmania, and presented new data from 2004-2005 which reportedly refuted the findings of other scientists. According to Hingston, the data from his latest survey was solicited by contacting other scientists, land managers and amateur naturalists, and asking them to report observations of more than 10 bumblebees in one day in native vegetation. 153 locations were reported as surveyed, 104 involving observations by individuals connected with universities and land management agencies. Active nests were reported from Cradle Mountain-Lake St. Clair National Park and from Maria Island National Park. We find several problems with the data. The sampling effort was undescribed, non-uniform and non-repeatable. Observers were at least in part solicited via advertisements in newsletters (e.g. <http://www.tasweeds.org> Edition 24, September 2004). The background given in the request introduces a potential major bias in the observers against bumblebees and in favour of finding >10 bumblebees/day. As there is no structured survey, the results are not repeatable and therefore have no scientific validity. There are no data on time of year (beyond September-May), how many of the 153 observations with >10 bumblebees were Hingston's, though he thanks 91 people for reports, whether bees were workers or queens, or what area was surveyed in one day (by foot or by vehicle). A single nest was actually found on Maria Island, not far from human habitation. How many were found in Cradle Mountain-Lake St. Clair NP? Finding >10 bumblebees a day should not be difficult under such an open arrangement and could still arguably be of a single bee. In his results, Hingston states:

‘This survey indicates that *B. terrestris* is breeding in native vegetation in all regions of Tasmania.’

Although a possibility, how has Hingston's survey indicated this, and without knowing the density of the population, how is this significant?

We also wish to refute several inaccuracies in the Introduction (Hingston 2006a). Goodwin, Steiner and Griffiths are named as ‘established and aspiring commercial breeders’. The author knows that this statement is incorrect and we question the motive for including it. Goodwin and Steiner were both long-term professional entomologists in the full-time employment of NSW DPI until retirement in 2007. Griffiths has been and still is an independent consultant to commercial rearing companies in the field of both bumblebee technology and biological control agents. It is also not correct that an application to import *B. terrestris* onto the Australian mainland was unsuccessful. The application has been ongoing and has followed due process since 1997.

Hingston *et al.* (2006) reported on the output of a single bumblebee nest located on Maria Island off the east coast of Tasmania. It was, according to the Abstract, reportedly in a Tasmanian National Park, isolated from urban and agricultural areas by 10 km of sea. The nest was, in fact, located approximately 2 km from gardens growing exotic plants in the historic village of Darlington, an area still occupied by campers and Parks employees. There are 90 introduced plant species on the Island. The size of the

nest, while large, is by no means unusual; output of nests in an area can also vary considerably from one year to the next (B. Donovan, R. Read, T. Marais, J. Thompson, N. Pomeroy, pers. comm. Auckland, 2007). It is entirely misleading to quote laboratory nest sizes overseas and occasional data for field nests as though they were the norm. What the large nest size does indicate is that resources were very favourable in that particular year at that particular site. Some Eucalypt species, presumably *E. globulus* common in the area, may well be a good food source when in bloom. There is no indication of where in the nest the pollen stores were collected for analysis, whether in recent cells or older ones, but it is unlikely the pollen stores from the *Eucalyptus* would have been utilised solely over several months. Stores generally are used up after a short period and replenished as needed.

Discussion in the paper on the output of non-diapausing queens has absolutely no relevance, nor has subsequent discussion on bivoltinism. This is sheer speculation not supported by facts. Maria Island has a temperate maritime climate with, as Hingston points out, mean monthly temperatures of 11.9°C (min) and 22.7°C (max) in February, and 2.8°C (min) and 13.4°C (max) in July. These temperatures are cool, too cool for *B. terrestris* to have more than one generation a year. Rainfall is fairly evenly distributed throughout the year (677 mm/year at Darlington), so flowering of vegetation would have been spread over several months. There is no reason to believe this colony was not founded by a queen that had undergone normal diapause. The ‘late’ nest may be a function of late emergence from hibernation in the spring and the fact that the nest went through to production of reproductives. Hingston has completely muddled three separate studies, that of Schmid-Hempel & Schmid-Hempel (2000) on mating frequencies of the queen (she mates only once), and that of Beekman & van Stratum (2000) and Duchateau *et al.* (2004) on sex ratios. Duchateau *et al.* (2004), referenced incorrectly in the paper as Duchateau *et al.* (2002), found that the sex ratio *at a population level* is biased towards equal investment in the sexes, and is moreover under queen control (*see also* Alaux *et al.* (2005), indicating the same). Thus the output of one colony has no relevance in estimating the area population level or success beyond that one colony.

Hingston goes on to misinterpret Gerloff & Schmid-Hempel (2005) on inbreeding depression and family variation as the authors apply it to Tasmania. The authors found that episodic inbreeding is normal in bumblebees and suggested that Tasmania might have been invaded by a ‘good’ family line, not that it suffered little or no inbreeding depression. We fail to see the relevance or understand the gist of the subsequent discourse on inbreeding in the Tasmanian population. A recent paper (Schmid-Hempel *et al.* 2007) examines inbreeding in the Tasmanian population in some detail. Hingston references his own paper for information on diploid male production following inbreeding (Hingston 2005b), but he conducted no work and his speculation on the effects of inbreeding and greater genetic diversity display a complete lack of understanding of population dynamics in bumblebees. Duchateau *et al.* (2004), Gerloff & Schmid-Hempel (2005) and Schmid-Hempel *et al.* (2007) provide a basic background to the dynamics of bumblebee populations relevant to Tasmania. Hingston (2005b) completely ignores the freedom from all major diseases found in the Tasmanian population, which is no doubt a major factor in increasing their population density and their successful establishment.

While this single colony appears to have performed well on *Eucalyptus* pollen, Eucalypts vary greatly in the frequency, timing, duration and intensity of flowering (Birtchnell & Gibson 2006), otherwise the swift parrot would have no trouble adapting to Eucalypts other than *E. globulus*. *Eucalyptus globulus* is a prolific nectar producer in some seasons, and appears to be providing suitable pollen resources for bumblebees for

Bumblebees may forage on native plants in bush areas, but are not abundant in these areas unless local resources are prolific over several weeks

part of the breeding season. Before general claims can be made about Eucalypts and their importance to bumblebees, much more research needs to be conducted, not just with this Eucalypt species, but with other Eucalypt species. Climatic tolerance, as Hingston concedes, is also a factor in establishment.

Conclusion

Several surveys in Tasmania from 1996 to 2005 record the spread of *B. terrestris* from Hobart to the north of the State, with concentrations in the southeast and northwest. Despite the fairly broad distribution, density of bees varied in different habitats, with most found in habited areas. Recent studies by Hingston *et al.* demonstrate a presence in several areas of mostly native bush, but surveys were poorly structured and abundance and persistence not measured. Several misleading statements have been made about the so-called ‘invasiveness’ of *B. terrestris* as a species, based on spread in Tasmania. The climate in Tasmania is temperate and favours such establishment, and many European crops, garden plants and weeds are available as food resources. The climate and vegetation in mainland Australia differs substantially and is not conducive to such spread.

5.3. Known impacts of *B. terrestris* on the environment in Tasmania

Background The potential impact of a new insect pollinator can be both positive and negative. Positive impacts are enhanced seed set, fruit set, and uniformity in shape, size and quality of fruit (both native and introduced plants). Potential negative impacts must also be addressed. The *degree of probability* that each potential negative impact will occur also needs to be assessed, and considered against potential benefits. The three-year HRDC EIS by the Tasmanian Museum (2000-2002) attempted to address the major issues as far as possible in the limited 3-year time frame (Hergstrom *et al.* 2002, 2005). The AHGA contributed financially to this study. A National Workshop was held in Hobart in late November 1999 to bring together as many interested parties as possible, in order to identify the key environmental issues. A steering committee of experts representing all sides of the debate then devised strategies to deal with those issues, which were, apart from distribution, which is not in itself a negative impact, (i) pests and diseases, (ii) effect on native pollinators, (iii) effect on native plants, and (iv) effect on weed species (Hergstrom *et al.* 2002). Thus, the terms of reference of the ensuing environmental impact study were agreed to by both proponents and opponents of the proposal. So far, Hergstrom *et al.* (2002, 2005) might reasonably be considered as the only study conducted and completed by researchers with no pre-conceived notions of or vested interest in the outcome.

5.3.1. Pests and diseases in bumblebees

Bumblebees generally are host to a wide range of parasites and predators (Macfarlane *et al.* 1995; Schmid-Hempel 1998; Hergstrom *et al.* 2002; Goulson 2003a; Allen *et al.* 2007); however, they share very few of these with honeybees or other bees. Those shared with honeybees are some viruses, a restricted range of protozoa, and some parasitic flies. The Tasmanian bumblebee population was sampled during the HRDC study (Hergstrom *et al.* 2002) and checked for internal and external parasites. Bees were found to be free of all but one external parasite, the phoretic deutonymphs of the mite *Kuzinia laevis*. This is a common associate of bumblebees, considered a benign pollen thief, although the Tasmanian bees were carrying very high numbers of these mites. It has only been associated with bumblebees, and not honeybees or other bees. A later, more detailed study of Tasmanian bumblebees (Allen *et al.* 2007) confirmed that of the

common parasites, only *K. laevis* was present, again in abnormally high numbers. 511 bees from 15 sites and 5 regions were examined. Viruses could not be analysed, but the successful establishment of *B. terrestris* in Tasmania suggests that at least no important ones are present, or that efficient vectors are lacking. Lack of parasites, disease and key predators such as Conopid flies is a very likely reason for the rapid establishment of *B. terrestris* in Tasmania, but the low genetic diversity may make them very susceptible to any future encounter (references in Allen *et al.* 2007). Notwithstanding, any bumblebees imported into mainland Australia from Tasmania would be sourced from clean stock and required to undergo strict quarantine procedures and treatment.

Tasmanian bumblebees left their parasites and pathogens in New Zealand when they migrated. They are remarkably healthy, but somewhat inbred

Conclusion

The possibility that the current population of bumblebees has had a negative impact on native bees and honeybees through transmission of parasites, predators and pathogens is highly unlikely and no evidence exists for it. A recent study confirms the absence of important parasites and predators of bumblebees in the Tasmanian population. Similarly, no evidence was found of honeybee pests and diseases carrying across to bumblebees, despite 15 years of co-existence. Bumblebees imported into mainland Australia from Tasmania would be sourced from clean stock and required to undergo strict quarantine procedures and treatment.

5.3.2. Impacts on native pollinators through competition for nectar and pollen resources

5.3.2.1. Native bees

Competition occurs when two or more species forage on the same resource plants and those resources are limited. Resource sharing is a natural process that may lead to co-existence, or in extreme cases may result in physical or temporal displacement of one of the species. However, pollinator webs are rather tolerant of species extinctions (Memmott *et al.* 2004). The presence of two or more species sharing the same floral resources does not automatically mean that one or more will be negatively impacted upon, rather, resource partitioning occurs (Eickwort & Ginsberg 1980; Dafni & O'Toole 1994; Dramstad & Fry 1995; Roubik & Wolda 2000; Potts *et al.* 2001, 2003a, b, 2006; Williams *et al.* 2001; Goulson & Darvill 2004). There are many facets to this partitioning. Habitats differ in plant composition, species and density. Bee species differ in foraging preferences, in collecting methods, in daily, seasonal and annual activity patterns, and in natural distribution range. Flowers differ in their attractiveness, architecture, and periodicity. The two rewards of pollen and nectar are often accessed separately, although nectar drives most foraging bouts. Relative humidity influences whether pollen or nectar is collected, and the production and concentration of nectar (Peat & Goulson 2004). The effects of competition are thus notoriously difficult to measure. Goulson (2003a) states that:

‘The outcome of interactions between exotic and native flower visitors depends on whether floral resources are limiting.’

The only way to test this unequivocally:

‘is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored.’

‘such experiments need to be well replicated, with replicates situated many kilometers

Conclusions of negative impact in Tasmania are based on unsupported conjecture. Many of the studies so far conducted are short term, the science questionable, and the focus unduly biased

apart, and conducted over several years. No such study has been carried out.’

We would agree with this. Much of the research that has so far been conducted in Tasmania is preliminary. The conclusions by some authors of serious negative impact are unjustified, having been based, in our opinion, on poor scientific methodology, inadequate data, and preconceived bias.

Tasmanian native bees have had to compete with each other and with a variety of other pollinators with which they have co-evolved. In relatively recent years they have also had to adjust to massive land clearing, pesticides, herbicides, foreign birds, European wasps and honeybees. The only impact studies on native pollinators in Tasmania have all been directed at potential competition from bumblebees, surely a very minor player in the overall scheme of survival. The relevant studies in Tasmania are reported in Semmens (1996, 1998), Hingston & McQuillan (1998a, 1999), Stout & Goulson (2000), Goulson *et al.* (2002a), Hergstrom *et al.* (2002), Hingston *et al.* (2002), and Hingston (2005a). Competition with native pollinators is presumed to occur primarily on native plants, so the feeding preferences of bumblebees on these plants have attracted most of the attention.

Semmens (1996) lists 14 native plant species and 156 introduced plant species on which bumblebees had been observed feeding. These were presumably located in southern Tasmania, as this was in the early days of expansion, but no details are given. He issued a supplementary list (Semmens 1998) of new flowers visited, to include six native and 40 introduced plants.

Hingston & McQuillan (1998a) restricted their survey to native vegetation, between September 1996 and June 1997, and included observations of honeybees and native bees at five sites for part of this period. There were located at Mt Wellington, Huon Road, Waterworks Reserve, Mt Nelson, and Coffee Creek. All these areas, though not stated, are not far from suburban areas of Hobart. Bumblebees were recorded at all sites in variable densities. Over a nine month period, 2160 individuals were observed foraging on 60 species of native plants, mostly belonging to the Myrtaceae, Fabaceae, and Epacridaceae. Similar foraging profiles were observed for several species of birds (Ford 1979), Colletid bees and *Vespa germanica*. *Bombus terrestris* visited predominantly plant taxa that supported a large number of other anthophiles, as one might reasonably predict. Of 66 native plant species listed, over a 10 month observation period, there were only eight with >75 visitations. The relative sampling effort is impossible to ascertain because the list includes those in suburban Hobart gardens with no sampling protocol described.

Despite only making their observations on native plants, the authors concluded:

‘The recording of *B. terrestris* foraging on 66 species of Tasmanian native plants countermands the claim [by Semmens 1995, 1996] that this species forages mainly on introduced plants.’

The reference should have been to Semmens (1996, 1998). The statement by Hingston & McQuillan (1998a) also contradicts the situation reported from New Zealand, where introduced plants were strongly preferred (Donovan 1980; Donovan & Macfarlane 1984). The authors make many allegations, with no supporting data, about potential negative effects of the common usage of floral resources with anthophilous insects and birds, the capacity to become naturalised in many areas of the Australian mainland, and even suggest that *B. terrestris* may compete with commercial honeybees in leatherwood (*Eucryphia lucida*). Yet such competition with honeybees has never been known to happen anywhere in the world.

Sharing of available resources amongst multiple pollinators is the norm. Competition may not be occurring if resources are not limiting

Despite the many unsubstantiated claims of negative impact, they also state:

‘competition may not be occurring...if these resources are not limiting.’

Relevant to this is that good supplies of nectar in native bush areas are sporadic over spring and summer, and likely to flush at the same time that native anthophiles are most active, and therefore resources may indeed not be limiting. The results of this study are largely negated in any case because of a failure to explain their methodology clearly. For example, the size of each plot is not defined, nor the time for each period of observation. These are important omissions, since their counts per plot reached 300 *B. terrestris* visits per day. At the known rate and frequency of forage flights of this species, depending on the area, it may represent the activity of just a single nest (Heinrich 1976b). The floral range within the observation areas are not mentioned either. The authors have also apparently failed to understand seasonal and daylight foraging patterns, which will significantly influence the density ratios between bumblebees and other bees during an observation period. Hergstrom *et al.* (2002), when surveying the same sites, described bumblebees as rare at Huon Road and Waterworks Reserve, and sporadically foraging at Coffee Creek and Mt Wellington, not exactly ‘thriving’.

Hingston & McQuillan (1999), in a further attempt to show that competition with native bee species is occurring, examined bee visitors to native bladder pea, *Gompholobium huegelii*, at a site on Huon Road, during a time (January 1997) when they considered resources were declining and therefore competition could occur. The only bee visitors noted were *B. terrestris* and two *Chalicedoma* spp., one of which was rare. The two quadrats of 2.4 m x 2.4 m were 3 m apart. They were monitored by a single observer for two days only. On the first day, all bumblebees were chased away from one quadrat, with quadrat ‘treatments’ reversed on the second day. Differences in various measures of foraging behaviour of *Chalicedoma* were estimated, e.g. number of flowers visited, and time of each foraging bout. *Chalicedoma* species have a rapid flight pattern and are difficult to catch (Hingston 1999), whereas *B. terrestris* are slow and lumbering, so the margin of error in this type of observational study would appear to be rather large.

An assumption (untested) was made that nectar levels were replenished in full overnight (and not removed by nocturnal visitors such as ants). The disturbance of chasing away bumblebees was assumed to have little impact on foraging behaviour of either species of bee in either quadrat, nor on ability to observe, at the same time, bee entry and exit into two separate quadrats, along with the number of flowers visited. In the afternoon (but not over the whole day), *Chalicedoma* foraged more heavily in the quadrat where bumblebees were chased away, which the authors attributed to depletion of the standing nectar crop in the control quadrat by bumblebees. There were, however, no significant differences between any of the behavioral variables over the course of the whole day. Thus, to hold this study up as showing that bumblebees will displace native bees on a broad basis is completely unjustified. Temperature variation alone could have accounted for differences in the afternoon. Differences in sunlight reaching the two quadrats in the afternoon were ‘solved’ by pooling the data. Knowing which quadrat was warmer in the afternoon, and by how much, is surely important? On the second day, the diurnal temperature ranges were reported to show a 3°C difference between maxima and minima. There is no mention of where this was measured, whether the nearest weather station or within a quadrat. (In public comments, 2006, Hingston reported he thought it might have been measured at the Hobart Weather Bureau). If within the study area, this is not a ‘slightly warmer day’ to a native bee sensitive to cold. That the temperature

The claim that B. terrestris will displace native bees is based on a single two-day study which had multiple design flaws

difference probably has a bearing on relative bee activity over the two days is demonstrated by the authors themselves. The mean number of flowers visited in the control quadrat on each foraging bout can be calculated from *Table 2* in the paper, for both species. There is only a 2.9% increase in the number of flowers visited by *B. terrestris* on the second, warmer day, but a 21% increase for the most numerous *Chalicedoma* species. The increase in the number of flowers visited by *Chalicedoma* per bout appears to be larger than that between quadrats with and without bumblebees.

An anomaly in data presentation in *Table 2* is apparent. A mean of 61 foraging bouts per day were reportedly conducted by *Chalicedoma* spp. in control quadrats, compared with 29 bouts for *B. terrestris*. If this day is 8 hours, then the mean number of foraging bouts per hour for *Chalicedoma* should be 7.63, not 14.75 as stated in *Table 1*.

On the second day, *B. terrestris* visited on average 6.43 flowers per bout, whereas *Chalicedoma* visited 4.24 flowers per bout (*Table 2*). Given that there were 60 flowers open in the quadrat, this does not appear to be heavy foraging pressure. Why would *Chalicedoma* not simply increase the number of flowers visited on each bout if resources were limited? If bumblebees had depleted all the resources in the morning before *Chalicedoma* started foraging, why did *B. terrestris* forage at the same rate in the afternoon as in the morning? Why did *Chalicedoma* increase its foraging rate in the afternoon in both quadrats? Nagamitsu *et al.* (2007) and Velthuis & van Doorn (2006) also criticise this paper, the former on the grounds that excluding bumblebees from one patch reduced the total forager density in that patch and alone could have caused the observed differences.

Reference in the paper's Discussion to standing crops of nectar being reduced by *B. terrestris* were credited to Pyke (1978) and Pyke & Balzer (1985). The association of the latter paper is to honeybees, but in any event, any organism which collects nectar can logically be expected to reduce its standing crop. The issue is whether there is enough nectar on a spatial and temporal basis to serve those needing it, and how soon it is replenished. Diurnal nectar production varies with the plant species and with weather patterns (Peat & Goulson 2005), and no information has been provided on nectar production in this plant to show that it was in any way deficient.

Two independent analyses of the statistics employed in this study (Anon 2004; McClay 2005b) were conducted. Both stated that because of a design flaw, the study does not have sufficient statistical power to confirm a displacement effect. There are only two treatments and two replicates, and only two degrees of freedom are available for testing treatment effects, rather than the 15 that were apparently used. The paper is an example of temporal pseudo replication. Thus, while competitive displacement *may* have occurred, the methodology used in no way justifies the conclusions. In our opinion, this was a poorly constructed study which should not have been accepted for publication. Repetition over several sites at different time periods should have been conducted. Hergstrom *et al.* (2002) attempted this repetition over several sites but found that bumblebee visitation rates were low and pollinator diversity much broader than Hingston reportedly observed. Experimental procedures are suggested in Paton (1996), Butz Huryn (1997), Manning (1997), Schwarz & Hurst (1997), Roubik & Wolda (2001) and Paine (2004).

Clearly, the conclusions reached by the authors are simplistic and not warranted. Paton (1996), Manning (1997) and Paine (2004) critique the conclusions of similar studies related to competition from honeybees. *Gompholobium* is not pollinator-limited, so it is also not correct to imply that pollination will likely be negatively impacted upon by competitive displacement of *Chalicedoma*, even should this have been shown. In fact, no data were taken to confirm or deny that this plant species was negatively impacted

The intricacies of foraging behaviour in bumblebees are very well described in the literature. Carefully planned studies are required to show long-term effects of any competition

upon by bumblebee visits. Yet this single paper is widely quoted in many scientific texts and articles as evidence of competitive displacement of native bee species by *B. terrestris*, which on such flimsy evidence raises disturbing questions about scientific rigour.

Stout & Goulson (2000) studied *B. terrestris* distribution across Tasmania but only made observations of feeding preferences. Bumblebees were reported to be ‘far more abundant on introduced flowers.’ They speculated on possible impacts previously mentioned, but conducted no studies to confirm their hypotheses.

Goulson *et al.* (2002b) quantified the abundance, diversity and floral preferences of flower-visiting insects from 15 November to 10 December 1999, at sites where bumblebees and honeybees were present, and compared them to sites where they were absent. Sixty seven sites were hand-examined and sticky traps were deployed at 122 sites within southeast Tasmania. The hand-examined sites were concentrated along roads, but encompassed much of the island except the far northwest and southwest. Honeybees, which have been present in Tasmania for 185 years, were found to be by far the most abundant bee species. There was considerable niche overlap between all bee groups in terms of flowers that they visited; however:

‘Sites where bumblebees were established had similar species richness, diversity and abundance of native flower-visiting insects as did sites where bumblebees were absent.’

Thirty six species of bees were found, but four native species predominated. Sixty three percent of inflorescences examined were of native plants, yet only 16.5% of bumblebee and 27.4% of honeybee observations were recorded on native plants. Three of the common native bee species were found predominantly on introduced weeds. Niche overlap did not take into account whether bees were collecting pollen or nectar, or possible differences between times of day that bee species feed. That this type of information is important is illustrated by Horskins and Turner (1999), who found that 90% of early morning visits by honeybees to flowers of *Eucalyptus costata* involved collection of pollen; they did not forage for nectar until native insects were active, so were not removing nectar before native insects could access it. Bumblebees tend to collect pollen in the middle of the day, depending on weather conditions (Peat & Goulson 2005). Conditions need to be dry or pollen will be difficult to groom off.

The authors concluded that bumblebees remained far more abundant in gardens, cultivated areas, and where there were substantial numbers of introduced plants. Their data:

‘do not suggest that bumble bees are having a significant impact upon native bee communities’.....‘the addition of (bumblebees) is perhaps unlikely to have an appreciable effect on small, short-tongued native bees.’

They concluded that:

‘This study should not be taken as evidence that bumblebees are having no ecological impact.’

They raised the possibility of competition with vertebrate visitors and effects of seed set on native and introduced weeds, but provided no supporting data. Broad generalisations about competition, niche overlap, potential and weed spread, from narrowly focused and limited studies, are all too common.

Search times in the study were concentrated between 11:00 and 15:00h, which

has been criticized by Hingston as being outside the main foraging times of *B. terrestris*; however, they do show relative abundance between vegetation types. *Bombus terrestris* peak foraging periods for nectar are known to be bimodal, in early morning and late afternoon (Herrera 1990). While the peak foraging activity for honeybees has been reported as mid-day (Corbet *et al.* 1993; Paton 1996; Thompson & Hunt 1999), other researchers found a bimodal pattern similar to that of *Bombus* spp. (Schaffer *et al.* 1979; Herrera 1990). The threshold for activity for *B. terrestris* may be lower (~5-10°C) than for *A. mellifera* (~8-11°C) (Heinrich 1979a; Corbet *et al.* 1993), but this may be irrelevant for the period of overlap in colony foraging activity in Australia, which would be in the spring and summer. It may thus be incorrect to state that *B. terrestris* will provide an add-on effect to that of honeybees by competing with native bees at hours when honeybees do not normally forage. Diurnal temperature range and nectar concentration will no doubt contribute to and drive much of this diurnal pattern (Corbet *et al.* 1979; Plowright & Lavery 1984).

Hingston *et al.* (2002) contributes several new native plant records where bumblebees were observed foraging, but again, in our opinion, the study was poorly constructed. They reiterate dire warnings of the consequences of bumblebee presence in Australia, but provide no supporting data for this extreme view.

Hergstrom *et al.* (2002, 2005) found a distinct preference of bumblebees for introduced plants. Only 11.1% of plants visited in the Royal Tasmanian Botanical Gardens in Hobart were native species, with a similar 10.9% of plants across Tasmania. A list is presented of over 200 plant species on which the public observed bumblebees foraging, which confirms this. As well as the three-year public survey, a scientific survey was conducted in seven areas of variable habitat in the Hobart area, plus observations were made in National Parks and in townships and sites across the State. The effect on other pollinators was studied by monitoring population densities of all pollinators.

Results were similar to those of Goulson *et al.* (2002b), in that honeybees were more numerous than all other pollinators on both native and introduced plants. On introduced plants, bumblebees were the second most prevalent pollinator, while native bees came second to honeybees on native plants. Native pollinators were more numerous in bush sites regardless of proximity to urban areas. Although bumblebees were polylectic, they showed strong preferences, in this case, for species such as lavender (120 sightings) and Lamiaceae. Only 20 of the 200 plant species (1028 sightings across Tasmania) had more than 10 sightings over the three years, of which only two genera with large flowers and good nectar supplies, *Banksia* spp. and *Eucalyptus* spp., were native.

The authors revisited Hingston & McQuillan's (1999) study on *Gompholobium* at Huon Road, discussed above, but expanded its scope. Three sites with this flower species were monitored from June 2000 to June 2002. Flower abundance was extremely low in the first two summers at Huon Road and Coffee Creek. When conditions were dry, no bumblebees visited at any site. Along Snug Falls track in December 2001, flower abundance was moderate, but no bumblebees were present. Flowers increased at two sites after heavy rain. At the Huon Road site, two adjacent quadrats 2 m x 2 m and 2 m apart were monitored, at five separate positions. Shooing bumblebees from one quadrat was planned, but the bees were so few in number that this was abandoned. Five further visits were made to the site in the following two weeks. The Snug Falls site was also monitored three times. At Huon Road, 16 potential pollinator species were recorded from the 10 quadrats monitored, as opposed to three at Hingston & McQuillan (1999)'s single site. Bumblebees represented only 10% of visitors, which included non-bees.

When all monitoring data are considered, bumblebees comprised 7% of observed visitors. At the Snug Falls track, the pollinator complex was different each time, with bumblebees not present till January 2002, when flowers were more prolific, when they represented 14% of potential pollinators. Flower abundance was not quantified in the report.

Independent analysis of this study (McClay 2005b) points out incomplete and inconsistent presentation of the data, making analysis difficult. Population counts of bees in themselves do not provide evidence that resources are being depleted. The issue of competition is not addressed directly, as bumblebees were rare and no *Chalicedoma* were present, so results cannot be compared directly to those of Hingston & McQuillan (1999). However, McClay concluded that:

‘Overall, the study indicates that flower-visiting communities on *G. huegelii* are diverse and vary over space and time. *B. terrestris* appears to be a minor component of this community at most times but increases its utilization of the plant when it flowers more abundantly.’

Hingston (2005a) compared visitation rates of *B. terrestris* to native and introduced flowering plants in his Hobart garden over a period of 133 days from November 2003 to March 2004. He reported that there was no preference for introduced over native plant species. Independent analysis of the statistical basis for this study (McClay 2005b) finds that it too is pseudo replicated, in that successive measurements from the same site on different dates are treated as replicates. The study is thus observational rather than experimental.

While the inadequacies of statistical approach are a concern, of more concern is that Hingston shows a complete disregard for the wealth of published information on the intricacies of foraging behaviour in bumblebees (*see* Prŷs-Jones & Corbet (1991) and Goulson (2003a) for a partial review of this well-researched subject). First, the floral composition of this garden must bias the result. The 12 ‘native’ plants include several species grown for their floriferous nature, whereas the 14 ‘introduced’ plants include not a single species associated with European flower gardens, but several vegetable plants such as kale, parsley, tomato, and Swiss chard, rhubarb, and four weeds, not known to be particularly attractive to *B. terrestris*; not surprising really that no preference for introduced plants emerged. The contention is not that bumblebees do not visit ‘native’ plants, or exercise choice, as Hingston must realise. Preference depends at least in part on the range of choices presented, and the naivety of the bees (Heinrich 1979b). High rewards of pollen and nectar naturally lead to preferential visits and a degree of flower constancy (Plowright & Lavery 1984; Goulson 1994, 2003a; Gegear & Thomson 2004; Gegear & Lavery 2005). The degree of relationship or similarity between plant species within the native or introduced group, and the flowering periods and organization of plants within the garden are not stated and presumably not considered, but all will influence the result.

Heinrich (1976a) observed that where plants were closely intermingled the effect of site specificity on flower fidelity will be at a minimum. Also, when bee populations are low, there may be less need for bees to discriminate between different flower types, as most of them could be providing suitable profits. Teräs (1985) showed that the daily distribution of bumblebees differs when continuous observations are made compared with the results of glance surveys made at 10 minute intervals. Hingston’s paper also ignores the fact that the foraging range of bumblebees is much broader than one small garden (Darvill *et al.* 2004; Knight *et al.* 2005; Martin *et al.* 2006; Greenleaf *et al.* 2007), so members of the one or several colonies involved may be doing most of their

None of the studies so far conducted in Tasmania has shown that *B. terrestris* is having or has had an impact on native bees or honeybees, or on native plants

foraging elsewhere and merely ‘sampling’ in this garden.

Familiarity with the intricacies of foraging behaviour in bumblebees would suggest that selection of the garden as the experimental site was inappropriate. The conclusions reached are too simplistic. Information on foraging behaviour, flower preferences etc. and assessment methods can be found in Heinrich (1976a, b, 1979a, b), Oster & Heinrich (1976), Eickwort & Ginsberg (1980), Goulson (1994), Dramstad & Fry (1995), Paton (1996), Stout *et al.* (1998b), Walther-Hellwig & Frankl (2000), Cane & Topedo (2001), Roubik (2001), Thomson (2001), Williams *et al.* (2001), Dramstad *et al.* (2003), Goulson (2003), Gegear & Thomson (2004), Goulson & Darvill (2004), Paini (2004), Gegear & Lavery (2005), Benton (2006), Morales & Aizen (2006), Potts *et al.* (2006), Raine *et al.* (2006b), Raine & Chittka (2007), <http://www.ecologyandsociety.org/vol5/iss1/> and many other papers. Even bumblebee species differ in the types of flowers they prefer (Goulson & Darvill 2004). We do not maintain that *B. terrestris* cannot or will not exist in native vegetation, just that they are much less likely to be attracted and sustained there, due to seasonality of flowering times, infrequent occurrence of flowering periods in some natives, and inadequate rewards of many native flowers. ‘Distribution’ is not equivalent to ‘abundance’ (Brown 1984). The experiences of Donovan and Macfarlane (1984) in New Zealand, Hergstrom *et al.* (2002, 2005) in Tasmania, Morales & Aizen (2006) in Argentina, and Inoue *et al.* (2007) in Japan, all arrive at the same conclusion: *B. terrestris* exhibits a strong preference for plant types associated with its natural range.

Conclusion

Despite claims to that effect by Hingston *et al.*, none of the several studies conducted in Tasmania to date shows that *B. terrestris* is having or has had any impact on native bees (or honeybees). Competition for resources *may* have occurred, but there is no indication that such resources were limited or that bumblebee abundance was sufficient to effect such limitation. Nor has it been shown that *B. terrestris* influenced native bee foraging behaviour or flower visiting fidelity, or that their reproductive output was adversely impacted. All researchers except Hingston *et al.* found that *B. terrestris* preferred to forage on introduced European plants. Although it was reported foraging on a broad range of native plants, it strongly favoured only a handful, which were those offering large rewards compatible with its high energy requirements. Most *B. terrestris* were located in areas where introduced plants were prevalent, and they were rare in areas of purely native bush.

5.3.2.2. Native plants

One possible impact that may result from *B. terrestris* visiting native plants is reduced or increased seed set through changes in pollinator association. The interest in studying the extent of use of native plants by bumblebees is linked to this. However, without carefully designed exclusion studies, no impact is likely to be proved, because pollination and seed set are complicated mechanisms, and pollinator assemblages are the norm rather than the exception. It should also be noted that the composition of visitor guilds may vary greatly between populations and years; population size may have an effect, but variation in flower visitor guilds is normal (Kwak *et al.* 2005).

Apart from a brief examination of seed set in *Gompholobium* by Hergstrom *et al.* (2002), no research has been carried out on seed set in native plants in Tasmania. Hergstrom *et al.* (2002) collected 200 pods from *Gompholobium* at the study site in Huon Road (1.12 bumblebee visits per hour), and 20 from Snug Falls (2.12 visits per hour). Seed number was slightly higher at the Snug Falls site (8.9 v 8.2 seeds/pod), but no statistical analysis is presented to assess the significance.

Nectar robbing has also been mentioned by Hingston & McQuillan (1998b) as having deleterious effects, but this is not necessarily so, and has been and is still a matter of debate (Brandenburgh 1961; Kendall & Smith 1975; Newton & Hill 1983; Stoddard & Bond 1987; Morris 1996; Maloof & Inouye 2000; Navarro 2000; Stout *et al.* 2000; Irwin *et al.* 2001; Maloof 2001; Irwin & Maloof 2002; Irwin 2003). It is a very common phenomenon among flowering plants; most species with tubular flowers or those with nectar spurs experience some form of nectar larceny (Irwin 2003). Variation on the level of nectar robbing can also occur in the same year and at different sites. The interactions and interrelationships can be very complex and not resolved easily (Irwin & Maloof 2002). *Bombus terrestris* has been known to nectar rob to reach nectar in flowers with corollas too long to permit legitimate access. This does not necessarily prevent pollination by the normal channel. Nor is this practice the sole preserve of bumblebees. Native bees such as *Xylocopa*, *Amegilla* and *Trigona* also nectar-rob. Both honeybees and native blue-banded bees have been seen accessing holes in bog sage, *Salvia uliginosa*, in a bumblebee-free environment, with the primary nectar robber unknown, but possibly ants (Steiner, pers. comm. 2005). Nectar robbing activities by *B. terrestris* in Tasmania were studied by Hingston & McQuillan (1998b) and Hergstrom *et al.* (2002) (*see following discussion*).

Hingston & McQuillan (1998b) observed bumblebees foraging on native common heath, *Epacris impressa*, at two sites, Coffee Creek and Hobart, on 13 days between January and April 1997. They examined plants for holes bitten at the base of the corolla. Eighty nine percent of flowers were accessed legitimately at Coffee Creek, but only 15% at Hobart. They concluded that the differences at the Hobart site were due to slightly longer corolla length and smaller bumblebees, encouraging nectar larceny because tongue length was too short to reach the nectar legitimately. While taking no records of seed set, they further predicted that nectar robbing will negatively affect reproductive success of *E. impressa*, and even plant community structure.

As *E. impressa* races in Victoria tend to have a longer corolla, the authors extrapolated this to predict nectar robbing by bumblebees of all *Epacris* in Victoria ‘providing that their flight periods and flowering phenologies overlap’.

This is yet another example of an evocative statement devoid of supporting evidence. The likely flight period of *B. terrestris* and flowering phenologies of the longer corolla pink races of *Epacris* in Victoria in fact do not overlap. Stace & Fripp (1977a, b) reported that pink and red-flowered races of *E. impressa* in Victoria flower in winter, when insect pollinators are not common (and when bumblebees would be in hibernation). They are likely bird pollinated. In western Victoria, pink races are rare, and white races flower in both spring (only bumblebee queens would be present) and winter (no bumblebees present). In eastern Victoria, the white-flowered races, the ones with the shorter corolla, flower in summer and are considered better adapted to insect pollination. Stace & Fripp (1977b) noted a variety of pollinators on this white race, including the two butterfly species *Vanessa kershawi* and *V. itea*. The eastern spine bill, *Acanthorhynchus tenuirostris*, has been observed taking nectar from the rare red-flowered race, and may be a legitimate pollinator. Hingston & McQuillan’s comments should not have been made without referencing published facts on *E. impressa* in Victoria.

Moreover, *E. impressa* is an outcrossing species (Fripp 1982), so nectar robbing, if it occurs, actually may have a beneficial effect through increasing the interplant flight distances of pollinators (Maloof & Inouye 2000; Irwin 2003).

Hergstrom *et al.* (2002) studied *B. terrestris* interaction with *E. impressa* in the southeast of Tasmania over 2.5 years. They set up 2 m x 2 m quadrats in each of 30

sites. Four stems of *E. impressa* per quadrat were examined every 4-8 weeks for pollinators (216 flowering periods, of which bumblebees were present at only eight). Seed capsules were collected and numbers of seeds counted. Capsules were also taken from another site at Mt Nelson, where nectar robbing by *B. terrestris* was common (ants were also robbers).

Both the number of capsules and seeds was significantly higher in the presence of bumblebees. It is also possible that a concentration of flowers attracting pollinators contributed to this result, but no data are presented to test this. The main pollinator of *E. impressa* in Tasmania is still uncertain as visitors (except ants) were rare. Ants collect nectar and may be worthy of study as possible nectar robbers or users, perhaps nocturnal (Schaffer *et al.* 1983).

Hingston & McQuillan (1998a) also claimed that bumblebees have the potential to impact on commercial honey production, by competing with commercial honeybees for the nectar of leatherwood, *Eucryphia lucida*. This conclusion was gleaned from observations of visits to this plant in a suburban garden and the Royal Tasmanian Botanic Gardens in Hobart (15 workers counted in total). This claim is repeated in an *Aussie Bee* article (*Aussie Bee*, 30 July 2003). There was no mention of bumblebees as a concern to leatherwood honey production in the recent submission from the Tasmanian Beekeepers Association to the 2007 Federal Enquiry into the Future Development of the Australian Honeybee Industry (submission #63, 2007). Loss of trees through felling and land clearing were the overriding concerns.

Eucryphia lucida is found primarily in high rainfall, cool temperate rainforests in the western and south-western part of the State, where *B. terrestris* has been recorded only in very low numbers. Ettershank & Ettershank (1992) found a very diverse insect fauna associated with leatherwood flowers and recorded no impact of honeybees on native insects. Honeybees and native bees removed approximately 90% of sugar over the course of the day (Mallick 2000). In another study, both honeybees and native insects were rarely seen before 12:00 hours on the warm days studied and not at all on the one cool day (Mallick 2001). The flowers received visits from a broad range of insect taxa. Most leatherwood nectar used for honey is produced in old-growth forests, because trees younger than 75 years old generally do not produce flowers. Flowering can be very variable (<http://sres.anu.edu.au/associated/fpt/nwfp/leatherwood/lw2.html>), with flowers produced for a restricted period of 4-6 weeks in summer. Flowers are long-lasting and produce nectar continuously throughout the day, and at a lesser rate at night. Commercial honeybee producers move their hives to take advantage of a nectar flow period, whereas bumblebees would be reliant on unpredictable supplies for many weeks. Considering all these factors, the likelihood of *B. terrestris* establishing in any numbers in west coast old growth forests, and then competing for leatherwood nectar with managed hives of honeybees, is extremely unlikely.

Conclusion

Claims were made by Hingston & McQuillan (1998a, b) that *B. terrestris* was negatively impacting on native plants through nectar robbing of common heath, *Epacris impressa*, and by reduced seed set in native pea, *Gompholobium* spp., and was affecting commercial honey production through removal of nectar from leatherwood, *Eucryphia lucida*. These claims do not stand up to rigorous scientific examination. Hergstrom *et al.* (2002) showed no decline in seed set of *Gompholobium* at higher densities of *B. terrestris* and an increase in seed set in *E. impressa*. There was a lack of any association between *B. terrestris* and commercial honey-producing areas of *E. lucida*, thus little likelihood of competition for leatherwood nectar with managed honeybee hives, as has

Claims that bumblebees will compete with managed honeybees for the nectar of leatherwood and Tasmanian blue gum are not supportable. Honeybees will always outcompete bumblebees

been claimed. A potential major negative impact on *E. impressa* in Victoria was claimed, but available information clearly shows that flowering periods would not overlap with foraging periods in the bumblebee life cycle.

5.3.2.3. Native birds

Many references have been made in the popular press, by Hingston in particular, of the harm that bumblebees are doing to endangered birds such as the swift parrot. The information underlying this contention is therefore examined in some detail. Research into potential impacts on birds in Tasmania has been restricted to a consideration of endangerment of threatened species such as the swift parrot and also the relative efficiency of pollinators of blue gum (*Eucalyptus globulus*) for seed production.

Hingston & McQuillan (1998a) reported monitoring of *B. terrestris* at five localities near Hobart between September 1996 and June 1997. With no supporting data, they inferred a serious impact of bumblebees on eastern spine bill, *Acanthorhynchus tenuirostris*, through feeding on *Epacris impressa* (376 total bumblebee visits recorded). They also recorded 51 visits to *E. globulus* at Mt Wellington, and on this basis, prematurely suggested additional competition for resources with nectarivorous birds on this plant. *Eucalyptus globulus* is found in coastal areas of eastern and south-eastern Tasmania, and also in small pockets on the west coast, on islands in the Bass Strait and in parts of Victoria, where it tends to form dense monocultures that have been seriously depleted over the years. It is also planted as a forestry tree.

Hingston & Potts (1998) found 7 bird and 71 insect species associated with *E. globulus* flowers in a 1997 survey. A total of 11 *B. terrestris* were recorded (0.4% of total anthophilous insects), against 1379 honeybees (49.6% of total). Because those insects that were recorded did not appear to contact the stigma, the authors concluded that birds, particularly parrots, are larger, thus more likely to contact the stigma and are therefore more reliable pollinators. The swift parrot, *Lathamus discolor*, is largely dependent on *E. globulus* pollen and nectar in its summer breeding range in south-eastern Tasmania. Despite the low bumblebee population, Hingston & McQuillan (1998a) and later Hingston & Mallick (2003) raised a red flag about foraging overlap with nectarivorous birds such as the eastern spinebill and swift parrot. Thrips were curiously excluded from the survey 'due to the impracticability of counting them'. Although little-studied as pollinators, some thrips species are attracted to flowers to feed on pollen and nectar, which makes them an ideal vehicle for pollen transfer (Terry 2001). The gum tree thrips, *Thrips australis*, for example, is a known inhabitant of *Eucalyptus* flowers in Australia, including Tasmania (L. Mound, pers. comm. to M. Steiner 2005), and should not be ignored in a consideration of pollinator efficiency.

Hingston (2002) found that flowers of *E. globulus* secreted nectar both day and night, and suggested that the plant had therefore evolved to exploit large, endothermic pollinators, such as parrots. *Eucalyptus* species generally vary in their nectar secretion period. Goldingay (2005) found that *Corymbia* (formerly *Eucalyptus*) *gummifera* secretes nectar both day and night with no clear diurnal pattern, but with considerable variation between trees and sample period, whereas other species in the Eucalypt family may secrete mostly at night. Many pollinators use Eucalypts, including birds, bats, possums and bees. *Eucryphia* also secretes nectar day and night (Mallick 2001), but is not bird pollinated. Hingston (2002) suggested that honeybees were numerous enough to displace nectarivorous birds on *E. globulus*, and may also reduce seed set and fitness. He did not present any evidence for this.

Hingston & Mallick (2003) again raised the spectre of native birds being negatively impacted upon by competition for nest sites and nectar. Yet competition for

nest sites is a non-issue because bumblebees, unlike honeybees, nest primarily underground in old rodent nests. In an address to *Birds Australia* on Member's Day (University of Tasmania, 2003), which was reproduced in various articles (e.g. *Feral Herald* vol. 1, July 2003, p.7), Hingston claimed that bumblebees, in concert with honeybees, are threatening the survival of the endangered swift parrot, *Lathamus discolor*, by feeding on nectar of *E. globulus*, a remarkable claim not supported by evidence of any impact.

Bumblebee nest density in favourable habitat in the UK is only <0.3/ha (Knight *et al.* 2005), and colony size and foraging range is much smaller than that of honeybees, just to name two of the many pollinators of *E. globulus*. Bumblebee foraging stops when nest supplies are adequate (Pelletier 2003), as they do not store food for more than their immediate needs. Thus the contribution of bumblebees to depletion of resources in *Eucalyptus* during periods of nectar flow is likely to be minimal.

Hergstrom *et al.* (2002), in re-evaluating this issue, monitored *E. globulus* flowers from September to December 2001 and again on 14 December 2002. Pollinator visitors were recorded over a 3-5 minute period, for a total of 24 monitoring periods at 18 locations. Of the total number of potential pollinators observed, bumblebees represented only 2% of visitors, honeybees 56% and birds 25%.

Hingston *et al.* (2004a) in 1998/1999 used cages with various mesh size to restrict access of different sized visitors to flowers. Only the lower parts of the tree were monitored (where they report that swift parrots rarely foraged). A broad range of potential pollinators visited, with honeybees again by far the most common visitor. Bumblebees were rare. Honeybees (and non-birds) were judged inefficient pollinators on the basis that their visits probably resulted in self-pollination rather than cross-pollination. 'Cross-pollination' in the experiment resulted in far greater seed set, but was obtained by hand dusting the birds with unknown amounts of pollen from other trees, which is not a comparable activity to insect pollination. Yet research by Patterson *et al.* (2004), not referenced by Hingston *et al.* (2004b), found that outcrossing rates in *E. globulus* were greater in the upper canopy and highly correlated with the degree of self-incompatibility of individual trees. They recommended screening seed orchards for trees with high self-incompatibility and restricting seed collection to these trees. There was no mention of parrots or other pollinators being limiting.

Not deterred by low incidence of bumblebees on *E. globulus*, and some doubt as to the usefulness of swift parrots in seed production nurseries, Hingston *et al.* (2004b) used *two* captive swift parrots daubed with pollen to support claims that the swift parrot was a much more effective pollinator during a single visit than a honeybee or bumblebee, a methodology scientifically unacceptable. That bees, particularly honeybees, are far more numerous, and may enable full seed production through multiple flower visits, does not appear to have been considered. Musk lorikeet, *Glossopsitta concinna*, was also deemed a potentially effective pollinator of *E. globulus* (Hingston *et al.* 2004c). Considering that they inhabit the entire tree and not just the upper canopy (Hingston *et al.* 2004a; Hingston & Potts 2005), the authors might find them more effective than swift parrots in seed production nurseries (but possibly not as practical as managed hives of honeybees).

The following information was posted in 2005 on *Ornithological News and Scuttlebutt* (Website of the Echuca and District Branch of Bird Observers Club of Australia). It is regrettably typical of some of the misinformation being presented to the public:

The greatest threat to the endangered Swift Parrot in Tasmania is habitat loss of larger Tasmanian blue gums (Swift Parrot Recovery Team)

‘Bumblebees may cause extinction of Swift Parrot. The introduction of Bumble Bees into Tasmania may result in the extinction of the Swift Parrot. Many Swift Parrots die by crashing into glass windows or meshed wire (e.g. around tennis courts). Habitat loss is another factor. But research in Tasmania by Hingston (&) Mallick has established that the main reason for their decline is honeybees consuming most of the nectar from the gums on which the Swift Parrot depends. Because bees are not active in early morning or when temperatures fall below 15°C, Swift Parrots have had a small window of time in which to feed on nectar built up overnight. But the recently introduced Bumble Bees start feeding much earlier at lower temperatures, denying the parrots the nectar which they require. If Bumble Bees find their way into Victoria’s box-ironbark forests, researchers believe it likely that the Swift Parrot will become extinct.’

In contrast, *The Swift Parrot Recovery Plan 2001-2005*, put out by the Swift Parrot Recovery Team (2001) (<http://www.deh.gov.au/biodiversity/threatened/publications/recovery/swift-parrot/>) and The Federal Department of the Environment and Water Resources website (http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=744, accessed 9 October 2007), do not mention bumblebees or honeybees as a threat to swift parrots. It is widely acknowledged that although the flowering of Tasmanian blue gum is a major factor affecting the reproductive success of the swift parrot, the loss of old trees through habitat destruction and fragmentation is the major cause of their decline (MacNally & Horrocks 2000; Swift Parrot Recovery Team 2001).

Swift parrots only breed in Tasmania. While *E. globulus* is the main source of nectar and pollen, the intensity of flowering varies greatly from year to year. In years when flowering is poor, and also in the small northern breeding population located between Launceston and Smithton, which is outside the natural range of *E. globulus*, swamp gum, *E. ovata*, may be used when *E. globulus* is not available. As swift parrots only spend the winter on the mainland in Victoria or NSW, even should *B. terrestris* establish there, the bees would be hibernating over the winter period and it is highly unlikely that any interaction between swift parrots and *B. terrestris* would occur there.

Conclusion

Several studies conducted in Tasmania examining the interaction of swift parrots, *B. terrestris* and Tasmanian blue gum, *E. globulus*, show that bumblebees are not frequent visitors to *E. globulus* and thus are highly unlikely to compete with swift parrots or any other pollinators, or have any impact on seed production of *E. globulus*. Both insects and several other birds are common visitors to *E. globulus*. It is disingenuous to claim, as Hingston has done, that bumblebees will result in the extinction of the swift parrot. The Swift Parrot Recovery Team considers that the greatest threat to swift parrots is habitat loss through felling of medium and large *E. globulus*.

5.3.3. Effect of bumblebees on weeds

A major consensus of the 1999 National Bumblebee Workshop, given the size and limited budget of the HRDC study, was that research on weeds would be the most fruitful area to pursue, with research assistance from other agencies (<http://www.tmag.tas.gov.au/workshop/proceedings.html>). The potential spread of exotic weed species through improved seed set, particularly of sleeper weeds, was the major concern. The environmental impact study (Hergstrom *et al.* 2002) attempted to address this with advice from a weeds advisory group that was set up. It was suggested that at least three weed species should be studied. After extensive monitoring in urban, rural and bush areas, weed species that were the most frequently visited and thus at most risk of greatly increased seed set were selected. These were Scotch thistle, *Onopordum acanthium*, greater trefoil, *Lotus uliginosus*, and tree lupin, *Lupinus arboreus*. Tree lupin is a

Californian native reportedly a serious weed in New Zealand (Stout *et al.* 2002; Goulson 2003b; Hanley & Goulson 2003) (outdated information) though not in Tasmania. It was speculated by the authors that bumblebees may be the missing pollinator in Tasmania. Other relevant studies conducted in Tasmania on weeds were those by Stout (2000), Stout *et al.* (2002), Hanley & Goulson (2003), and Hingston (2006b).

Hergstrom *et al.* (2002) collected seed pods from many sites across the State over 2-3 years, with >30 sites per weed species. For tree lupin, there was both an increase in healthy pods and in healthy seeds per pod at sites where bumblebees were present, giving a potential 29.7% increase in seed set. For Scotch thistle, there was an overall reduction in seed set of 13.2% over two years where bumblebees were present. For greater trefoil, there was a significant increase in number of healthy pods per stalk, and in seeds per pod, in one year only, to give an overall 40.2% increase in healthy seeds per pod. The actual number of bumblebees and the diversity and abundance of other pollinators is not recorded, nor the percentage of sites where bumblebees were present, nor the degree of aggregation of the particular weed species, nor diversity of plant species available. On the basis of this study, the evidence for a causative relationship is largely circumstantial.

Stout *et al.* (2002) studied pollination of tree lupin by honeybees and *B. terrestris* at 20 sites where the latter was present, to examine whether bumblebees might enable tree lupin to become a more serious environmental weed in Tasmania. Both bee species access tree lupin for pollen only. One hundred and twenty patches of tree lupin were monitored for 10 minutes each during November and December 1999. A total of 140 *B. terrestris* and 132 honeybees were observed. The authors reported a positive relationship between the proportion of flowers setting seed and seed set and visitation rates by bumblebees and combined bees. They concluded that *B. terrestris* was an effective pollinator, but so also were honeybees where bumblebees were less dominant. Bumblebees dominated at 11 sites and honeybees at eight, with an inverse relationship between them which suggested to the authors that bumblebees may be competitively displacing honeybees. Other workers on other plant species have found the opposite (Holmes 1961; Thomson 2004, 2006; Forup & Memmott 2005; Walther-Hellwig *et al.* 2006, Goulson & Sparrow 2008). Observations were made between 0945h and 1600h; bumblebees often start foraging earlier than this and this may have impacted on later honeybee visits. The authors concluded that it is possible that *B. terrestris* would have little additional impact on seed set because of the pollinator services already provided by honeybees, but that:

‘Generalisations about the effects of exotic bees on Tasmanian ecosystems should not be made from a limited number of studies, however, and further research is needed.’

Stout *et al.* (2002) quote Williams & Timmins (1990) as stating that tree lupin is one of the 33 worst environmental weeds in New Zealand. Hanley & Goulson (2003) and Goulson (2003a, b) all quote Stout *et al.* (2002) for this information, so it is second-hand. However, tree lupin’s status now appears to have been downgraded to a minor weed in New Zealand, possibly because it is attacked by a fungal pathogen which has seriously affected stands, including those used for sand-dune stabilisation (Douglas *et al.* 2004).

Hanley & Goulson (2003) discussed the urgent need for more research to examine the role of pollinators on fecundity and population dynamics of introduced plants, noting that no serious attempt had been made to quantify this role as yet, and that surprisingly little was known of the pollination biology of weed species in new environments, nor of the interaction between introduced weeds and introduced

Bumblebees are unlikely to contribute to spread of exotic weeds on mainland Australia for a variety of reasons, but primarily because most weeds are not pollinator-limited, or do not depend on the services of a pollinator

pollinators.

Hingston (2006b) conducted a study on *Agapanthus praecox* and concluded that bumblebees were probably the major pollinator of *Agapanthus* in suburban Hobart. The experimental methodology was poorly constructed and the conclusions not scientifically provable. For example, the number of days sampled and number of sites were not defined, the relationship between honeybee numbers, bumblebee workers and queens might be expected to be variable over the 7 January to 5 March time-period, the temperature during the observation period and the seed set were not determined, and it was not possible to compare the relative number of visits accurately. The statement in the methodology that 'Visitors to flowers of *Agapanthus* were observed opportunistically in suburban Hobart between 7 January and 5 March 2006 at various times of the day', and summary data showing 262 bumblebees and 63 honeybees were observed during this time, has no scientific rigour. *Agapanthus* was establishing feral populations prior to the arrival of bumblebees. Claims have since been made implicating bumblebees in their increased weediness, but this study demonstrates neither increased weediness nor that bumblebees were responsible.

Hingston is reportedly also conducting studies on *Rhododendron ponticum*, white-edged nightshade *Solanum marginatum* and butterfly bush, *Buddleia davidii*. These are discussed in Section 7.1.

Conclusion

Limited studies have been conducted in Tasmania on whether bumblebees have the potential to spread weeds such as Scotch thistle, greater trefoil, tree lupin, and *Agapanthus*. The results are inconclusive and for the latter poorly constructed. Examination of the potential for spread of several weeds suggested by the Weeds CRC and others as being at greatest risk from the services of a specialist pollinator strongly suggests that bumblebees will have no additional impact. Improved pollination and seed set over and above that of honeybees and other native anthophiles has yet to be demonstrated.

Summary of Section 5

Distribution records show that *B. terrestris* is located across much of Tasmania, but is rare in areas of native bush, with nests, where present, smaller and less persistent than in urban and semi-urban areas.

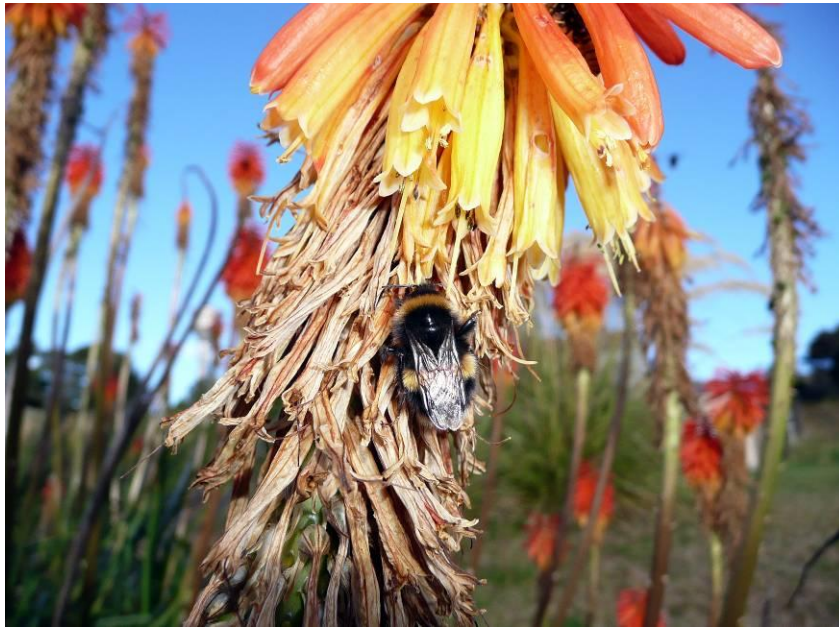
Despite claims by Hingston (2005a) that *B. terrestris* shows no preference between native plants and introduced plants, five other research studies in Tasmania (and others in New Zealand) have shown a distinct preference for the introduced plants with which this species co-evolved in its native environment. This does not preclude visits to Australian native plants nor suggest that all native plants are unattractive. Indeed, those few native plants offering high rewards in terms of nectar and secondarily pollen will be sourced more frequently. In areas of native bush, low bumblebee numbers, lack of continuity in food supplies, and different foraging preferences should favour native pollinators.

Limited studies have been conducted on the impact of *B. terrestris* on native bees and native plants. The studies were not definitive because of design flaws, particularly in methodology, and a lack of understanding of bumblebee foraging behaviour and the complexities of this type of study. Pollinator assemblages were broad in the few plants that were studied, and contradictory results were often obtained by Hingston & McQuillan (1998b, 1999), Hingston *et al.* (2002, 2004b), and Hergstrom *et al.* (2002,

2005).

Despite attempts by Hingston to link the demise of threatened bird species such as the swift parrot to bumblebees, there is no evidence for this association. His own studies and those of Hergstrom *et al.* (2002) show limited visitation to *E. globulus*, a preferred and important nectar resource in swift parrot breeding areas in Tasmania.

Studies on weeds have been limited in scope and do not demonstrate any persistent increase in propagule pressure sufficient to cause concern over weediness potential.



Bombus terrestris audax queen on *Kniphoffia* in New Zealand. European wasps were also present, possibly responsible for the larger holes in the florets made to access pollen in stamens. Photo courtesy M. Steiner.

6. ASSESS THE LIKELIHOOD OF THE SPECIES BECOMING ESTABLISHED IN THE AUSTRALIAN MAINLAND ENVIRONMENT

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Introduction The questions regarding likelihood of establishment of *B. terrestris* on the Australian mainland are all interrelated. Distribution range affects the area of potential impact; floral resources, ground habitat and climate affect distribution; climatic extremes, local predators and pathogens and temporal floral resources will affect nest success and size; local native pollinators, honeybees and bumblebees will vary in competitive abilities and their interactions will vary depending on availability of floral resources, population density and floral preferences.

Tasmania has a temperate, maritime climate similar to New Zealand, and shares many European weeds, forage plants and garden plants in settled areas, so the wide distribution of *B. terrestris* across Tasmania is not unexpected. Mainland Australia has quite a different climate, except in south-eastern coastal areas, so the extent of distribution will always be much more limited and thus the *potential* impacts similarly limited.

Choice of *B. terrestris* subspecies may also have an impact on ability to establish. The finding of *B. terrestris* on wharves in Victoria and Queensland in 2003, one near a recently berthed New Zealand ship, can hardly be isolated incidents during 130 years of *B. terrestris* presence in New Zealand. The fact that no establishment has thus far occurred in Australia, despite the more favourable climate on the coast and several attempts at introduction in the past, might be taken as some indication of the difficulties of successful establishment on the mainland.

6.1. Life history of *B. terrestris* relative to establishment potential

A brief discussion of the life history of *B. terrestris* is appropriate to an understanding of if, and when, bumblebees might survive or impact on native flora and fauna, and the relevance of observational studies so far conducted. A more detailed discussion is contained in Appendix III (for a good description and diagrammatic illustration of the life cycle see also <http://www.bio-bee.com/site/> and <http://www.bumblebee.org/>).

A bumblebee colony may comprise eggs, larvae, pupae, queens, workers (non-reproductive females), and males, but they are not all present at the same time until later in the summer. Unlike the situation with honeybees and European wasps, a bumblebee colony survives for only a few months (Sladen 1912; Alford 1975; Goulson 2003a; Benton 2006) and contains active foragers for only about 3 months. In temperate climates, activity begins with overwintering queens in early spring, who found that year's colonies. Queens are gradually replaced by increasing numbers of workers, and

Bumblebees have annual spring- and summer-active colonies which die out after new queen production. These queens hibernate underground until the following spring

finally males and new queens appear in mid-late summer. In temperate climates, the population is negligible during the late autumn and winter months. Even in early spring, the young queens surviving the winter will be too few to offer any serious competition for food resources with other anthophiles.

Each queen emerging from hibernation independently finds a nest site, usually in an abandoned rodent burrow already containing suitable nesting material. She provisions it with the nectar and pollen she has collected, and starts laying eggs. The eggs hatch and progress through larval and pupal stages to become worker bees some three weeks later. There are three separate broods, each producing greater numbers of workers (Duchateau & Velthuis 1992). Once there are enough workers to take over foraging and nest duties, the queen stays within the nest laying eggs. After about two months, in the last brood, if colony size is large enough and food is plentiful, the first males and then new queens develop instead of workers.

Diapause triggers maturation of the queen's ovaries, without which egg laying cannot occur

A new queen produced in a mid-late summer colony stays in the maternal nest for a few days building up her fat body and honey stomach. She may use colony resources or forage for herself, returning to the nest after each foraging bout (Alford 1975). She needs enough reserves to be able to diapause for an extended period of several months (Beekman *et al.* 1998), as she does not feed during this state. When she is on average six days old, if she has enough food stored, she leaves the nest in search of a mate and does not return. After mating, usually with a single male who leaves a plug to prevent further matings (Schmid-Hempel & Schmid-Hempel 2000), she seeks a suitable site for overwintering and digs into the ground some distance, usually under leaf litter at the base of trees (Alford 1975). Once the new queens have left, the remaining colony dies out. Initially the new queen in her burrow is easily disturbed, but eventually she enters a torpid diapause state, from which she is not easily aroused until this process is completed (Sladen 1912). She then stays in her hibernation site in a quiescent state induced by low temperature (Hodek 2002), until increasing temperature in the spring encourages her to come out to forage, in order to build up her food reserves again.

It is important to recognise that in nature ovaries do not develop unless and until diapause has been completed, and egg laying does not commence until maturation of the ovaries is complete, a process taking some weeks.

What is the possibility of establishment if there is an escape from a commercial hive? We believe from studying the biology of this species that it is minimal.

A commercial hive on delivery contains a queen, who cannot and does not wish to escape, and ~50 workers, who can come and go while the exit and entrance holes are in the open position. Some workers forage and others remain to look after the nest. After a few weeks, if it is not replaced, the hive will switch from worker production to that of first males and then queens, although the numbers of each can be very variable with often no sexual forms produced. New queens, except for unusually small ones, will be prevented from leaving the hive by the hole size of the queen excluder.

In order to mate, queens, even if they escape the hive, must be ~6 days old and males ~12 days old (Tasei *et al.* 1998; Baer & Schmid-Hempel 2000). There is no nectar in the tomato house, so if she escapes she is likely to return to the nest constantly to access the sugar supply. Males feed within the hive for 2-4 days but do not return once they have left the hive (Alford 1975). Usually they feed on flowers, and set up patrol routes where females can find them to mate. In the greenhouse, they would have no nectar available to them, and no pollen as they do not buzz pollinate, so it is doubtful they would survive long enough to mate. Thus both queen and male must circumvent the netting and exit the greenhouse as well as the hive in order for mating to occur. If the queen does find a mate, it will likely be with one of her own brothers, thus there may be

The possibility of a queen escaping from a managed hive system in a greenhouse and successfully founding a colony in the wild is very small

inbreeding depression with reduction in hibernation survival and colony foundation success (Gerloff & Schmid-Hempel 2005). Some diploid males may be produced in any succeeding generation, these with low life expectancy (Buttermore *et al.* 1998).

Depending on the time of year and location, the climate and resources may or may not be suitable for surviving a long period of diapause, particularly because to escape through the queen excluder, she must be undersized and thus less likely to survive diapause (Beekman *et al.* 1998). Predators may also kill her. Most queens in any case fail to survive to the next season (Goulson 2003a). If she does survive diapause, and about 80% of queens do not (Benton 2006), she will again need to find suitable pollen and nectar supplies to replenish her fat body, find a suitable underground nest site in unknown territory, and establish a nest which must be very successful to be able to produce queens for the next generation. Thus the odds are strongly against establishment of a feral colony originating from managed hives in a greenhouse.

Schmid-Hempel *et al.* (2007) concluded that the founder population in Tasmania may have consisted of as few as one or two queens, but that they would have been from a 'good' family line. She/they would also have been pre-mated and may have concluded diapause at time of arrival. The survival and dissemination of *B. terrestris* in Tasmania from such a small founder population was an unusual and extremely fortuitous circumstance.

In Mediterranean areas and in the south of its natural range, some subspecies have a summer diapause (aestivation) instead of, or as well as, a winter diapause. This has led to suggestions that *B. terrestris s. l.* will adapt to the hotter Australian climate by aestivating or avoiding diapause altogether. Because an understanding of this process is critical to determining likely establishment and distribution of the species in mainland Australia, an extensive review of diapause issues follows.

6.2. The issue of diapause as it relates to area of establishment

In this section, several questions critical to this issue are addressed:

- i) *Is diapause facultative or obligate in B. terrestris?*
- ii) *What evidence is there for non-diapause in B. terrestris in nature?*
- iii) *If diapause is facultative, is there potential for continuous reproduction of B. terrestris in warmer climates?*
- iv) *Is there a cost or a benefit of non-diapause to the fitness of future generations?*
- v) *What is the significance of sex ratio on population density and survival?*

Diapause is defined as an extended resting period, or torpor, where an organism remains relatively inactive and metabolic activities are largely reduced, in order to survive periods when conditions are too harsh to survive normally. It is a physiological state, usually relating to unfavourable periods in climate or resources. In insects, it is generally genetically controlled, but the environmental conditions that the insect experiences often determine if and when diapause occurs and the extent of the diapause (Leather *et al.* 1993). The terms hibernation and diapause are often used interchangeably, but are not strictly comparable. Diapause is roughly equivalent to hibernation when it occurs through winter, and to aestivation when it occurs in summer. The triggers for beginning and ending the two processes may be different. For bumblebees, there are still gaps in our knowledge, particularly for aestivation (pers. comm. M. Duchateau to M. Steiner, 2007).

Diapause (a long resting period) is innate in bumblebees and permits survival during unsuitable climatic or low resource periods. It is automatic for new queens after taking on food stores

New queen bumblebees in temperate climates enter into diapause in the summer months, with *no known climatic triggers*, and continue it through the winter, responding to warmer temperatures in early spring by emerging and renewing their activity. Hibernation, strictly speaking, is only the winter part of the process. Hodek (2002), in a general discussion paper on aspects of diapause development, stated that diapause could be divided into two phases, a slow first period (horotelic process) and a faster second period (tachytelic process). The second tachytelic process is subject to outside influences such as temperature and photoperiod. It is generally recognised that in temperate climates, the first horotelic process is usually already completed in early/mid winter, and that the observed dormancy or hibernation is then simply temperature quiescence (a tachytelic process). So, for a queen bumblebee, if diapause is concluded early, she may remain in her burrow in a quiescent state until warmer temperatures enable flight and foraging activity. The onset and duration of diapause is independent of temperature (Beekman *et al.* 1998) and programmed genetically, with a certain minimum period of several months required that appears to vary with subspecies and between individuals. Duration of diapause under controlled conditions is consistently correlated with many variables of colony development, colony productivity, and sex ratio (Beekman & van Stratum 2000; Duchateau *et al.* 2004).

Hodek (2002) stated that cool temperatures, even when not necessary for completion of diapause, may lead to synchronous resumption of post-diapause morphogenesis, and help to maintain the viability of post-diapause insects. Thus diapause, while entailing a cost in terms of the percentage of queens surviving the process, can also be seen to offer benefits to long term survival of the species. For the purpose of this review, we use the term *hibernation* loosely to refer to the period of diapause which is completed in late winter/early spring, and *aestivation* to refer to summer diapause.

The range of latitude of establishment of the UK subspecies *B. t. audax* is approximately 42-57°N in the UK, 41-43°S in Tasmania, and 35-46°S in New Zealand. For all subspecies, *B. terrestris sensu lato*, the latitudinal range is approximately 30-60°N, from southern Scandinavia to the northern coast of Africa (*Figure 1*, Appendix I). In the southern part of the natural range of *B. terrestris s. l.*, summers are hot and dry with few available resources, whereas winters are cool and wet, with adequate resources, but limited to only a few species in terms of flowering plants, notably *Arbutus* spp. (Rasmont *et al.* 2005; P. Rasmont, pers. comm. to M. Steiner, January 2008).

Hibernation is a general rule for the northern populations of *B. terrestris* and bumblebee species in general, but *B. terrestris* is unique among European bumblebee species in that some of its Mediterranean populations and subspecies aestivate to avoid the hot dry period with little or no flowering vegetation (Estoup *et al.* 1996). These aestivating populations become active in the winter (Maciel Correia 1991; Estoup *et al.* 1996; Velthuis & van Doorn 2004a; Gösterit & Gürel 2005). The coming of the rains in late autumn, which results in flowering of Mediterranean plant species, is also the trigger for the end of aestivation (de Jonghe 1986; P. Rasmont, pers. comm. to M. Steiner, January 2008). Emergence from aestivation can be triggered by watering a substrate in which queens are buried. Apart from the observed effect of rain in precipitating emergence, the triggers for onset or termination of the aestivation process have not been well studied. Both aestivation and winter diapause appear to be able to switch on juvenile hormone synthesis, initiating ovariole development. Only then can eggs be laid. Both aestivation and hibernation are considered true diapause (P. Rasmont, pers. comm. to M. Steiner, January 2008).

Hodek (2002) states that in contrast to aestivation, there is usually no cue or

stimulus terminating winter diapause (we presume this applies to the horotelic phase). While there may be physiological differences between the two diapause processes, the cues for the end of the quiescent stage may themselves be different, with rising temperature completing hibernation and rain completing aestivation. There is some observational evidence for a short hibernation in addition to aestivation for *B. t. lusitanicus* in Portugal (Correia 1991), and in four other subspecies indigenous to Mediterranean countries (P. Rasmont, pers. comm. to M. Steiner, January 2008, summarised in *Table 1*), although overlap of two populations which respond differently does not appear to have been ruled out experimentally. There is also some doubt about diapause capability in *B. t. canariensis*, a very distinct subspecies (P. Rasmont, pers. comm. January 2008).

Diapause is thus considered innate in *B. terrestris* and also other temperate-climate *Bombus* species, and is likely genetically linked. Ovaries usually do not develop naturally unless a period of diapause is experienced, thus there is also a physiological requirement, in most cases, for diapause.

The large area occupied by *B. t. dalmatinus* encompasses a wide range of climatic conditions, which appears to be reflected in the diapause plasticity of its populations, even over a narrow geographic area. It may also, of course, reflect as yet unidentified geographic gene pools within this vast landscape. For example, one of four ecotypes from Turkey had a significantly later switch point to laying of haploid eggs and colonies produced more queens; the incidence of *Nosema bombi* was also lower (Yeninar *et al.* 2000). *Bombus terrestris dalmatinus* is a preferred species in commercial rearing not just because of favourable colony characteristics, but because of diapause flexibility within the subspecies which allows manipulation of colony production.

Table 1. Diapause experience of some of the *B. terrestris* subspecies. Information supplied by P. Rasmont, January 2008.

<i>Bombus terrestris</i> subspecies	Area occupied	Generations/ year	Aestivation	Hibernation
<i>audax</i>	UK	1	N	Y
<i>terrestris</i>	Continental Europe, N of latitude 45°N	1	N	Y
<i>dalmatinus</i>	SE, SW France	2 (?3)	Y	Y (short)
	Anatolian west coast	1	Y (long)	N
	Turkey, Anatolian Plateau	1	N	Y
	Urals and Altai	1	N	Y
<i>xanthopus</i>	Corsica	2	Y	Y
<i>sassaricus</i>	Sardinia	2	Y	Y
<i>africanus</i>	Tunisia	1	Y	N
<i>lusitanicus</i>	Portugal ¹	2	Y	Y

¹ Information from Maciel Correia (1991)

All the Mediterranean subspecies can switch into aestivation if exposed to hot, dry conditions, and into hibernation (but short, as little as 3 weeks) if exposed to cold (P. Rasmont, pers. comm. January 2008). A three-week hibernation period for the northern subspecies is insufficient for survival. For both the northern European subspecies, *B. t. audax* and *B. t. terrestris*, a long period of diapause, 3-6 months optimum, is the norm,

and aestivation is unknown (Estoup *et al.* 1996; D. Griffiths, A. van Doorn, P. Rasmont, pers. comm. to M. Steiner, 2007/2008).

i) *Is diapause facultative or obligate?* Historical literature states that *B. terrestris* has one generation a year in temperate regions, with a long period of several months hibernation (e.g. Sladen 1912; Cumber 1949; Free & Butler 1959; Alford 1969, 1975; Prÿs-Jones & Corbet 1991; Beekman *et al.* 1998; Goulson 2003a; Benton 2006). The hibernation period of the UK subspecies *B. t. audax* is generally shorter in New Zealand than in the UK (Cumber 1954; Alford 1969; Donovan & Wier 1978) (3-6 months in New Zealand instead of 6-9 months). This is readily explained by the warmer climate, which brings queens out of hibernation sites earlier, and to the season-long availability of nectar and pollen resources and adequate rainfall.

Until recently, it was always assumed that diapause in bumblebees was obligate, although, as previously noted, aestivation occurred in southern subspecies of *B. terrestris* (Maciel Correia 1991; Velthuis & van Doorn 2004a; Gösterit & Gürel 2005; Rasmont *et al.* 2005). Maciel Correia (1991) in Portugal, working with an unnamed local subspecies, possibly *B. t. lusitanicus*, reported that there was a large flight of queens (generation A) in winter from the end of January till late April (winter average 19°C), and a second flight (generation B) in summer from the end of June to mid July. Generation B queens had a summer quiescent period spent hidden in mild and slightly damp places, under minimal cover, and they re-emerged in mid September to found colonies. New queens (generation A) from these emerged at the end of November and early December, hibernated deep in the ground, and after a short diapause period, emerged from the end of January. Thus there appear to be two generations a year in this region, one with a long aestivation and one with a short hibernation. Similarly, Rasmont *et al.* (2005) reported *B. terrestris* (?*ssp. terrestris*) was polyvoltine in southeastern France with a short winter diapause in January/February. De Jonghe (1986) conducted limited crossing experiments with *B. t. terrestris* from Switzerland and Belgium and *B. t. xanthopus* from Corsica. There was no limitation to fertility of F1-crosses, although the true extent of hybrid inviability must be tested in crosses of the F2 and F3 individuals. F1-individuals from both *B. t. xanthopus* and *xanthopus-terrestris* crosses were observed to have a shorter mean diapause (121 days (range 43-159 days) for *B. t. xanthopus* and 132 days (range 20-228 days) for *B. t. xanthopus-terrestris* crosses) than northern European subspecies (210-260 days). De Jonghe stated that 'The tendency to a short diapause seems to be genetically fixed'. Diapause duration of *B. t. xanthopus* and *xanthopus* crosses was also characteristically very variable, with individuals that started diapause on 1 August emerging from mid-October to mid-March (presumably in Belgium). Emergence of the F1-generation from hibernation in outside cages was apparently stimulated by rainfall and not temperature, as de Jonghe noted had been similarly observed for *B. t. xanthopus* in Corsica. The trigger of rainfall to end diapause rather than temperature is interesting if it too is genetically linked. It also might explain the wide variation in emergence dates in Belgium, because rain in Belgium is unpredictable, whereas it is quite precisely timed in the Mediterranean.

In the early days of breeding bumblebees in captivity, diapause for several months was an inconvenience, because supplies were needed all year round in greenhouses. The shortfall of queens in late summer was made up by those of aestivating *B. t. dalmatinus* from Turkey, and by *B. t. audax* from New Zealand, where seasons are reversed. In attempting to circumvent the necessity of a long diapause period, it was discovered that a brief period of CO₂ narcosis of mated queens mimicked diapause in effect, by causing maturation of the ovaries (Röseler 1985). However, there

are costs to fitness associated with this practice, so it is no longer used routinely (Pomeroy & Plowright 1979; Tasei 1994; Kukuk *et al.* 1997; Pelletier 2003; Velthuis & van Doorn 2004a). Early researchers such as Horber (referenced in Velthuis & van Doorn 2006, see also Hodek 2002) also used a period of high temperature and high light intensity to circumvent diapause. CO₂ and high temperature might therefore be considered tachytelic processes. With in-house continuous breeding rather than collecting from the wild, manipulation of the diapause period is employed to provide colonies year-round. In commercial rearing, tests indicated that survival is greatest if bumblebees are stored at 5-6°C for a minimum of two months and then kept at 27-28°C and 60-65% RH to bring them out of diapause and into production (Velthuis & van Doorn 2004a, 2006). Even then, queens in artificial rearing will not lay eggs unless they are stimulated with younger bees or CO₂.

Duchateau & Velthuis (1992) discuss the problems encountered in early rearing of bumblebees for commercial use. They reference early methods for breaking diapause using CO₂ anaesthesia, and a more natural method of refrigeration at 6°C. CO₂ narcosis reportedly causes early production of males at the expense of workers. Also, the pollen used in artificial rearing is honeybee-collected pollen and not necessarily ideal for bumblebee nutrition (Génissel 2002). The outcome of colonies, in terms of numbers of workers and queens produced, is unpredictable because this variation is genetically programmed in nature (Duchateau *et al.* 2004). It is a problem even today for commercial rearers. The relative number of queens, males and workers that are produced is linked to whether the time between the switch point (when the queen starts producing haploid eggs) and competition point (when workers start to become aggressive and produce their own eggs) is short (<15 days needed for queen production) or long, but the mechanisms controlling each point are not fully understood.

Several people involved with commercial rearing of bumblebees have reported that some queens found a nest and lay eggs without apparently going through diapause (Tasei 1994; Beekman *et al.* 1999; Fliszkiewicz 2002). Tasei (1994) and Tasei & Aupinel (1994) reported on the effect of duration of CO₂ narcosis, age of mated queens, temperature following narcosis and following photoperiodic regime on delays to egg laying. A light period reduced egg laying delays, and resulted in a higher survival rate and longer lifespan of young queens post-diapause (Tasei & Aupinel 1994; Amin *et al.* 2007). Some queens were noted to found a nest without CO₂ treatment, although it was assumed that CO₂ narcosis would be needed to activate egg-laying.

Beekman *et al.* (1999) were interested in factors that influenced diapause induction, and whether diapause, although assumed to be obligate, might, in fact, be facultative. They referred to instances of apparent non-diapause in commercial cultures, and referenced bivoltinism in Tasmania (Buttermore 1997) as a demonstration that non-diapausing queens occur in the field, although we question whether variation in colony founding time or simply a second generation might provide an alternative explanation. Pathogens may also affect ability to diapause. *Nosema bombi*, a protozoan often present in natural and commercial cultures, can delay or prevent diapause if severe (Goulson 2003a). Beekman *et al.* (1999) reared queens in the laboratory which apparently did not undergo diapause (subspecies not reported). This trait could apparently be selected for (to some extent), thus the authors came to the conclusion that diapause was facultative rather than obligate. We question the methodology and some of the suppositions that were made in these experiments. The 'treatment' units were laboratory-reared queens, originally from a colony initiated in 1988. They were mated with siblings, held together for one week, and then placed individually with honeybees or an anaesthetised bumblebee worker for up to six weeks until egg-laying occurred. Conversely, the field-

caught queens used as a 'control' were reared for one generation only in the laboratory. Diapause of the new generation queens was broken with CO₂, so the experimental units to be compared were treated differently and unnaturally. As previously noted, CO₂ narcosis is known to produce deleterious effects. The 'control' colonies produced 17% non-diapausing queens. Four lines of 'non-diapausing' queens from the laboratory colony went on to produce variable and inconsistent degrees of non-diapausing queens over five generations, with means of 20.3, 38.5, 70.2 and 43.1% 'non-diapause' in the second, third, fourth and fifth generation respectively. The 'non-diapause' iso-female (single original female) selection lines could not be maintained, which the authors thought was possibly a result of inbreeding. They stated that:

'In a temperate climate it is unlikely that true non-diapause (non-diapause in each generation) exists'; for early emerging queens, 'In the field we would expect bivoltinism instead of true non-diapause'.

Beekman *et al.* (1998) earlier found that there was no effect of temperature during diapause on diapause survival, at least for the range of temperatures used (-5°C to 15°C). Thus we are unsure how Beekman *et al.* (1999) determined that the 'non-diapausing' queens in their experiment, which were up to 7 weeks old, had not actually completed diapause, albeit for a short period. The authors also raised this possibility, but dismissed it on the grounds that there had been no rise in temperature. Could it be that ovary development was stimulated by other means, for example by the addition of honeybees or a bumblebee worker, which are needed in artificial rearing in order for the queen to lay eggs?

Beekman & van Stratum (2000) studied the effect of a diapause period of 0, 2 or 4 months on colony characteristics. The set up and experimental methodology was similar to that described in Beekman *et al.* (1999), and suffered from the same problems in methodology. Thus the two month and four month 'diapause treatment' queens were subjected to CO₂ narcosis to simulate diapause, whereas the 'non-diapause' queens were not. The authors found that 'non-diapausing' colonies produced fewer workers and more queens in a shorter time.

Claims that diapause is not obligate are ill-founded. Exceptions are very rare in nature and unknown at the population level

This information has been used by respondents, including Beekman, to argue that diapause may not occur in Australia, thus there will be no limit to northward spread into subtropical climates, that colony fitness will not be compromised if queens do not diapause under warm climate conditions, and that there may actually be an advantage in terms of greater queen output. We strongly question these assumptions on several grounds. The sample size used for 'non-diapausing' colonies in Beekman & van Stratum (2000) was small (n = 10) compared with alternative treatment colonies of n = 27 and n = 21 for colonies with diapause-duration of 2 and 4 months respectively. Given the innate variability in nest size in bumblebees, this may well lead to a lack of robustness in the significance of the results. Gerloff (2001) also found in his inbreeding experiments with *B. terrestris* that family line had a strong influence on results, with some inbred lines fitter than outbred ones. Given also the large among-colony and among-family variation in fitness traits measured, there is considerable doubt about the validity of the conclusions that Beekman & van Stratum (2000) reached. There are also the questionable effects of CO₂ on the two 'diapause' treatments, and the possibility that the 'non-diapause' queens may actually have had a short diapause. A short diapause period is known to result in a higher output of queens (Duchateau *et al.* 2004), thus the claim that superior colonies were produced by 'non-diapausing' queens is questionable. Breeders have long recognised that stimulation of the ovaries is required for queens coming out of diapause to mature and for egg-laying to occur. Moreover, there is a

suggestion in the paper that a more female-biased sex ratio is produced by non-diapausing colonies in a second generation, because they can be certain of the presence of males produced by diapausing colonies. This appears to us to possibly stretch the cognitive abilities of bumblebees.

One might reasonably assume that if true non-diapausing queens exist in nature, an unknown factor other than diapause, perhaps high temperature or CO₂, would be required to provide a stimulus for ovary maturation.

More recent research sheds light on the possible causes of non-diapause, without claiming that ovary maturation and colony development can proceed regardless. The role of the fat body in enabling diapause has been known for some time (Alford 1975). Fliszkiewicz (2002) in Poland investigated the causes of lack of diapause in commercial rearing of *B. terrestris*. Three factors were significantly different between queens which did and did not experience diapause. These were ovary length (much shorter in non-diapausing females), sperm number in the spermatheca (low numbers in non-diapausing females), and size of the abdominal fat body (much smaller in non-diapausing females). She also queried conclusions reached on laboratory-reared queens, which differed from those caught in the wild, suggesting an inadequate understanding of artificially reared bumblebee colonies. In a further study, Fliszkiewicz *et al.* (2007) reiterate that 'In closed cultures, young inseminated queens have been observed not to fall into the state of diapause, which leads to losses in rearing' (Bilinski (2002) referenced). This latest research showed that the fat bodies of diapausing queens were characterised by a higher mean content of dry matter and a higher content of fat compared with non-diapausing ones. Thus one could speculate that building up reserves in the fat body is critical to entering a resting stage, which enables the bee to avoid unfavourable conditions such as winter cold or lack of resources, and that lack of such reserves might delay or even prevent onset of diapause, and implies a cost to lack of diapause that would likely affect long-term survival.

Mating does not appear to be a trigger for diapause, as had originally been suggested to us, nor to be necessary for its completion (Alford 1969, 1975; Schousboe 1994). Schousboe (1994) reported the existence of up to 11% of spring queens of *B. terrestris* in Denmark without semen in the spermatheca (sample size was rather small). It is unknown whether these were a result of poor mating (males insert a plug after mating to prevent further mating) or lack of mating, but hibernation appeared to have taken place. There was no mention of development of ovaries sufficient to found a colony. Only males could be produced from such a colony, as eggs would be haploid.

In New Zealand, all four bumblebee species that were introduced from the UK rapidly switched to southern Hemisphere seasons. The largest population was found during the summer months, despite food supplies being available year round. Hopkins (1914), who was involved in the first importations of bumblebees from the UK, notes that:

'so far not a trace of any change in habit (except perhaps in the calendar period of hibernation) has been noticed in the bees from those natural to them in their ancestral home.'

Young queens from a colony of the normally aestivating subspecies *B. t. sassaricus* from Sardinia, Italy went into hibernation at 5°C for at least 3 months (M. Duchateau, pers. comm. September 2007), as did *B. t. dalmatinus* (Estoup *et al.* 1996). We question whether this merely indicates plasticity, or a genetic pre-disposal to winter diapause, or at least physiological and/or environmental influences precipitating diapause.

There does not appear to be a genetic change away from hibernation-diapause capability towards aestivation. Estoup *et al.* (1996) also suggested that the differences between northern and southern populations with respect to diapause/aestivation may indicate genetic differentiation. They noted also that the markers linked to genes for diapause are most unlikely to be detected and would not necessarily show up with microsatellite data unless the resolution was improved. While southern *B. terrestris* subspecies which normally aestivate will hibernate if given suitable conditions, as far as we are aware, no-one has tested the ability of northern subspecies such as *B. t. audax* to aestivate, either in the short or long term. Given that they do not experience climatic conditions which might precipitate aestivation, there is little reason to expect that they would have this capability. Velthuis & van Doorn (2004a) state that, 'generally speaking, these two populations, aestivating and hibernating, are isolated subpopulations (located on islands, for instance), although in some cases there may be some exchange of genetic material (mountain versus lowland population).' A. van Doorn (pers. comm. to M. Steiner, December 2007), agreed that aestivation ability appeared to be confined to southern subspecies, and that *B. t. terrestris* and *B. t. audax* did not aestivate. Aestivation is usually tied to both hot and dry conditions. Where populations overlap, the subspecies are not clearly separated and there may be individuals which can both hibernate and aestivate, as appears to be the case in Portugal (Maciel Correia 1991). *Bombus terrestris audax* is not known to aestivate in New Zealand or elsewhere. McClay's CLIMEX map (Figure 6, Appendix I), with the broader projected distribution of *B. terrestris s. l.*, includes several subspecies able to aestivate. As previously stated, rain rather than rising temperature has been observed to trigger emergence. If aestivation is genetically linked (de Jonghe 1986), then it has no relevance to *B. t. audax*, and the narrower distribution in Figure 7, Appendix I, is more valid if this subspecies is used.

Thus the degree to which diapause is facultative rather than obligate appears to us unanswerable until more is known about the triggers for beginning and ending each phase of the process, how subspecies differ, and how much of each process is genetically controlled. However, some form of diapause is certainly the norm in *B. terrestris*, and aspects of it are genetically controlled.

ii) *What evidence is there for non-diapause in nature?* The extent of non-diapause in nature has not been established, but inadequacy of food reserves has been shown by Fliszkiewicz (2002, 2007) to be a major factor in preventing diapause. Alford (1975) reported that many of the so-called queens that are reported foraging late in the year have reduced fat bodies and probably will not enter hibernation, thus they will not survive. Such individuals are frequently diseased or may be physiologically workers rather than queens (workers do not build up fat bodies and do not diapause/hibernate). On the other hand, unmated queens, stated to be rare in nature, may build up sufficient fat bodies to hibernate, though it is not known if they might found a colony the following spring. Because eggs would be haploid, these would be capable of producing only male offspring and would have no workers, so it is very unlikely. Stimulation of the corpora allata (secretory bodies in the brain), is necessary for ovaries to develop. This normally occurs during the final stages of hibernation (also as a result of exposure to CO₂ narcosis). Alford (1975) suspected that any non-diapausing queens might remain in the vestiges of the maternal nest to establish a colony rather than start their own, but there was no evidence for this. Velthuis (pers. comm. to M. Steiner July 2005) also reported that occasionally young, mated queens of various subspecies skip diapause, but that the colonies remain small. He suggested that it was possible that these individuals were closer to being workers, and that this should be interpreted as an intercaste

characteristic rather than a (potential) flexibility linked to climate differences.

Appearance of bumblebee queens in the winter months, as has been reported in New Zealand (Donovan & Wier 1978) and Tasmania (Buttermore 1997; Hingston *et al.* 2002), may be a result of a brief early warm spell bringing queens out of hibernation, or in response to generally warming temperatures. If the warm temperatures are prolonged and floral resources are available, then nest initiation may occur, with an early production of workers. In any one area, overlap in colonies will occur naturally because of variation in length of diapause and site-specific differences in temperature at overwintering sites. In a warmer climate, it thus becomes more likely that the hibernation period will be shorter and that a second generation is possible, so long as floral resources sufficient for survival and breeding are constantly available over the several months needed for the colony to complete development. Prÿs-Jones and Corbet (1991) and Goulson (2003a) noted that winter flying queens were now sometimes observed in England.

Thus while non-diapausing queens are not uncommon in commercial rearing, the extent to which they occur in nature, or contribute to a second generation, or enable winter-active populations, has not been investigated, but they are probably rare. Whether they occur or not is of doubtful practical significance. In a cold climate, non-diapausing individuals would not survive the winter and lack of resources during this time, so if the characteristic were genetically linked, it would be selected out. As a minority, non-diapausing queens would probably not maintain genetic purity even if they did survive.

Throughout its extensive range, despite prolonged exposure to local climatic conditions over many centuries, there is no evidence for a non-diapausing population among any of the subspecies of *B. terrestris*.

iii) *If diapause is facultative, is there a potential for continuous reproduction of B. terrestris in warmer climates?* We consider such an occurrence to be an extremely unlikely event. The availability of suitable resources, along with temperature and rainfall, has largely governed the seasonality of bumblebees in different areas. Rasmont *et al.* (2005) analysed the dietary suitability of pollen and nectar from the strawberry tree, *Arbutus unedo*, for honeybees and *B. terrestris* in southeastern France. He states that in Mediterranean areas, *B. terrestris* is polyvoltine with an autumn generation (authors referenced in Rasmont *et al.* 2005). During winter, few plants are available to provide nectar and pollen. In this region, which includes Spain, France, Italy, Greece, and Turkey, *B. terrestris* is almost solely dependent on the winter-flowering *A. unedo* for the winter generation. Its pollen is a highly suitable diet for bumblebees (though not for honeybees). Another species of this tree, *A. andrachne*, is spring flowering and the one on which Dafni monitored *B. terrestris* outside his office window in Israel (Dafni & Shmida 1996). This raises an interesting question about the degree of plasticity of the *B. terrestris* life-cycle, and suggests that plant suitability and periodicity in the area invaded is extremely important for adaptation to environments which are climatically challenging. The aestivating Mediterranean subspecies are clearly very vulnerable, particularly as *A. unedo* is being removed in some areas to reduce fire risk (P. Rasmont, pers. comm. January 2008). The presence of this one genus of plants may have been the factor that enabled establishment of *B. terrestris* in the far south of its range, possibly now supplemented by irrigated urban gardens and cultivated crops.

What might happen in a constantly warm climate? The marginal mosaic model applied to *B. terrestris s. l.*, of which the natural latitudinal range is 30-60°N, predicts that there will be thermoregulatory strictures placed on the species at the extreme temperature ends of its distribution, and that overall density will be very low at these

Summer diapause (aestivation) is common in Mediterranean populations. Rain rather than warmer temperatures triggers awakening. Aestivation in *B. t. audax* is unknown, so adaptation to a hotter climate is very unlikely

B. terrestris
is at the
margins of its
latitudinal
climatic
range in
southern
Australia and
so any
population
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transient and
bee density
low

margins, with a tendency to extinction on a local or temporal scale (Hengeveld & Haeck 1982; Williams 1986; Guo *et al.* 2005; Williams *et al.* 2007). This model would conceivably provide the best fit at a subspecies level. Pockets of survival will be resource driven, often temporary, and possibly dependent on high altitude conferring cooler temperatures. High temperatures much above 30°C inhibit foraging, require workers to spend time fanning the nest instead of foraging, and result in high mortality of immatures (Goulson 2003a; Weidenmüller 2004; van Doorn 2006; Velthuis & van Doorn 2006). Warm, humid conditions will also increase fungal pathogens in the colony (Pouvreau 1970). The causes of non-diapause so far identified point to a lack of fitness in the individual, which may be partially offset in commercial rearing by a continuous supply of food. We might speculate that low population density and lack of synchronisation of generations will reduce mating opportunities and also result in non-episodic inbreeding. Gerloff (2001) and Gerloff & Schmid-Hempel (2005) examined the effects of inbreeding depression and found that episodic inbreeding is not necessarily detrimental in bumblebees, but reinforces differential representation of families in the population. Maternal family line strongly influenced the percentage of queens successfully founding a colony. The authors suggest that successful colonisation of new areas such as Tasmania from an extremely small founder population may be a result of invasion by a 'good' family line, combined probably with little interspecific competition, few parasites and a benign climate.

Bombus terrestris is a cold-adapted species, particularly in its northern ranges, which can be expected to perform best in temperate-climate conditions. Queens that mate and hibernate early in the season survive hibernation more frequently and form larger colonies than those that do so later. It is very unlikely that in a semi-tropical climate, at the edge of its climatic tolerance, colonies will be more successful than in a temperate climate, just because the life cycle is shorter and there may be another generation or two a year. In fact, survival is far more likely to be jeopardised under these conditions.

iv) *Is there a cost or a benefit of non-diapause to the fitness of future generations?* If there is a genetic component to non-diapause, and the need to diapause is selected out (though it is difficult to see how this might happen), survival will depend primarily on climate and resources being favourable to queen production *every month of the year*. Beekman *et al.* (1998) investigated the effect of pre-diapause weight and size of queens on diapause survival and post-diapause performance, finding a minimum weight of 0.6g necessary for queens to survive diapause. With no diapause, a higher percentage of low weight, poor quality queens might survive to found colonies. Beekman *et al.* (2000) found that in artificial rearing, queens gradually became lighter. Inbreeding was discounted, but a deficiency of scarce nutrients caused by deficiencies in honeybee-collected pollen was a probable cause. Thus a lack of suitable food may result in a decrease in weight of queens, which, without the rigours of diapause, may survive to perpetuate their genes. Non-diapause may be expected to incur a cost to fitness and therefore long term survival, and its low incidence in nature confirms this view. The colony itself is not perennial but is started anew by young queens with each cycle. We can see no clear benefits of continuous cycling, but these would in any case be site- and context-specific and very dependent on resources and pressure from predators, pathogens and parasites.

v) *What is the significance of sex ratio on population density and survival?* Beekman & van Stratum (2000) claimed that their 'non-diapausing' colonies raised a higher number

of queens and sexual offspring and should rear a more female-biased sex ratio. This has been used to imply superior output of queens in warmer areas of Australia should no diapause occur.

Three papers referenced deal with sex ratios in bumblebees (Bourke 1997; Beekman & van Stratum 1998; Duchateau *et al.* 2004). An interesting characteristic of bumblebee colonies is that they tend to specialise in either male or female sexual forms, termed a split sex ratio. The split sex ratio goes some way towards prevention of inbreeding. In a colony producing both sexes, males are produced before females. Males are the 'cheaper' sex to produce.

Bourke (1997) and Beekman & van Stratum (1998) reported that sex investment ratios in bumblebee populations are male-biased. Where resources are scarce, colonies are more strongly male-biased, with fewer workers. They found differences between laboratory and field populations in the relationship between colony size and sex ratio. In the field, sex ratio is biased towards males when resources are scarce and colony size is small. In laboratory cultures, the number of females produced was independent of colony size, perhaps a reflection of food quantity or quality. This again points to the need for caution in applying laboratory results to the field.

Duchateau *et al.* (2004) studied a greater number of colonies than Beekman & van Stratum (1998) and found that the number of queens and males produced in each colony was related to the duration of hibernation-diapause. The timing of the switch point from worker eggs to male eggs being laid was strongly affected by hibernation duration of the queen. A long diapause period led to large first and second worker broods, an early switch point, and a male-biased sex ratio. A short diapause period with a late switch point and early competition point resulted in production of mostly queens. Conversely to the earlier laboratory results showing a male-biased sex ratio, Duchateau *et al.* (2004) found that, population-wide, patterns of sex-allocation actually showed equal investment in the sexes. After the competition point, workers contribute to male production, and in laboratory studies boost the apparent sex ratio in favour of a strong male bias. However, they argue that in nature, workers have no realistic options to capitalise on their contribution, leaving queens in effective control of sexual output. This favoured a 1:1 sex ratio at the population level.

The split sex ratio innate in bumblebees makes it difficult to realistically determine area population density from a small colony sample size. Queens are energetically expensive to produce and only a small number of colonies obtain sufficient resources to progress to queen rearing. A short diapause is one of the factors favouring queen rearing (Duchateau *et al.* 2004), so warmer climates might appear to favour population increase (up to the point where temperature becomes limiting in other ways). Queen production, and worker oviposition about 12 days later, seems to be an evolutionary compromise between ecological constraints, kin-selected interests and colony quality (Duchateau 2006). The work of Duchateau *et al.* (2004) suggests that population-wide patterns of sex-allocation will continue to show equal investment in the sexes, with queens in the driving seat.

In summary,

1. Diapause is the normal condition experienced by *B. terrestris* in both its natural and adopted ranges, which allows the species to survive periods of unfavourable climate or lack of resources. In Mediterranean climates, aestivation may supplement or replace hibernation. There is some evidence to suggest a genetic component for each

Bumblebee colonies specialise in production of either males or queens. Very few colonies are successful and go on to produce new queens. Only 15% of colonies are successful in New Zealand

type of diapause, which is linked to the local subspecies. The triggers for onset and completion of diapause are not well known.

2. Non-diapause is reported in laboratory rearing, but whether it is true non-diapause or is linked to a rearing artefact has not been well established. Non-diapause in natural populations has been linked to disease and to lack of food resources and sperm in the spermatheca, and would normally confer a disadvantage. An inability to become dormant during unfavourable periods is more likely to result in selection against this trait. Its incidence and significance in nature has not been investigated, but it appears to be rare.
3. At a population level, there are no known *B. terrestris* subspecies without a period of diapause, thus, there is no reason to believe that the situation will be any different in Australia.
4. A colony is always annual, with a natural progression from eggs to workers, then in some cases males and queens, after which it is finished. Only new queens survive the season or are able to diapause.
5. In warm-temperate areas the life cycle is shorter and there may be more than one generation a year. It has not been established whether the small winter populations of *B. t. audax* observed in New Zealand and Tasmania are derived from diapausing or non-diapausing individuals, to *Nosema*-infected individuals, or is simply due to an overlap in colony foundation time.
6. Colony size is intrinsically very variable, with the sex ratio under queen control. Nests generally specialise in males or queens, termed a split sex ratio, though some produce both, or more often, only workers. This trait is shared by other bumblebee genera. There is no reason to believe there will be any fundamental changes in biological characteristics in Australia.
7. While a warmer temperature may speed up the bumblebee life cycle, too high a temperature is detrimental to other facets of their existence. Most of Australia (at and above latitude 30°S) is at the limits of known climatic tolerance of this species (Perth, WA is 31.56°S, Coffs Harbour, NSW is 30.18°S). Aestivation in *B. t. audax* is unknown. Without this ability, survival of this subspecies is very questionable in areas with high temperatures and the more appropriate CLIMEX model is *Figure 7*, Appendix I, with the far more limited projected distribution.
8. For Mediterranean subspecies such as *B. t. dalmatinus* which can aestivate, survival at high temperatures is also questionable, as the cue for completion of the process is rain, which in its natural range arrives predictably in late autumn after a dry summer. Thus the CLIMEX model for *B. terrestris s. l.*, *Figure 6*, Appendix I, may not be appropriate in the Australian climatic context.

It is worth noting that if aestivation occurred in Australia, any temporal overlap with Australian bees, which are mostly summer-active, would be minimal.

6.3. The range of habitats the species could inhabit, and how abundant could it become in these habitats

This topic has been discussed in Section 5 with respect to the Tasmanian situation. If climate is suitable, then a range of habitat types on the mainland *might* support *B. terrestris*. However, abundance of bees is also needed for a significant impact to occur, and this will likely vary greatly with and within habitat-type, from one month or year to the next and from one vegetation patch to the next. There is no evidence from its settlement of New Zealand or Tasmania that the population has changed in any of its characteristics compared to that in its ancestral home. As in Tasmania, should establishment occur, abundance will most likely be less than that of native bees in native

There would be many constraints on bumblebee survival and abundance in mainland Australia, not limited to climate

bush, and greater than native bees in urban areas and other habitats with a high percentage of introduced plants (Goulson *et al.* 2002b; Hergstrom *et al.* 2002). Hedgerows, headlands and unimproved pasture rich in legumes are recognized as good sites for nests and food sources in Europe and New Zealand (Goulson 2003a; Goulson & Hanley 2004); however, these are not a common feature in the mainland Australian landscape.

It has been suggested that bumblebees would compete with native birds and mammals for tree cavities, but this is not correct as their strong preference is for underground, protected sites in rodent holes, and none has been recorded from tree cavities (Alford 1975; Donovan & Wier 1978; Harder 1986; Goulson 2003a). Further, above-ground sites would be exposed to high summer temperatures and also to birds, ants, and other predators. Hergstrom *et al.* (2002) found very poor uptake of, and survival in, above-ground nests in Tasmania. On the other hand, lack of suitable ground nesting sites may well affect both establishment and abundance, particularly in native bush. Nest density in favoured habitat in the UK was estimated at 0.29 nests/ha (Knight *et al.* 2005) and 13/km² (Darvill *et al.* 2004), from which their foraging range may extend more than a kilometre.

Pests and diseases in mainland habitats may also limit their survival or abundance. Studies of the Tasmanian population have so far found a very low pest and disease incidence (Hergstrom *et al.* 2002; Allen *et al.* 2007). However, bumblebees generally are potentially host to a wide range of predators and parasites (Macfarlane *et al.* 1995; Schmid-Hempel 1998; Hergstrom *et al.* 2002; Goulson 2003a). Birds, spiders, ants, robber flies (Asilidae), foxes, rodents, wasps and various nest commensals are some of the potential predators (Goulson 2003a) that might preclude or limit establishment of any feral populations on mainland Australia. Parasites include Conopid and Sarcophagid flies, Braconid and Mutilid wasps, and a variety of viruses, prokaryotes, fungi, mites and protozoa. Predators are less likely to be host-specific than parasites, which appear to be absent in the Tasmanian population. As bumblebees in Tasmania are still in an expansion phase, it can be expected that any new relationships between parasites and predators have not yet had time to develop.

Bumblebees collect food only for their immediate needs (Heinrich 1979a; Pelletier 2003), so are vulnerable to starvation during extended periods of hot or wet weather, which limit foraging. Unlike honeybees, they do not store food to carry them over periods of shortages, thus very short periods of just three days without a food source will result in the demise of the colony.

Only larger, well-supplied colonies are able to produce reproductive females and males. To achieve this, a sequence of suitable flowers for 12-15 weeks is needed (Macfarlane, pers. comm. to S. Goodwin 1997). There is a high mortality rate of both queens and of colonies (Sladen 1912; Donovan & Wier 1978; Barron *et al.* 2000; Hergstrom *et al.* 2002; Goulson 2003a), with few nests producing queens (Free & Butler 1959; Donovan & Wier 1978; Müller & Schmid-Hempel 1992; Goulson *et al.* 2002; Duchateau 2006). Some colonies in New Zealand are reported to be unusually large (Donovan & Wier 1978); however, the size is very variable from one location or year to the next (pers. comm. B. Donovan, R. Read, N. Pomeroy, J. Thompson; T. Marais, Auckland, October 2007). The population in New Zealand has been relatively stable over many years, and may be limited by a lack of suitable nest sites or by pests and diseases. Only 15.5% of nests were found to have completed their developmental cycle in New Zealand, with very few queens producing reproductive nests (Donovan & Wier 1978). Nests in unsuitable habitats will fail to produce any new queens (Hergstrom *et al.* 2002; Goulson 2003a). Maximum nest size at peak production is less than a thousand,

Temperatures much above 30°C are detrimental to survival of both foraging bumblebees and immature stages in the nests

usually considerably less (Donovan & Wier 1978; Goulson 2003a; Benton 2006). In a closely related species, *B. lucorum*, large maximum colony size was strongly correlated with nest foundation early in the season (Müller & Schmid-Hempel 1992).

Nest temperature is kept at 30-32°C (Alford 1975; Goulson 2003a; Weidenmüller 2004). Higher temperatures may melt the wax honey pot and also the wax covering the brood. Worker response to higher temperatures is to cease foraging or caring for brood in order to fan the nest and cool it (Vogt 1986; Weidenmüller 2004; van Doorn 2006). Both these factors have implications for survival in hotter climates in mainland Australia, which effectively includes the entire landmass (<http://www.bom.gov.au/climate/averages/>).

Conclusion

Bombus terrestris in Tasmania has inhabited a range of habitats, though density in each habitat varied, with few bees in native bush and larger populations in urban areas. Variation is similarly expected within similar climatic zones in mainland Australia, should *B. terrestris* become established there. These suitable climatic zones are much more limited on the mainland, being restricted to the coastal south and south east. Many known and unknown factors may mitigate against successful establishment, so even though climate may be suitable in a particular area, persistence of colonies to the following season is not a 'done deal'. Abundance in natural areas is highly unlikely. All regions in Australia experience high temperatures at some time in the year that have the potential to seriously disrupt bumblebee survival.

6.4. The ability of the species to compete with native insects and animals for nectar

Nectar feeders in Australia potentially include a wide range of native insects (e.g. bees, ants, microhymenoptera, moths, thrips, hover flies), birds (e.g. honey eaters, parrots) and other animals (possums, flying foxes, bats), with little flower constancy. Some discussion on this issue has already taken place in the original submission (Goodwin & Steiner 1997 URL: <http://www.tmag.tas.gov.au/workshop/append2.html>). None of this overlap has any relevance if competition is not occurring to the extent of impacting on reproductive output of native fauna, and if nectar and pollen resources are not limiting. A high density of bumblebees, more typical of urban and semi-urban areas, in itself indicates that resources have not been limiting.

First, any establishment of *B. t. audax* that might occur on the mainland would likely be in regions with a climate similar to the UK, New Zealand and Tasmania. For Mediterranean subspecies able to aestivate, expansion might occur into areas with a Mediterranean climate and suitable winter forage, but this would still limit the species to far southern Australia.

Because bumblebees have been much maligned in Tasmania, several studies attempting (unsuccessfully) to prove negative impact have been conducted there. Such studies were planned to indicate potential impact on the mainland, but their status in other countries where they are long-established must surely be of greater relevance. So far, only a worst case (and highly unlikely) scenario has been forecast for the Australian mainland, with little consideration for supporting evidence, and totally at odds with knowledge of the species elsewhere. So what indications are there in countries where *B. terrestris* is indigenous that competition with native insects and other animals for nectar is occurring or has occurred? In the UK and New Zealand, all bumblebee species, including *B. terrestris*, are considered highly beneficial insects, not pests. A degree of competition for resources is considered the normal situation in nature, threats to pollinators are significant but rightly blamed on human activity, and no bad publicity has

In its established range, including the UK and New Zealand, bumblebees are not considered pests but beneficial insects

prompted the initiation of studies designed to show otherwise.

The establishment of *B. terrestris* (?*subspecies dalmatinus*) on the island of Hokkaido, Japan, has led to concern over displacement of native bumblebee species with overlapping life styles. As yet studies have only pointed to circumstantial evidence for the decline in one species, possibly related to lack of nesting sites, while other studies show no effect, most likely because of resource partitioning (Heinrich 1976a; Ranta & Lundberg 1980; Ginsberg 1983; Steffan-Dewenter *et al.* 2000; Goulson 2003a; Goulson & Darvill 2004; Nagamitsu *et al.* 2006).

The subject of competition has already been defined and discussed in Section 5 with respect to Tasmania. Before claiming a negative impact on native insects and animals, those impacts must be shown. So far, none of the studies in Tasmania has identified a negative impact, despite claims to the contrary. As in New Zealand, where *B. terrestris* has been widespread for many years as an introduced species, there is no evidence of displacement or competition with native pollinators. Thus, the interaction and impact on mainland Australia in similar climatic zones, which are primarily limited to southern coastal areas, can reasonably be expected to be negligible.

Pollinator assemblages and mechanisms of pollination in all but a few Australian native plants are poorly researched and understood, but foraging and biological characteristics of bumblebees are well known, so it is quite possible to make an educated assumption on likely interaction and impact. Claims by Hingston (2005a) that bumblebees exhibit no preference between introduced and native flowers suggest that he is ignorant of bumblebee foraging habits, despite a wealth of literature on the subject (*see* Section 5 for discussion). It is well known that bumblebees do not visit flowers in a haphazard fashion. Like other polylectic social bees, they exhibit flower constancy, though to a lesser extent than honeybees (Eickwort & Ginsberg 1980; Goulson 2003a), because learning how to handle a particular type of flower takes time and is energetically taxing (Goulson 2003a; Peat & Goulson 2005). Some native bees are polylectic, and some specialize to varying degrees (Armstrong 1979; Hingston 1999). Polylectic does not equate to 'no preference'. On a single foraging trip, bumblebees may show fidelity to one particular flower type, particularly if flowers are large and clustered and known from previous sampling to be rich in rewards (reviewed in Goulson 2003a). These flowers are generally those of introduced rather than native plants. Low rewards may cause a bumblebee to switch flower preference, possibly sampling several flower types if rewards are still low (Heinrich 1979a, b).

Despite an innate sense of rewards associated with a particular plant type, bumblebees with no experience must still go through a learning process to choose which flowers in a particular area are most profitable to visit, and how to handle each type (Eickwort & Ginsberg 1980; Peat & Goulson 2005). They usually choose flowers that face upwards or horizontally and offer a substantial landing platform, and rarely choose pendulous flowers (Prÿs-Jones & Corbet 1991). Many Australian native flowers in areas where climate is suitable for establishment are small and plants are scattered; these are easier for small native bees with shorter tongue length to access. For bumblebees, if small native flowers are all that is on offer, choosing a particular species on which to forage may be abandoned in favour of general sampling. Thus, finding that a bumblebee visits as many native flowers in a garden as introduced ones cannot be assumed to be a case of 'no preference'.

The economics of random sampling, in terms of visitation rate, handling time and handling competency, may produce marginal returns and so affect colony survival or preclude queen production. Survival in native bush is therefore never going to be easy.

On the basis of known biology in many other countries, competition sufficient to impact on native insects and other animals in Australia is considered highly unlikely

Bumblebees are also non-aggressive towards other species when sharing feeding sites, unlike trigonid bees, many flower-feeding birds and *Vespula* spp. (Thompson 1989). They will not chase away native pollinators. Conversely, the Australian native blue-banded bee, *Amegilla* sp. has frequently been observed chasing honeybees away from favoured flower patches (pers. observ., M. Steiner). Larger size is not an indication of aggression or dominance.

Conclusion

The ability of *B. terrestris* to compete with native insects and animals for nectar in mainland Australia is predicated on suitability of climate and resources in the range of habitats encountered. On the basis of experiences in Tasmania and New Zealand, where climate allows establishment, density of *B. terrestris* is likely to be low in native bush, and of no consequence in urban and semi-urban areas, where resources are unlikely to be limiting. Thus, competition sufficient to impact on native insects and animals is also predicted to be of no consequence.

6.5. The probable effect of Australia's climatic conditions on hive number, size and ability of new queens to survive

The effect of mainland Australian climate will be to limit the potential distribution of *B. terrestris* compared with that in Tasmania or New Zealand, because the temperature over much of the continent is either too high or at the upper limits of survival capability. Colony size and individual size of social insects is also generally smaller in non-seasonal climates (Kaspari & Vargo 1995) Both Tasmania and New Zealand have a cool to warm temperate climate, with adequate rainfall and few temperature extremes. The long-standing colonial influence has resulted in an English landscape across settled areas, with many introduced weeds, pasture and garden plants. Climate variation in mainland Australia has produced many distinct, unique habitats to which native bees and other anthophiles are adapted, but areas of temperate climate with good rainfall are restricted to a southern and south-eastern coastal strip. A consideration of ability to survive climatic extremes across the country is a prerequisite for defining suitability of habitat and other limiting factors in any one area. The AHGA recognized that being able to predict the potential distribution in mainland Australia with some degree of certainty was very important, and so commissioned two studies based on modeling climatic parameters.

CLIMEX modelling suggests only a limited potential distribution for B. terrestris on the mainland, particularly for the temperate subspecies B. t. audax.

Predicted distribution The CLIMEX modeling system that was used (Sutherst *et al.* 2004)

‘allows the user to estimate potential geographic and seasonal abundance of a species in relation to climate. The fundamental assumption of CLIMEX is that any species range is limited by their response to climatic factors.’

The first report considered only Australia (Hergstrom 2003), while the second was an updated, more comprehensive study (McClay 2005a). The latter is appended as Appendix I. Using CLIMEX version 2 (Sutherst *et al.* 2004), McClay developed two models on which he based two separate predictions.

Model 1 was based on the current distribution of *B. terrestris s. l.*, which covers the known range of all 9-11 *B. terrestris* subspecies, and Model 2 on *B. t. audax* distribution in the United Kingdom, New Zealand and Tasmania and the climatic parameters of those areas. The *B. t. audax* model (Model 2), when applied to Europe, still predicts a potential distribution across much of continental Europe and into northern Spain and Italy, which is occupied by other *B. terrestris* subspecies (*Figure 4*, Appendix

Parameters for diapause and aestivation were not included in the two CLIMEX models developed, and may well place further restrictions on potential distribution

I). When applied to mainland Australia, the predicted range includes Kangaroo Island off South Australia, the coastal south and higher elevation areas of south-eastern Victoria, the southern tip of New South Wales north almost to Sydney, and some areas around the Armidale area of New South Wales (*Figure 4*). This model fits closely with that of Hergstrom (2003). Incomplete documentation of the parameters that Hergstrom used (McClay 2005b) does not permit a closer analysis, nor its publication. In the alternative McClay model for *B. terrestris s. l.* (Model 1), the predicted area with suitable climate on mainland Australia is, not surprisingly, much more extensive (*Figure 6*, Appendix I). It includes almost all of Victoria, south-eastern coastal areas of South Australia, the eastern half of New South Wales, coastal areas of southern Queensland and higher elevation areas around Cairns and around Bowen, and coastal areas of Western Australia from Eyre to Geraldton. This model is much more all-embracing. It assumes, we believe incorrectly, that although geographical boundaries have separated subspecies, climatic adaptations have not been genetically reinforced, despite long periods of isolation over thousands of years.

Which of the two models is appropriate? The extreme natural range of *B. terrestris s. l.* extends from latitude 60°N to 30°N (except 28°N for the cooler-climate Canary Island subspecies *B. t. canariensis* (*Figures 2 and 3*, Appendix I). One might reasonably anticipate that in the Southern Hemisphere this would equate to 30°S to 60°S. However, Model 1 for *B. terrestris s. l.* in Australia predicts establishment as far north as 15°S, which would be well outside this range. Model 2 for *B. t. audax* predicts a range of 35°S to 45°S, except for a small area around Armidale at 30°S. Both models, as one would expect, encompass Tasmania. Little establishment is predicted for west-central areas of Tasmania, which encompass much of the World Heritage Area. This confirms the results of surveys by Hergstrom *et al.* (2002) and Stout & Goulson (2000), but contradicts the predictions of Hingston *et al.* (2002). How does this compare with countries outside its natural range, where *B. terrestris* has been documented as establishing? New Zealand extends from ~50°S to 35°S, and Japan from 45°N to 30°N, where most of the feral population (not *B. t. audax*) is reported in the northern island of Hokkaido. Santiago in Chile is approximately 35°S. Uruguay is 30-35°S. Thus, known establishments outside the natural range encompass the same range of latitudinal limits. Further refinement of the model requires more specific biological information on aestivation and diapause requirements.

No bumblebee colonies are produced in hot dry conditions, limiting establishment potential in much of Australia

Griffiths (Appendix II) has argued strongly that isolation under different climatic conditions for thousands of years is likely to reinforce adaptive changes genetically, with which we agree. Recent information obtained from researchers long-familiar with *B. terrestris* biology in Europe sheds further light on this issue, and is discussed in Section 6.2. The missing factor that would limit northward expansion of *B. terrestris s. l.* in Model 1 to a maximum latitude of 30°S is unknown, but rain during the summer would bring southern subspecies (if selected) out of aestivation when temperatures are too high for survival. Considering the importance of this phenomenon as an ancestral trait of *B. terrestris*, this omission may well cast doubts on the broad distribution predicted in Model 1. Model 1 includes several subspecies able to aestivate, but because *B. t. audax* has never been observed to aestivate, this may obviate McClay's assertion that this model equally applies to this subspecies. Even if it did aestivate, rain is the trigger for emergence, so this would only work in a Mediterranean climate, and only if suitable forage plants were available through the winter. A cool wet season is needed to produce the next generation. None of the *B. terrestris* subspecies are active or produce colonies in hot dry conditions. Thus we believe that there will also be climatic limitations on northward spread of Mediterranean subspecies such as *B. t. dalmatinus*.

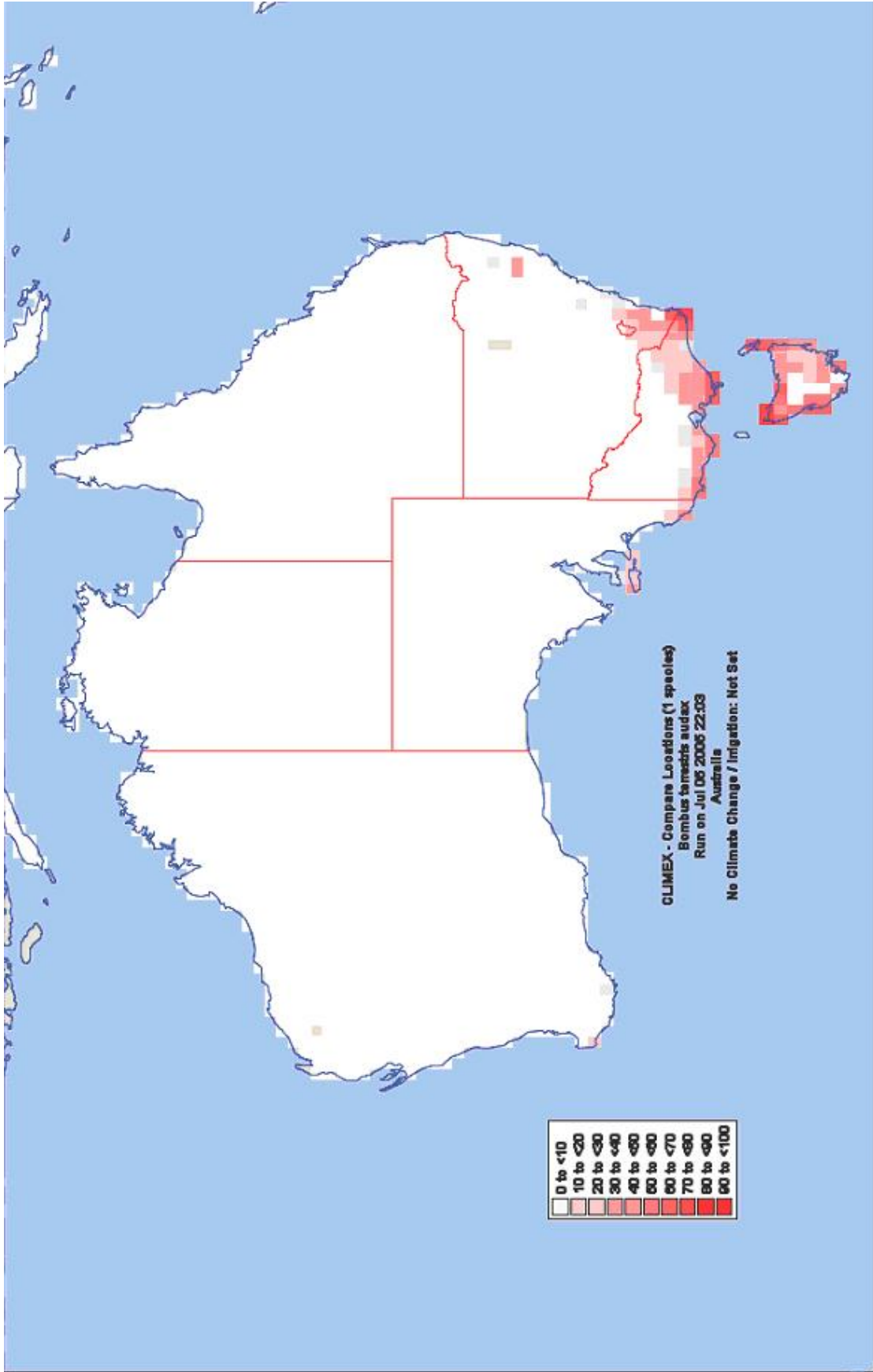


Figure 4. Predicted distribution of *Bombus terrestris* ssp. *audax* in Australia according to the CLIMEX® model. (McClay 2005)

Additional stress factors potentially affecting predicted distribution Hot-wet, hot-dry, cold-wet, cold-dry stress indices were not used in the CLIMEX models either, as predictions appeared to fit observed known distributions. However, the climate in Australia's northern regions, which is hot-wet, does not correspond to that in southern areas of its natural range in Europe, which is hot-dry. Improvements in biological information on cues for aestivation and diapause may allow refinement of the models in the future. Suitable areas may depend on altitude conferring lower temperatures, and are seldom contiguous, so geographical isolation may also serve to limit spread. It should also be remembered that the type of projected distribution discussed does not take into consideration any other limiting factors such as the availability of floral resources and nest sites, nor the influence of known or unknown predators, pathogens and parasites, nor climatic extremes (e.g. drought, high temperatures, floods), any or all of which may preclude establishment in the long or short term.

The importance of subspecies differences in *B. terrestris* It has been reported earlier that all the subspecies of *B. terrestris s. l.* can be distinguished on morphological grounds (Chittka *et al.* 2004; Peat *et al.* 2005). Chittka *et al.* (2004) and Raine *et al.* (2006a) argued against a purely adaptive explanation for observed behavioural differences between some populations of *B. terrestris*, suggesting genetic drift, exaptation (change in the function of an earlier biological adaptation) and pleiotropy (multiple physical effects caused by changes in one or a pair of altered genes) as alternative explanations for these differences. This view is supported by the work of Widmer *et al.* (1998), who distinguished six haplotypes through molecular studies. The haplotype for *B. t. audax* was unique within the group.

Although molecular work conducted by a number of agencies shows varying levels of divergence of some of the subspecies, few studies have been conducted as yet that would show specific physiological differences such as different temperature and humidity tolerances. Given the long geographic isolation of several of the subspecies and the extremes of the climatic range they inhabit, it is unlikely that no climatic adaptation has occurred, but ability to aestivate in hot climates may well be one such adaptation. For *B. t. audax*, isolated in a cool temperate climate for over 7,000 years, with diapause inherent and with a unique haplotype, some genetic drift has undoubtedly occurred. Accordingly, we disagree strongly with the conclusions of the author of the CLIMEX report, that there are essentially no proven differences between *B. terrestris audax* and *B. terrestris s. l.* that cannot be explained by simple geographical isolation, thus that the expanded range in Model 1 is just as likely a scenario for *B. t. audax* as Model 2 or by implication, as it is for Mediterranean, North African and south-eastern Asian subspecies.

The situation in northern Israel and Jordan (Dafni & Shmida 1996; Potts *et al.* 2001, 2003a, b, 2006; Al-Ghzawi *et al.* 2006) may offer some insights. Both have highland areas in the north allowing a Mediterranean climate of cool wet winters and hot dry summers, in which *B. t. dalmatinus* survives to some extent. They do not occur as feral populations south of these highlands, despite their widespread use in irrigated crops and greenhouses (S. Steinberg, pers. comm.).

When an organism is exposed to such long periods of isolation, prevailing selective pressures will trigger genetic drift within its genotype. Indeed, isolation *per se* is recognized as a very important building block in the evolutionary progression of species formation. It can be reasonably argued that the not inconsiderable circumstantial evidence suggests that *B. t. audax* has evolved a genotype based towards living in a cool, moist, temperate climate. Even in the UK, this distribution is skewed towards the wetter southwestern regions (Alford 1973; Williams 1986). The limited genetic base of *B. t.*

audax in Tasmania would also argue against the ability to adapt to an extreme range of climatic conditions. Thus, subspecies will differ in adaptive response to climate. Dr Griffiths has included a further discussion on this issue in Appendix II.

Relevance to subspecies differences in *Apis mellifera* A comparable situation exists for honeybees with respect to divergence in subspecies characteristics. There are at least 30 subspecies of the western honeybee, *Apis mellifera*, which have evolved in response to environmental conditions and which cover different geographic areas, much like *B. terrestris* and its subspecies. As is probably the case for *B. terrestris*, all the subspecies can interbreed given the right conditions, but can be differentiated on the basis of physiology, natural history, and biology. These characters are fixed genetically, so that a colony cannot readily adapt itself when transferred to a different kind of environment. Nine of these subspecies originate in Europe, 12 in Africa, and nine in the Middle East (http://en.wikipedia.org/wiki/Western_honeybee). Each subspecies is recognized as having different character traits which have remained unchanged over centuries (Ruttner 1976). The so-called black bee from northern Europe, *Apis mellifera mellifera*, was first imported from England onto the Australian mainland in 1822. It was adapted to the cool climate of its natural range in Europe and evolved over millions of years (The British Beekeepers Association, http://www.bbka.org.uk/articles/honeybee_family.php). *Apis mellifera ligustica* was imported from Italy some 40 years later, as it is better adapted to higher temperatures, and it is now the dominant species on the Australian mainland. *Apis m. mellifera* and *A. m. ligustica* were both imported into Tasmania, in 1814 and 1879, respectively. Despite some hybridization elsewhere on the island, only pure *A. m. mellifera*, the black bee, is found in cooler climate areas.

Other climatic factors affecting hive number, size and survival of new queens Survival of bumblebees within the favourable climatic range will not be uniform from year to year. As with New Zealand, Tasmania and the UK, bees are likely to be far more abundant in areas and years with good rainfall, but not floods (Hopkins 1914; Harder 1986), and where favoured weeds, forage plants and garden plants are available continuously throughout the breeding season. Higher population density in urban areas and botanic gardens is thus likely.

Weather conditions (cold, heat, rain) may have a profound temporal and seasonal effect on interactions of bumblebees with their surroundings (and on observers and observation periods) (Peat & Goulson 2005; Peat *et al.* 2005). Studies based on limited sampling periods of short duration are thus of little value in understanding the complex interactions that may occur between floral resources and pollinators, yet in the context of Tasmania, far too many inferences have been drawn from them.

Temperature will affect the number of pollinator visits and visitors and the potential for competition. Cold is unlikely to be limiting to survival, except in higher elevation areas, as *B. terrestris* hibernates during winter months and has good cold tolerance (Heinrich 1979a; Prÿs-Jones & Corbet 1991; Goulson 2003a). Nor is ability to forage at lower temperatures of much relevance, because Australian mainland temperatures are not limiting in the summer months when most native bees are active.

Research studies overseas have concentrated on low temperature tolerance; there are few studies at higher temperatures. Nest temperature is generally kept at a stable $30 \pm 1^{\circ}\text{C}$ (Goulson 2003a; Weidenmüller 2004; Velthuis & van Doorn 2006). Much higher temperatures will melt the wax cap on the brood and larvae will die, so nests will need to be very well protected to escape summer temperature extremes on the mainland. Weidenmüller (2004), examining the fanning response of workers to nest temperatures,

found that the mean of the threshold distribution within colonies ranged from 27.7–28.7°C air temperature and 1.6–2.5% CO₂ concentration. To avoid temperatures above 30°C, which would impair brood development, the colony needs to respond strongly even at temperatures below 30°C. This is achieved by a large number of workers with response thresholds around 28°C.

Other information on high temperature tolerance of *B. terrestris* has been gained from working with managed hives in greenhouse situations. Bees forage between 10°C and 30°C but prefer 15–25°C (Koppert Biological Systems, <http://www.koppert.nl>). At 33°C, pollination in tomato greenhouses is reduced (S. Steinberg, pers. comm. to M. Steiner 2005). Kwon & Saeed (2003) found that foraging activity in a greenhouse capsicum crop was highest at 25.7°C; foraging activity decreased by ~70% at 32.7°C. A. van Doorn (2006) similarly reported that bumblebees stop foraging in a greenhouse at 32°C. A temperature of 40°C dramatically reduced pollination activity and colony longevity (ChiTung & FengKong 1996). In Italy in plastic tunnels, bumblebees stopped foraging at 27°C (Koide & Hayashi 1993). Unlike bumblebees, honeybees can forage at temperatures >40°C, regurgitating nectar to provide evaporative cooling.

Excessive heat is clearly a major factor in limiting survival of bumblebees, with an energy cost to thermoregulation at sub-optimal climates (Williams 1989). As previously mentioned, *B. terrestris*, as a temperate species, prefers to forage during early morning and late afternoon. Despite a single report (Hingston 1997) of *B. terrestris* foraging at temperatures well above 30°C, such instances are rare and foraging activities are generally restricted to cooler parts of the day. Foraging at high temperatures may indicate that resources are limited during preferred foraging times, or that the short-term supplies in the colony are running out, but this is not a sustainable situation. Single event extremes, not a rarity in Australia, can be catastrophic. As an example, a *Trigona* sp. that was successfully imported into Israel from Australia for pollination services survived several seasons until one >40°C day killed them all (S. Steinberg, pers. comm. to M. Steiner 2005).

Most native bees in Australia, while poorly studied, have relatively short periods of activity and these are mainly during the summer months (Dollin *et al.* 2000). They have presumably evolved to tolerate high temperatures and may be adapted to cope with more concentrated nectar (Herrera 1990). Bumblebees prefer nectar at concentrations of 40–50% (Corbet *et al.* 1979), which may influence diurnal foraging periods and floral preferences relative to native animals. Nectar concentration generally increases during the day and declines later in the afternoon (Plowright & Laverty 1984), possibly reinforcing the avoidance by bumblebees of mid-day high temperatures.

The need for water Experience from commercial rearing indicates that the species will not establish in areas where the relative humidity falls below about 60% (D. Griffiths, pers. comm. 2005; Bilinski 2000; Duchateau 2000). Free water must also be available. Annual rainfall below 400mm will also not support colony development (R. Macfarlane, pers. comm. to S. Goodwin 1997). Australia's natural condition is for drought, and this has worsened in recent years and is unlikely to change for the better. The lack of water generally will likely lead to more and more restrictions on broad acre irrigation, limiting free water and introduced weeds, and thus further limit the ability of a temperate, rainfall-limited pollinator to survive. On the other hand, underground nests are susceptible to flooding (Hopkins 1914). Water, of course, is necessary to floral development and nectar production (Peat & Goulson 2005). In a drought these will certainly be limiting.

Nest size and number Nest size in New Zealand has been reported as unusually large, with an average of 150-200 workers, with a total yearly production of about 900, 120 of these new queens (Donovan & Macfarlane 1984). Nest size is innately very variable in *B. terrestris* (Donovan & Wier 1978; Duchateau & Velthuis 1992; Goulson *et al.* 2002; Goulson 2003a; Duchateau 2004; Duchateau *et al.* 2004; Hergstrom *et al.* 2002). It will depend on many factors, including resources available to new queens pre-and post-diapause, size of queens, length of diapause, emergence time from hibernation, pathogens, parasites and predators, and availability of resources over the period of colony development. There is no evidence of evolution of social traits in New Zealand or Tasmania that may have enhanced productivity and ecological success. Colonies on mainland Australia are likely to be smaller and more transient than those in New Zealand and Tasmania, except in urban areas or Botanic Gardens, because of the marginal climate suitability and extensive areas of native bush.

The disused burrows of rodents are very often used as nest sites (Sladen 1912; Donovan & Wier 1978; Goulson 2003a), as these provide insulating material necessary for the brood. It should be made clear that bumblebees do not usurp these nests. Rodents, other small mammals and reptiles often predate bumblebees in their nests (Sladen 1912; Free & Butler 1959; pers. comm. B. Donovan, R. Read, T. Marais, J. Thomson, N. Pomeroy, Auckland, New Zealand, October 2007). Lack of suitable nest sites may well prove limiting; there is competition between queens for suitable sites which often results in the death of competitors (Plowright & Lavery 1984; Prÿs-Jones & Corbet 1991; Barron *et al.* 2000; Hergstrom *et al.* 2002). Failure to find a nest site also results in a high mortality rate of queens. Available nest sites in Tasmania, even in Hobart, appeared to be limiting (Hergstrom *et al.* 2002) as several were re-used and competition was evident. However, favoured sites will be fought over, while less-favoured sites may go vacant (Sladen 1914; Alford 1975). Even in favourable habitats in the UK, nest density of *B. terrestris* was only 0.29 nests/ha (Knight *et al.* 2005). This may give some idea of the maximum density likely. It is possibly more realistic to assess the likelihood of any nests being established.

A very relevant, well-established ecological theory is that of the marginal mosaic model and similar models, which state that animals and plants are generally more abundant near the centre of their distribution ranges than near their edges (Hengeveld & Haeck 1982; Brown 1984; Williams 1986, 1988, 1989; Guo *et al.* 2005). If population density is plotted against an environmental gradient (temperature/latitude), then the spatial distribution of population density along any transect which runs through the centre of the species' ranges will tend to resemble a bell-shaped surface. The natural latitudinal range of *B. terrestris s. l.* is approximately 30°N to 60°N. The known range of *B. t. audax* is for the UK 50-58°N, Tasmania, Australia 41-42°S, Hokkaido, Japan 42-45°N, and New Zealand 35-47°S. Mainland Australia ranges from 12-38°S, with Sydney at 34°S, Brisbane 27.5°S, Melbourne 38°S, Perth 32°S, and Darwin 12.5°S. The extreme northern edge of potential establishment would thus run between Cervantes in WA and Armidale in NSW, with temperature as the main limiting climatic factor and adequate rainfall a secondary factor. Good resources might enable pockets of short term survival, which could be renewed periodically from a source population in a more favourable zone, but the population north of Sydney and Perth would always be close to possible extinction, with overall abundance in mainland Australia low.

Establishment on the mainland, should it occur, is likely to be restricted in area, with low density, transitory populations, and thus B. terrestris will have negligible impact

Summary of Section 6

The question of whether *B. terrestris* can establish on the mainland has been addressed at

some length, because issues such as competition and weed spread are only relevant to areas where the species might survive.

It must be emphasized that there is no intention of releasing bumblebees outside of greenhouses, so the question then becomes, what is the likelihood of establishment following mishap with secure hives, or for that matter unpredictable and accidental arrival in cargo? Both possibilities are very small.

Even should a queen bee escape into the environment and be successfully mated, the problems discussed in this Section relative to successful survival and propagation suggest that the likelihood of feral establishment is very low. Climatic modeling, particularly if the subspecies *B. t. audax* is considered, suggests that only very limited areas of the mainland will be suitable. Thus if commercial hives are sourced from a population of the temperate subspecies *B. t. audax*, then the affected area will likely be restricted to coastal regions of the southeast of the mainland below latitude 30°S.

Further limitations apply through the need for either a prolonged winter cold period in order to complete diapause, or an inability to enter or successfully complete aestivation. If establishment and production of new queens should occur, they would still require suitable nest sites and food resources for a period of four to five months, and a period of cooler weather in which to establish and raise young. Nest sites and food resources are likely to be limiting, particularly in native bush. Predators such as birds and ants may also preclude long-term establishment.

It is therefore concluded on present evidence that establishment of *B. terrestris* on the mainland of Australia is unlikely, but should it occur, the area will be restricted and the density of nests and individuals which may result is predicted to be low and their impact negligible.

7. THE PROBABLE CONSEQUENCES OF THE SPECIES BECOMING ESTABLISHED

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Introduction The Terms of Reference ask that in reply to Section 7, we should infer and extrapolate from studies of other species, with particular reference to *Apis mellifera*. However, in respect of *A. mellifera* it should be noted that *Bombus* and *Apis* are quite dissimilar in lifestyle, behaviour, physiology and genetic composition and such extrapolations have limited usefulness. Honeybees (in the absence of Varroa) will always be far more widespread and numerous than bumblebees and other bees in the Australian environment. Their colonies are perennial and can be very large, they can store food, they can forage at greater distances, and they have different races which extend climatic tolerance over much of Australia. They also visit a much broader range of plants than bumblebees. Thus the question is whether bumblebees would really make much difference to pollination systems in Australia. Their disadvantage is that they are large and stand out - if they were small and insignificant, we doubt this debate would be happening. The exotic ladybeetle *Hippodamia variegata*, which originates from Europe and China, was detected in QLD in 2000 and spread extremely rapidly through NSW, VIC, SA and WA, as it did when it arrived in North America. It had all the hallmarks of an invasive species. It may well have displaced native ladybeetles, native aphids and other aphidophagous insects, yet it was treated as a welcome addition to the fauna, with few questions asked. Instead of the curiosity and warmth that bumblebees evoke in their home ranges, bad publicity has made them a target for environmentalists and governments here. This emotive response cannot be justified on the evidence presented, or under the circumstances of the proposed importation. The AHGA accepts that the legislation advises a precautionary approach to all introduced pollinators. Nevertheless further imports of the Canadian leafcutter bee *Megachile rotundata* have been accepted as recently as 2005 (Anderson 2006), with a commendable degree of cooperation between agencies. A similar model might have worked well for *B. terrestris*, but was never put forward as an avenue that the AHGA could pursue. Approximately one million leafcutter bees were imported from Canada during each of the 2002-03, 2003-04 and 2004-05 Australian lucerne growing seasons. There have been losses of *M. rotundata* due to Australian parasitoids and predators (Woodward 1994, 1996), and also climate, limiting establishment. These might also be relevant to bumblebee establishment in

There are recent precedents for importation of exotic bees into Australia, namely the Canadian leafcutter bee Megachile rotundata

Australia. Otherwise there have been few concerns expressed since its release. This is despite the presence of similar leafcutting bee species in Australia, and low numbers of non-indigenous parasitoids in imported material. The level of safety with *B. terrestris* would be higher as there are no similar bee species in Australia and material would not be field collected, significantly lowering the possibility of natural enemy transfer. The ability to rear *B. terrestris* in an enclosed environment would enable new material to be kept securely in isolation and bred for a proscribed number of generations to ensure freedom from exotic pests and pathogens.

Linkages with European wasps, rabbits and cane toads made by opponents of the importation are not relevant. *Vespula germanica*, *V. vulgaris* and other vespid wasps are known to produce perennial colonies in other countries in the warmer areas of their natural range (Ross & Visscher 1983; references in Harris 1996; <http://www.issg.org/database/species/references.asp?si=896&fr=1&sts>). Only a small minority of wasp colonies in New Zealand and Australia are perennial (East 1984; Harris 1996; Ward *et al.* 2002; B. Donovan pers. comm. November 2006). Harris (1996) estimated only 10% of colonies overwintered at two sites monitored in New Zealand. Bumblebees, except for a few tropical species, have never been known to produce perennial nests (Goulson 2003a); *B. terrestris* certainly does not. Bumblebee queens may usurp recently established nests, but only one queen survives (Sladen 1912; Goulson 2003a). In *Vespula* nests, many queens may coexist (Leathwick *et al.* 1999; Ward *et al.* 2002). *Vespula* nesting behaviour in New Zealand and Australia has probably not evolved differently from in its natural range, but is more a reflection of a warmer winter climate, rainfall differences and more availability of resources. Other major differences are the high output of wasp queens, whereas only a few bumblebee nests produce queens; the much larger size of the colonies, even annual ones; multiple mating, and no split sex ratio. *Vespula vulgaris* has a strong inbuilt need for diapause, and is only weakly established or has died out in Hawaii, and is also not as strongly established in mainland Australia. *Vespula* wasps are aggressive, predaceous and contribute directly to loss of biodiversity (Thomas *et al.* 1990). It is not reasonable to compare them with bumblebees.

No *Bombus* species are indigenous to Australia, so there is no likelihood of there being a gene pool within Australian bees that could conceivably permit mating, let alone hybridization. It seems logical, therefore, that 'impact' on mainland ecosystems can best be assessed by reference to the impact which *B. terrestris* has had upon the fauna and flora of its native habitat, in addition to New Zealand where populations have stabilised over >130 years. Across these vast and divergent areas, *B. terrestris* (and all other *Bombus* species for that matter) is considered only as a benign and efficient pollinator. It has *no pest status* in any of these areas. It coexists with many thousands of species of native bees and with honeybees. Only recently has it been suggested that there is a negative impact from introductions made outside its natural range, notably in Japan. Even here, the main concerns are related to Japan's native bumblebee species: transfer of pathogens, hybridization, and overlap in resource use. These issues are important but do not have relevance in the Australian context. Japan has more than 15 existing species of bumblebees. It remains to be seen whether one more species will make a truly significant impact, except conceivably through pathogen or parasite transfer, which appears to us the most important issue, but a manageable one. So far negative effects are being inferred but have not been proven. Loss of bumblebee species, abundance and habitat is the overriding concern of many nations. The root causes of many of these losses are the same as those for native bees and other anthophiles, and relates primarily to vegetation and climate change caused by human activity.

We would argue that the only *probable* consequence of the species becoming

Linkages of bumblebees to European wasps, rabbits and cane toads are not relevant and simply an attempt at scaremongering

Concerns about interbreeding, pathogen transfer and resource overlap with closely related bumblebee species are not relevant to Australia. It has no native *Bombus* species

established is improved pollination of a wide range of horticultural crops through a managed hive system, leading to improved seed set, yields and quality of those crops. Possible consequences relating to establishment, weed spread, and changes on pollinator associations are much more difficult to predict, but on the basis of present evidence and precautions outlined in Section 10, are considered unlikely to eventuate. If the CLIMEX Model 2 (Figure 7, Appendix I) for *B. t. audax* is accepted as predicting potential establishment on the mainland (based on climate alone) of the subspecies accessed from Tasmania or New Zealand, then any potential conceived impact must be considered as minimal.

7.1. Effects on rates of pollination, gene flow and seed set among agricultural and environmental weeds, including those identified by the Cooperative Research Centre for Australian Weed Management (Weeds CRC) as ‘sleeper’ environmental weeds

The potential for spread of introduced weeds, particularly so-called ‘sleeper’ weeds, (those so far perceived as not weedy because of lack of an efficient pollinator or other mechanism of spread), is generally acknowledged by all parties as the one issue of any real concern, or at least the one where control cannot be easily exercised. Even then, several scenarios are possible:

- A. Bumblebees do not establish outside greenhouses in mainland Australia.
- B. Bumblebees establish outside greenhouses, but either in such low numbers, or for such a short period, that the impact is non-existent or negligible.
- C. Bumblebees establish outside greenhouses in larger numbers but in very restricted habitats.
- D. Bumblebees establish feral populations in a variety of habitats, but do not contribute to increased weed spread, because existing species are already optimally pollinated by honeybees and native bees, are self-pollinating, or are spread vegetatively.
- E. Bumblebees establish over a broad area in a variety of habitats and cause spread of one or more sleeper weeds, possibly also contributing to the spread of existing weeds.

Scenario A is the ideal scenario, at least for greenhouse growers, and we believe achievable through use of hives fitted with a queen excluder, screened greenhouses, and additional precautions outlined in Section 10. Scenario B is comparable to Scenario A in terms of no impact on weed spread, but would imply that at least some queen bees have escaped from greenhouses, but in an area or at a time unsuited to establishment. Scenario C might be possible in the limited climatic areas previously identified (Figure 4, Section 6) if little attempt is made to apply restrictions on usage, and if weeds or surrounding vegetation provide habitats with good floral resources. This is most likely to occur in agricultural areas bordering settled areas and along roadsides. Knowledge about existing weeds in those areas would assist in decision-making about any action needed. Cost-benefits associated with weed management against improved crop production and pesticide reduction should also be considered. The broader establishment implied in scenario D is not supported by the evidence or arguments presented in previous Sections. However, even should widespread establishment occur, there is as yet no evidence that increased weed spread will eventuate. New Zealand and Tasmania are examples of this scenario. Scenario E has been touted by those vociferously opposed to importation of *B. terrestris* onto the mainland as the environmental disaster likely to occur. It has no basis in established fact and is very unlikely.

Dr Rachel McFadyen of the Weeds Cooperative Research Centre was contacted regarding potential sleeper weeds. In her replies and those of others she contacted, were

The only probable consequences of B. terrestris becoming established are improved pollination of horticultural crops and reduced pesticide use

included all solanaceous and leguminous weeds, specifically tree lupin (*Lupinus arboreus*), tree lucerne (*Chamaecytisus palmensis*), *Leucaena leucocephala*, *Desmodium*, *Solanum* spp., gorse (*Ulex europaeus*), Siratro, greater trefoil (*Trifolium pratense*), Scotch broom (*Cytisus scoparius*), lupin (*Lupinus polyphyllus*), foxglove (*Digitalis purpurea*), comfrey (*Symphytum officinale*), myrtle-leaf milkwort (*Polygala myrtifolia*), *Rhododendron* and *Impatiens*. Some of these are already well-established and have been for many years in the absence of bumblebees. Wilson & McFadyen (2000) argue strongly for release, without full testing, of biological control agents against weeds in the ‘developing world’, as offering greater benefit than risk, yet Dr McFadyen has argued strongly against *B. terrestris* being allowed to enter mainland Australia as being an unacceptable risk. This dichotomy in approach to risks appears to us rather curious. Further, it is difficult to argue a case for general increased weed spread due to the activities of bumblebees, given the present preponderance of honeybees and their broad-ranging pollinating abilities. Native bees also utilise exotic plants and weeds (Dollin *et al.* 2000). The doubt is reinforced by various authorities. Hanley & Goulson (2003), relative to the Tasmanian situation, state that:

‘this clear preference [of exotic bees] for introduced weeds is insufficient in itself to determine whether the spread of weeds is in fact facilitated by exotic bees’

(see also Butz Huryn & Moller (1995), Butz Huryn (1997), Perley *et al.* (2001), Goulson (2003b). Butz Huryn (1997) argues that

‘most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic, or primarily reproduce vegetatively.’

Therefore it is only sleeper weeds that need consideration. It has been implied that the lack of a suitable pollinator is the only reason that some alien plants have not or will not become major weeds (Hanley & Goulson 2003). This is far too simplistic. It should be made clear that only a few of these weeds are ‘sleepers’ because they lack a suitable pollinator. There are likely many reasons why spread of a particular weed species has not occurred. Similarly, the fact that a weed such as tree lucerne is more of a problem in New Zealand than it is in Tasmania and mainland Australia, does not necessarily make *B. terrestris* the missing link. In New Zealand, it has been a cultivated species for over 100 years and has been widely planted. Nor is it a major problem in its original habitat, where several species of bumblebees are present. Herbivory, pests and diseases, opportunity, commercial value, spread by humans and many other factors come into play. Information on some of the more important weed species are discussed in more detail here. Many of the weeds of concern in New Zealand and Tasmania are a problem primarily because few people are attempting to control them, not because efforts are failing.

Most weeds do not rely on insect pollination for seed set or spread

Tree lupin, *Lupinus arboreus*, is listed as a potential environmental weed in Australia (<http://www.weeds.gov.au/>). It is a native of California and was introduced to stabilise sand dunes in New Zealand, Tasmania and Australia. In New Zealand, it is now considered only a minor weed. Its usefulness as a sand-dune stabiliser was compromised by anthracnose, *Colletotrichum lupini* (Douglas *et al.* 2004). Another anthracnose species, *C. gloeosporioides*, is present in Western Australia (http://www.clima.uwa.edu.au/_data/page/921/2005-2006_annual_report3.pdf) and in Tasmania ([http://www.dpiw.tas.gov.au/inter.nsf/Attachments/JCOK-64GA7P/\\$FILE/Qtine_Update_April04.pdf](http://www.dpiw.tas.gov.au/inter.nsf/Attachments/JCOK-64GA7P/$FILE/Qtine_Update_April04.pdf)), which might limit tree lupin spread there. Tree lupin is established in small pockets in Victoria

and is regarded as a sleeper weed. It was introduced into Tasmania in the 1920's, also to stabilize sand dunes, and has naturalised in scattered, but extensive populations (Stout *et al.* 2002). It has previously been discussed in the Tasmanian context (Section 5.3.3). As it appears to be kept well under control by anthracnose, any weed threat appears to have abated.

Hanley & Goulson (2003) quoted Stout (2000) and Stout *et al.* (2002) as claiming that both *L. arboreus* and *C. scoparius* are self-incompatible and rely entirely on pollination by bumblebees in order to reproduce. Nowhere is this stated in either paper. They also quote Stout *et al.* (2002) as determining that seed set in *L. arboreus* has increased in Tasmania as a result of the recent introduction of *B. terrestris*. This is misleading as this study showed no significant difference from seed set achieved by honeybees. Honeybees and bumblebees were rarely at the same sites. The authors actually concluded that the spread of *B. terrestris* may not alter the fecundity of *L. arboreus*, because of the pollination service already provided by honeybees. While bumblebees are also an effective pollinator (Stout 2000), the numerical superiority of honeybees makes them the most important and more contentious pollinator. Individual bumblebees in Stout's study visited only a small number of flowers per plant, whereas honeybees are favoured by being collectively flower constant.

Stout *et al.* (2002) quote Kittelson & Maron's (2000) investigation into seed set in tree lupin, stating that dehiscence occurs five weeks after pollination (actually 5-7 weeks), but then they assessed seed set only two weeks after observing bee visits. This suggests that there may not have been a direct relationship between bee visitation rate and the seed set measured. This was a limited study which took place in November and December 1999, giving rather ambiguous results.

Kittelson & Maron (2000) also reported that both honeybees and bumblebees (*Bombus vosnesenskii*) were the primary pollinators of tree lupin at their California site, though many small insects (ants, thrips etc.) are also found in the flowers. They found that *L. arboreus* is a self-compatible perennial that reproduces through a mixture of selfed and outcrossed pollinations. Self-pollination must be facilitated.

It is by no means certain, therefore, that *B. terrestris* has had, or will have, any impact on spread of tree lupin in Tasmania and no claims for such can be made for the mainland, particularly as honeybees are similarly ubiquitous. Susceptibility to anthracnose should also limit spread of this weed.

Tree lucerne, *Chamaecytisus palmensis* = *Cytisus proliferus*, is native to the Canary Islands. It was introduced to New Zealand from California in the late 19th or early 20th century, and is regarded as a useful fodder and bee forage plant, though also as an environmental weed requiring management. It was also introduced into Tasmania and mainland Australia as a fodder crop, and is highly valued as such and still promoted for this purpose (Fowler *et al.* 2000):

<http://www.dpi.nsw.gov.au/agriculture/field/forage-fodder/crops/tagasaste;>

<http://www.weeds.asn.au/weeds/txts/treelucerne.html;>

<http://www.eddept.wa.edu.au/deo/midlands/Landcare/liyh/treefarming.htm;>

[http://www.envbop.govt.nz/land/media/pdf/lm19.pdf.](http://www.envbop.govt.nz/land/media/pdf/lm19.pdf)

Currently, tree lucerne exists as mid-to-large stands in higher rainfall areas of Victoria, South Australia, Western Australia, and New South Wales. Both bumblebees and honeybees acted as nectar robbers in tree lucerne in New Zealand, though bumblebees were the most efficient pollinators (Webb & Shand 1985). Self-pollination was also possible. Pod production in the latter study was found to vary greatly between

branches of individual trees and also between trees. The number of mature seeds per pod (~5) is similar to figures given by Stout *et al.* (2002) and Hergstrom *et al.* (2002) for *L. arboreus*, and seems to be a constant 50% of initial seeds. The seed production per pod is thus relatively stable, but this needs to be balanced against the proportion of flowers setting pods, which can be quite low. Only 5% of the ovules of a naturalised population and 16% of a cultivated population developed into viable seeds (Webb & Shand 1985).

Tree lucerne flowers in late winter/early spring, peaking in August and September. This would be a time when only a few overwintered queen bumblebees would be foraging, together with honeybees and honeyeaters (<http://www.esc.nsw.gov.au/Weeds/Sheets/trees/T%20Tree%20lucerne%20or%20tagasaste.htm>), which collect only nectar. Thus, *B. terrestris* would be likely to contribute very little to increased seed set. The level of concern expressed does not appear to be matched at a State level. Tree lucerne is not a declared weed in Tasmania (<http://www.weeds.asn.au/weeds/txts/treelucerne.html>), and the NSW State Government is still promoting it as a fodder crop (<http://www.dpi.nsw.gov.au/agriculture/field/forage-fodder/crops/tagasaste>).

Scotch broom, *Cytisus scoparius*, is an invasive species in native vegetation in Tasmania (<http://www.dpiw.tas.gov.au/inter-nsf/>). It was introduced into Australia around 1800 as an ornamental, and is now naturalised on over 200,000 ha, mostly in Victoria, with 10,000 ha in NSW in the Barrington Tops (http://www.weeds.crc.org.au/documents/broom_management.pdf) (see also 1998 Broom Management Workshop, 2000). It also occurs in South Australia and Tasmania (Memmott *et al.* 1993) and is a declared noxious weed. The population dynamics of Scotch broom in its native range are strongly influenced by its natural enemies (Parsons & Cuthbertson 1992; Memmott *et al.* 1993; Fowler *et al.* 2000). It is thus the target of a number of biological control programs, currently hampered in New Zealand by the fact that potential agents also attack tree lupin and tree lucerne, considered of some value (Fowler *et al.* 2000).

Research in Japan (Suzuki 2003) and the United States (Parker *et al.* 2002) identified honeybees as one of the main pollinators of Scotch broom. At Parker's 1997 study sites in Washington State (Parker 1997), broom was very pollinator-limited. Visitation rate to flowers by a suite of five bumblebee species and honeybees was low (3-30%) and differed between sites and year. Hand pollination experiments giving much higher fruit production suggested that this species was pollinator limited. However, Knight *et al.* (2006) caution that such pollination experiments are not a reliable indicator of potential increase in propagule pressure by an additional pollinator. In California, honeybees were the main visitors to Scotch broom, with only one *Bombus vosnesenskii* observed in 72 hours of observation at each of two sites (Parker *et al.* 2002). The flower visitation rate was very low. Parker & Haubensach (2002) also found *C. scoparius* to be pollinator-limited in central California. In this case, honeybees, *Xylocopa* sp. and *Bombus vosnesenskii* were observed visiting, but species were not categorized as to relative visitation rates. Results were site-specific.

Stout (2000) studied pollination of *C. scoparius* in the UK at two nearby sites where it was the only major forage resource. Visitation rate by primarily *B. terrestris* was low and open flowers were preferred over untripped ones. Honeybees were not much in evidence, but unstated was that Varroa mite had been present for 8 years and few feral honeybees remain. Honeybees were much more efficient pollinators of broom at Barrington Tops, NSW, where 84% of flowers set fruit after a single honeybee visit, higher than the 33% in Japan and suggesting site specific effects (Simpson *et al.* 2005). This underlines the site-specific nature of pollinator-plant interactions, and the dangers of generalizing from very limited studies, for both honeybees and bumblebees.

Scotch broom is pollinated by honeybees and is not pollinator-limited in Barrington Tops, NSW. Bumblebees will therefore not increase its weediness

Additional pollination services to broom in Australia by a single species of bumblebee, which may or may not become abundant, is therefore very questionable. Parker & Haubensak (2002) also concluded that:

‘the role of mutualisms in promoting or restraining invasions is likely to vary considerably among invaded communities’.

Modelling of broom populations at Barrington Tops by Stokes *et al.* (2006) suggested that the addition of *B. terrestris* would cause no change in areas already heavily infested by broom, as is typically the case in invaded areas in Australia. In New Zealand, broom is not visited much by bumblebees (pers. comm. B. Donovan, R. Read, N. Pomeroy, T. Marais, J. Thompson, Auckland, October 2007).

Bee keepers regard broom as a good source of pollen for their honeybees. Broom is such an entrenched, intractable and successful invader that the addition of bumblebees is unlikely to make any significant difference to the problem. It seems to have done rather well for itself and will best be controlled by a biological control program. Containment of spread of scotch broom in any new areas is still an essential weed management tool.

Hingston has recently implicated bumblebees in the spread of *Agapanthus*, *Buddleia*, *Rhododendron* and white-edged nightshade, *Solanum marginatum*, in Tasmania, prior to research being conducted, and without any pre-bumblebee baseline data on the distribution and abundance of these plants (Aussie Bee <http://www.zeta.org.au/~anbr/bumblebees-and-weeds.html>). His conclusions have been broadcast to the media before a scientific study has been conducted. It is misleading to imply that the four plant species are invasive in other parts of the world as a result of bumblebee pollination. Other pollinators and factors play a substantial role in their weed status, and their invasiveness in many areas is highly questionable. *Buddleia* is mostly adapted to butterfly pollination (hence its common name of butterfly bush), *Agapanthus* and *Rhododendron* are still being extensively planted and sold from nurseries, and an annual *Rhododendron* festival is being promoted in Blackheath, NSW. One presumes these weeds are quite easy to find in the bush and remove, if indeed they are considered a present or future problem.

No evidence has been presented for bumblebees feeding on white nightshade, *Solanum marginatum*. While bumblebees are buzz pollinators, and useful for tomato pollination when they are presented with a monoculture of them, *Solanum* spp. provide only pollen and not nectar (hence a sugar supply is needed in commercial hives) and are not preferentially visited in the wild. None of these four weed species is mentioned as a problem weed in New Zealand, despite the presence of four species of bumblebees, including *B. terrestris* (see Butz Huryn & Moller (1995) re: honey bees and weed spread).

Rhododendron, *Rhododendron ponticum*, has been highlighted by opponents of the submission as an emerging weed likely to be made worse by the introduction of bumblebees. This is based on proliferation of exotic rhododendrons in the UK and Ireland, where they have been extensively planted for many years as an ornamental and as a windbreak (Stout *et al.* 2006; Stout 2007a, b). It has been and continues to be propagated and sold by the Nursery Industry in Australia. The potential distribution area is probably quite limited; however, if there are genuine concerns about this plant, then this practice should end, and an eradication program should be implemented. There are no bumblebees in the Blue Mountains, but if rhododendrons are becoming weedy there, this begs the question of why such obvious weeds are allowed to proliferate. The reason

that *Agapanthus* and *Rhododendron* appear to have increased in Tasmania since bumblebees arrived may be independently a result of exceeding a critical propagule pressure (Holle & Simberloff 2005; Lockwood *et al.* 2005; Simberloff 2005), and/or because of extensive planting.

Agapanthus, *Agapanthus praecox* Hingston (2006b) conducted a short term study on *Agapanthus praecox* and concluded that bumblebees were probably the major pollinator of *Agapanthus* in suburban Hobart. The experimental methodology was poorly constructed and the conclusions not scientifically provable (see Section 5.3.3). *Agapanthus* was establishing feral populations prior to the arrival of bumblebees. Claims have since been made implicating bumblebees in their increased weediness, but this study does not demonstrate either increased weediness, or that bumblebees are responsible for this.

White hedgenettle, *Solanum marginatum*, is already a problem weed in Australia, where it was first introduced in the early 1900's. It spreads rapidly by vegetative means as well as by seed. There does not appear to have been any study carried out in Australia on pollination mechanisms, but large numbers of fruit and seeds have been reported (Silverleaf nightshade. NSW DPI Primefact 237, 2007), suggesting that this plant may not be pollinator-limited. While bumblebees may be able to buzz-pollinate *Solanum* species, this does not make them a preferred food source that is frequently visited. Most *Solanum* species have small, single flowers which would be accessed only for pollen, since they do not provide nectar (Anderson & Symon 1988; Martine & Anderson 2007). As yet, no association has been shown between bumblebees and the increased population of this weed, which is subject to a Statutory Weed Management Plan in Tasmania. There are a great many species of *Solanum* in Australia, both introduced and native, which are visited by a wide range of native bees (Anderson & Symon 1988; Dollin *et al.* 2000; Martine & Anderson 2007). Moreover, many Australian bees are buzz pollinators, including *Amegilla*, *Xylocopa*, *Lestis* and *Nomia*, and others extract pollen by larceny. *Trigona* is also a common pollinator. Thus *Solanum* species are in all likelihood not pollinator-limited in Australia, and bumblebees would thus not contribute to any increased spread.

Australia has many buzz-pollinating native bees which already pollinate *Solanum* species

Himalayan balsam, *Impatiens capensis*, is a weed of lake and stream banks and moist areas, so it is unlikely to be a problem weed in mainland Australia. We can find no listing for it as occurring as a weed or otherwise within Australia. It has been present in New Zealand since 1909 and is described merely as 'adventive', despite four species of bumblebees being present (http://www.nzpcn.org.nz/exotic_plant_life_and_weeds/detail.asp?WeedID=1721). Pollinators elsewhere include several species of bees, 10 moth species and wasps (Mumford 1988; Beerling & Perrins 1993).

Japanese honeysuckle, *Lonicera japonica*, is a problem weed already in parts of Australia, as it is in New Zealand. In New Zealand and other countries it primarily spreads vegetatively. Fruit and seedlings are rare in New Zealand (Williams & Timmins 1997), and in the US (Larson *et al.* 2002) despite bumblebees being present. Several pollinators, including various bees and particularly nocturnal hummingbird moths, are known to effect pollination in Japan, with increased seed set reported but not measured (Larson *et al.* 2002). Seeds require a 60 day period of dormancy at 5-8° C to germinate, thus it is extremely unlikely that any increased seed set of *Lonicera* by bumblebees will be an issue in Australia.

Other weeds mentioned

Leucaena is essentially a tropical species which has spread from Darwin to northern NSW. Eco-climatic overlap looks rather unlikely. Gorse and foxglove were low on the list of visited preferred weeds in New Zealand (Hanley & Goulson 2003). Honeybees also visit them. Despite a recorded increase in seed set of greater trefoil in Tasmania, this plant requires high rainfall and grows mostly along roadsides (Hergstrom *et al.* 2002), so has limited potential for invasiveness in mainland Australia. Desmodium spp. are semi-tropical and tropical, self-pollinating, and contain important cultivated forage plants, so they do not appear to be relevant. Senna contains both native and exotic species which exist primarily in semi-tropical and tropical areas. Senna acclinis is an endangered native species pollinated by several native buzz-pollinating bees (Williams 1998.) Because several buzz-pollinating bees (e.g. Amegilla, Xylocopa, Amphylaeus, Hylaeus, Lasioglossum) already exist in Australia which service buzz-pollinated plants such as Solanum and Senna, these plants may well not be pollinator-limited (Anderson & Symon 1988; Martine & Anderson 2007). Polygala myrtifolia is widely cultivated in gardens in Australia and is reportedly a prolific seed producer in the absence of bumblebees. In its native South Africa it is visited by Xylocopa, a carpenter bee, which has representatives in Australia. The flowering period is September/October, when only queen bumblebees would be foraging. Fabaceae, Boraginaceae and Lamiaceae contain many genera in Australia and have no specific requirements for bumblebee pollination as far as we are aware, though their flower architecture suggests that they are more likely to be favoured by long-tongued bumblebee species than by the shorter-tongued B. terrestris.

Published information on named 'sleeper' weeds gives no credence to claims that importation of B. terrestris will 'awaken' them on the mainland

Thus, as indicated in the original submission, unless evidence is provided of plants likely to be elevated to notable weediness by bumblebees, we must assume that no association is known. Those suggesting many of these weeds do not appear to be familiar with their biology or pollination requirements.

Gene flow in weeds Gene flow can be promulgated by many insects other than bees. Flower-inhabiting thrips, for example, both native and introduced, can carry pollen over large distances as they are often wind-borne. Individually they may carry few pollen grains, but because they can occur in plague proportions their total impact may be larger. Their contribution is largely ignored, yet they may have a substantial role to play in pollination of weeds (Faegri & Pijl 1979; Terry 2001). No-one has so far considered their role in pollination and outcrossing rate, nor become emotive about alien species, of which there are many. Bumblebees do not forage far from their nests and tend to flower constancy (Goulson 1994, 2003a ; Gegear & Thomson 2004; Gegear & Lavery 2005), so they will effect gene flow far less than honeybees and some other anthophiles.

Conclusion

Published information on 'sleeper' weeds cited as being most at risk of spread by B. terrestris gives no credence to the claims that importation of B. terrestris will result in a substantial increase in their spread. Further comments and conjecture about other weeds on the list would appear to be unproductive until and unless some serious consideration is given to the real likelihood of interaction with B. terrestris. Information is particularly needed on weed pollination mechanisms, climatic overlap and likely bumblebee abundance. The Weeds CRC, although asked, did not provide any information on pollination mechanisms of weeds that were specified as at risk of spread, nor their current distribution, nor potential distribution based on ecoclimatic modelling. It is therefore difficult to make any quantitative or qualitative assessment of the real 'risk' posed by B. terrestris. The AHGA is sympathetic to the immensity of the general weed problem in

Australia, but believes that the provided list of weeds deemed at risk of specialist pollinator services was not well considered. In any case, it does not accept that in reality there will be any increased risk of spread of ‘sleeper’ weeds, given the precautions for containment outlined in Section 10, the low risk of feral establishment and suitable climatic area for persistence, and the limited annual activity period of *B. terrestris*.

7.2. Impacts on seed set in native plants caused by nectar and pollen removal by *B. terrestris* and by potential failure of *B. terrestris* to correctly contact the anthers or stigmas

This question has largely been addressed in Section 5.3.2. with regard to Tasmania and studies conducted there, and in Section 6, regarding the likelihood of the species becoming established on the mainland. Australia has a wealth of native pollinators, far more than New Zealand, and thus few plants are likely to be pollinator-limited or specific in their requirement (Thomson 1881; Heine 1937; Armstrong 1979; Memmott & Waser 2002; Newstrom & Robertson 2005; Rodrigues 2006; Donovan 2007).

Effect on seed set Studies in Tasmania (Section 5.3.2) have found no evidence that *B. terrestris* has had any direct impact on seed set in native plants, except for a positive increase in seed set of *Epacris impressa* in one season at some sites, despite nectar robbing, and a non-significant small increase in seed set of *Gompholobium* (Hergstrom *et al.* 2002). Nor has any evidence been found of indirect impact through changes in density or behaviour of native pollinators, including native bees and birds. Several studies in New Zealand have indicated that any effects are minimal, because there is little overlap in resource use (Donovan 1980; Newstrom & Robertson 2005; Kelly *et al.* 2006). A positive impact on seed set is also possible, but more long-term studies are required to demonstrate a significant effect either way.

Nectar robbing Nectar robbing by biting holes in the base of plants with long corollas is partially dealt with in Section 5.3.2.2. Hergstrom *et al.* (2002) mentioned an unsubstantiated report of poor seed set in faba beans in Tasmania, yet research on the effects of nectar robbing on this plant is contradictory (Poulsen 1973; Newton & Hill 1983). Malouf & Inouye (2000) reviewed 18 studies of the effects of nectar robbers on plant fecundity, and found six showed a negative effect, six a positive effect, and six no effect (*see also* Goulson 2003a). Ants are very common nectar robbers and there is certainly no shortage of them on mainland Australia, in a wide range of habitats. There are 1275 described species of ants in Australia, many of which are carnivorous (Shattuck & Barnett 2001). They rob nectar both day and night, but observational studies have taken no account of their possible substantial contribution to reduced nectar flow and seed set. One must presume that plant species have evolved to effect pollination despite their visits. Some native bees such as *Xylocopa* and *Amegilla* also nectar rob, as do European wasps.

Changes in gene flow A change in population structure of native plants through a different pattern of pollen transport by non-native bees has been raised as a possibility (Goulson 2003a, b). This is effected by differing distance of movement between plants by various pollinators. For bird-pollinated plants, a change to bee pollination may promote self-pollination rather than cross-pollination, as birds may travel further between flowers. Such studies are very difficult to conduct and effects hard to detect. There is presently no data for or against such a contention in relation to bumblebees. Because most plants are serviced by many pollinator species, it is unlikely that changes in gene flow will be

significant. The role of thrips in gene flow has also not been considered.

Effect of floral preferences on visitation rate and seed set Floral preferences of native bees are reviewed by Armstrong (1979) (see also the original submission to import *B. terrestris* (Goodwin & Steiner 1997 URL: <http://www.tmag.tas.gov.au/workshop/append2.html>)). Although native pollinators are presumed to be better adapted at pollinating native plants than bumblebees and honeybees, this is not necessarily so (Butz Huryn 1997; Goulson 2003b). There is a paucity of information on the suite of pollinators for any given native plant species, but a specialized relationship between plants and pollinators is the exception rather than the rule. Honeybees and bumblebees exhibit a degree of flower constancy (Goulson 1994, 2003a; Gegear & Thomson 2004; Gegear & Lavery 2005; Benton 2006) and tend to work trap lines, but for bumblebees this pertains more to preferred, introduced plants than to native ones. Little is known of the habits of native bees in this regard, but it is likely to be variable between species (Hingston 1999). There may actually be improved pollination of some native plant species by exotic bees, to the overall benefit of all (Butz Huryn 1997; Memmott & Waser 2002). Again, whether an impact is significant or negligible depends on both the presence and abundance of *B. terrestris* at critical periods.

In New Zealand, a report to the New Zealand Ministry of Agriculture and Forestry (Perley *et al.* 2001, see <http://www.maf.govt.nz/mafnet/rural-nz/sustainable-resource-use/biodiversity/convention-on-biological-diversity/>) concluded that:

‘there is not a single intensive study that demonstrates that pollination failure influences population dynamics of either rare or abundant native plants. Most threatened plants are impacted by introduced grazers and habitat loss rather than lack of pollination’.

Kelly *et al.* (2006) argued against the importance of introduced animals as pollinators and dispersers of native plants in New Zealand, because native plants were seldom visited.

No negative effect on seed set of native plants has been documented

Conclusion

Limited studies in Tasmania to evaluate whether *B. terrestris* affects seed set in native plants through nectar robbing or pollen and nectar harvesting found no discernible effect except for a slight increase in seed set of *Epacris impressa* and *Gompholobium*. By extrapolation and from existing knowledge of the biology and foraging preferences of *B. terrestris*, no significant effect on seed set of native plants on the mainland is anticipated.

7.3. Impacts on native bee and native insect pollinators from competition from *B. terrestris* The broad distribution and abundance of honeybees on mainland Australia, and controversy surrounding their impact as competitors of native pollinators, has led to attempts to link the potential of *B. terrestris* to establish and impact similarly. It has also been suggested that bumblebees will have an add-on effect, removing whatever narrow window remains for foraging opportunities for native pollinators. These are incorrect assertions and we therefore consider it important to remove the linkages between these two quite separate species.

Honeybees in the mainland environment Honeybees have been present in Australia since 1826 (Doull 1973; Paton 1996). There are at least 500,000 managed hives in Australia that contribute to the honeybee population every year (Paton 1996), as well as unknown numbers of feral bees. At least two subspecies were introduced to broaden the climatic range that they could inhabit. While the high numbers of honeybees in some areas would suggest that competition with at least some native animals and some impact on native

plants may be occurring, data presented in support of this is equivocal (Paton 1993; Paton 1996; Manning 1997; Schwarz & Hurst 1997; Horskins & Turner 1999; Goulson 2003a; Paine 2004; Moritz & Hartel 2005). Paton (1996), Manning (1997) and Paine (2004) in particular provide excellent reviews of research conducted on the impact of honeybees in Australia. They reported that much published research in Australia is of limited value because experiments were poorly designed or not conducted over enough sites or time periods to produce clear-cut evidence of an impact. Butz Huryn & Moller (1995) and Butz Huryn (1997) made a similar assessment in New Zealand. The add-on effects of habitat fragmentation and destruction with competition for limited resources would suggest that native birds may be more vulnerable to competition than native bees.

Any impact of B. terrestris will be negligible compared with that of the much more populous and widespread honeybee

Suggestions for protocols for in-depth studies on native flora and fauna are given in Paton's (1996) comprehensive review and in Paine (2004) and should be promoted to provide some definitive background information on which to make proper assessments of the impact of change. Regrettably, it is difficult to escape the conclusion that these much needed studies are being put in the 'too hard basket' in favour of headline-grabbing, very limited studies designed to galvanise public opinion against bumblebees.

Comparison between bumblebees and honeybees It is not planned to introduce bumblebees into the environment except in greenhouses. Even with escapes, a CLIMEX study (Figure 7, Appendix I) (McClay 2005a, also Section 6.5) predicts that potential establishment of *B. terrestris audax* will be restricted to temperate areas in the southeast of the country. Limited research on *B. terrestris* in Tasmania, and years of co-existence in New Zealand and in their natural range, suggests that honeybees will always be more populous and widespread than bumblebees. Colonies of honeybees last several years, can be very large, and often contain thousands of individuals which forage all year. Bumblebee colonies exist for less than a year and contain at most hundreds of individuals, which actively forage for only 3-4 months. Honeybees collect nectar and honey not only for present need, but to store for future need. Bumblebees collect only for immediate needs, so have no stores to tide them over shortages. There are major differences in foraging preferences and communication abilities. Any impact, either positive or negative, will be on a much smaller scale than that of commercial or feral honeybees. Honeybees, in themselves, may negatively impact on bumblebees at shared food resources (Holmes 1961; Eickwort & Ginsberg 1980; Thomson 2004, 2006; Goulson & Sparrow 2008).

Any competition with native flower-visiting insects is anticipated to be limited and transitory

Bumblebees and native pollinators It is difficult to see that any case for significant competition of bumblebees with native bees and birds has been or could be sustained. The only relevant studies on bumblebees in Tasmania (Section 5) show no impact on native bees or birds, despite claims to the contrary. Most native bees reproduce in late spring and summer when floral resources are plentiful, lessening the impact further. Despite differences in climate and floral and native bee diversity, New Zealand is an example of successful integration of *B. terrestris* into the natural environment. No-one has accused bumblebees there of being the equivalent of a rabbit, possum or European wasp. Their benefits as a pollinator of forage, fruit, and vegetable crops in greenhouses are widely acknowledged. Similarly, the leafcutter bee *Megachile rotundata* was introduced into South Australia in the 1980's for lucerne pollination (Woodward 1994, 1996; Anderson 2006), with no known negative effects on the natural environment; it is not abundant and has remained narrowly distributed. The fact that a bee is not native does not necessarily imply a negative environmental impact.

Aussie Bee, a website committed to appreciation of native bees, has devoted

several articles to encouraging opposition to importation of *B. terrestris*, while completely ignoring information attempting to present a more balanced view (Carruthers 2004). It also devoted an article to the pleasures of assisting in the export of several nests of the Australian native bee *Trigona carbonaria* to Japan in 1999 and 2000, despite knowing the species was exotic to that country (<http://www.uq.net.au/~zzrzabel/our-bees-in-japan-2.htm>), perhaps suggesting a need for greater objectivity on their part.

Conclusion

On the basis of known biological traits of *B. terrestris*, the experience of 130 years of occupation of New Zealand and 16 years in Tasmania with no demonstrable negative effects, and predicted limited distribution on the mainland, any competition with native anthophiles is anticipated to be limited and transitory. Suggestions have been made that bumblebees will have a similar or add-on effect to that of honeybees in the Australian environment. While both are exotic bees, there are major differences in their biology which will limit the temporal and spatial abundance of bumblebees compared with honeybees and greatly reduce opportunities for competitive interaction with native insects.

7.4. Impacts on native vertebrates that utilize nectar and pollen resources from competition with *B. terrestris*, especially threatened species

It has been suggested that birds and some mammals may potentially be impacted upon by competition with *B. terrestris*. The arguments that have been made in the previous Section with respect to limited competition with native bees also apply to native vertebrates. Factors suggestive of competition that may lead to a negative impact are abundance of the exotic bee, high levels of niche overlap, evidence of resource depression, and displacement of the native pollinator. Whether this effect is temporary or sustained is also critical. Very similar accusations of negative impact have been made against honeybees over many years. A review of research and arguments in the honeybee debate are put forward by Paton (1996), Manning (1997), and Paini (2004) in Australia, and by Butz Huryn & Moller (1995) and Butz Huryn (1997) in New Zealand. They should be required reading, as many of the protocols suggested for more definitive experimental studies are also relevant to bumblebees.

Hingston and various co-workers claimed a severe negative impact on the threatened swift parrot, *Lathamus discolor*, and eastern spine bill, *Acanthorhynchus tenuirostris*, in Tasmania. This is refuted in Section 5.3.2.3. Birds supposedly at risk on the Australian mainland are again the swift parrot, the helmeted honeyeater, *Lichenostomus melanops cassidix*, and the regent honeyeater, *Xanthomyza phrygia*. A review of research relevant to named 'birds at risk' in mainland Australia follows to put these claims in perspective.

The Swift parrot includes parts of Victoria and New South Wales in its winter range, where it depends largely on dry forests and woodlands of box-ironbark for nectar. Bumblebees, even if present, hibernate during this period, so the issue of competition and any impact is irrelevant. For the two honeyeaters, no research has been conducted on any association with bumblebees. The Federal Threatened Species Scientific Committee (2003) concluded that:

‘No information is currently available to determine the extent of any possible impact on these honeyeaters due to bumblebees should they become established in mainland Australia’.

The Regent honeyeater is restricted to drier open forests and woodlands of south-eastern Australia. Their decline is almost entirely due to habitat fragmentation and massive land clearing. This species is very dependent on four key eucalypt species (*E. albens*, *E. melliodora*, *E. leucoxyton*, and *E. sideroxyton*) for nesting habitat and nectar, which have been widely cleared and harvested. Insects are also a necessary dietary component. Honeybees have been mentioned as potential competitors for the remaining nectar, but these too would appear to be scapegoats for the degradation caused by human activity. It is difficult to see how bumblebees could in any way be considered a threatening process, particularly in dry eucalypt forests.

The Helmeted honeyeater is endemic to Victoria and is now extremely rare. These birds inhabit streamside lowland swamp forest, feeding on insects and sugary secretions from manna, lerp and honeydew. They also take nectar from eucalypts and fruits when available. As with other critically endangered species, the decline has been caused by extensive destruction of their habitat by man. Some remnant patches have been destroyed by fire. The native bell miner, *Manorina melanophrys*, is also named as a threat. Honeybees are *not* mentioned as a threat; it is highly improbable that bumblebees will be. This did not prevent an attempt to have *B. terrestris* listed as a Key Threatening Process under the *Federal Environment Protection and Biodiversity Conservation Act 1999*, which was officially rejected.

Despite the lack of evidence of any existent or likely threat, State Governments in Victoria and NSW were persuaded to include *B. terrestris* as a key threatening process in their legislation for all three bird species (see Sections 8 and 9).

Conclusion

There is no evidence to implicate bumblebees as a threat to native birds feeding on nectar and pollen. It is abundantly clear that man is the key threatening process for bird species such as swift parrot, helmeted honeyeater and regent honeyeater, through land clearing, fire, and resultant habitat loss.

7.5. The potential impacts on the lifestyle and health of humans should *B. terrestris* establish in or near human settlements

Despite all the negative publicity emanating from some elements in Tasmania, bumblebees are generally popular with the public there, as they are in other countries (http://findarticles.com/p/articles/mi_qn4158/is_20060527/ai_n16436889). There are many programs in the UK and Europe aimed at encouraging children to study and work with bumblebees (e.g. Griffiths & Robberts 1996; Kwak 1996; Goulson & Darvill 2006), which does not suggest that they are a hazard. Websites devoted to encouraging bumblebees around homes and gardens are numerous. Bumblebees are defensive when nests are invaded, but are not aggressive (Prÿs-Jones & Corbet 1991); their nesting sites are seldom observed and are located where they will rarely be disturbed accidentally.

While bumblebee queens and workers (not males) are capable of stinging, this is a rare occurrence. Stings are no doubt painful, but there are no after-effects for the great majority of people. Nevertheless, anyone with an allergy to honeybees (cross-allergy does not necessarily occur) should take the relevant precautions (Riches 2003). Millions of bumblebees are released annually into greenhouses while workers are in the crop, and

There is no evidence to implicate bumblebees as a threat to the Swift Parrot and other endangered native birds feeding on nectar and pollen. Man is clearly the key threatening process

stings are not common. Similarly, bumblebees are handled in mass production facilities with no protective equipment. *Aussie Bee*, an Australian website devoted to improving knowledge of native bees, reports (<http://www.zeta.org.au/~anbrc/bumblebeeharm.html>) that:

‘Bumblebees can sting repeatedly and they defend their nest ferociously. Reactions to stings include severe itching, swelling, nausea, vomiting, defecation, difficulty in breathing, low blood pressure and loss of consciousness. Fortunately severe reactions to stings are rare but bumblebees can sting without provocation. ‘

This is completely and provocatively misleading. It is atypical behaviour for a bumblebee and describes the reaction of someone with a severe allergy to bee venom. This issue has been addressed in several recent international publications, which make clear that the risk to the general public is considered negligible and that appropriate treatment is available if necessary (Kochuyt *et al.* 1993; Jong *et al.* 1999; Stern *et al.* 2000; Bucher *et al.* 2001; Bilo *et al.* 2005 a, b; Bonifazi *et al.* 2005a, b; Roll & Schmid-Grendelmeier 2005; Groot 2006). Occupational exposure from the widespread use of bumblebees in greenhouses necessitates a contingency plan in case of allergic reactions, as is the case with those who work with honeybees or are known to be sensitive to bee or wasp stings (<http://www.koppert.nl/cgi-bin/x0127.pl?lang=e>). We have seen no reports from New Zealand or Tasmania that would indicate the public has any special concerns about being stung by bumblebees, indeed a few people we spoke to in Tasmania reported hand-collecting them to take home with them.

In another article on native bees (<http://www.zeta.org.au/~anbrc/faq.html>), *Aussie Bee* reports that 1490 Australian native species can sting, and that they can sting more than once and it is possible to be allergic to the sting. Presumably this is not much of an issue.

Conclusion

Reports emanating from a small core of people in Tasmania and Australia, that bumblebees are a menace because they sting aggressively and repeatedly, are completely at odds with global experience of their generally non-aggressive nature, and the positive public image of them around the world, where they are an accepted and common inhabitant of gardens and countryside. The risk of being stung is negligible, and primarily related to occupational exposure for those working closely with them. Treatment of people with specific allergies is similar to that for honeybee stings.

Summary of Section 7

Consideration of the possible areas of impact of *B. terrestris* on mainland Australia suggests that *Bombus terrestris* will not constitute a threat to native bees, other pollinators, native plants or people, any more than it does in its native range or adoptive ranges. Recent claims of negative impact in Tasmania have been based on conjecture and poor science, and have ignored the wealth of published scientific literature on the biology and ecology of this species. In the unlikely event that *B. terrestris* establishes significant feral populations in mainland Australia, the only conceivable negative consequence is spread of some weeds, though this has yet to be demonstrated, and would depend on substantial populations and pollination services over and above that of the common honeybee. Of those weeds suggested as sleeper weeds by the CRC, none was shown to be at risk of increased spread.

Bumblebees are non-aggressive. They sting only rarely, as do many native bees. Honeybees are a much grater hazard in this regard

Recent claims of negative impact of bumblebees in Australia are based on unsupported conjecture and poor science

8. OTHER RISK ASSESSMENTS UNDERTAKEN ON THE SPECIES

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8.1. Commonwealth risk assessment. The Department of Environment and Heritage received a nomination in 2001 of a Key Threatening Process under the *Environment Protection and Biodiversity Conservation Act 1999*, for ‘Changes to plant-pollinator associations caused by bumblebees, *Bombus* spp.’. The nomination was considered by the Threatened Species Scientific Committee (TSSC), and was rejected (the full response can be found on <http://www.deh.gov.au/biodiversity/threatened/nominations/bumblebees.html>). An attempt was made by the instigators of this nomination to have it considered before the environmental impact study in Tasmania was completed (Hergstrom *et al.* 2002) and without notifying researchers and other interested parties of their intention. It is to the credit of the committee that it awaited the results of this study and gave due consideration to submissions both for and against the nomination. The questions and conclusions are as follows:

A. Could the threatening process cause a native species or an ecological community to become eligible for listing as Extinct, Extinct in the Wild, Critically Endangered, Endangered or Vulnerable?

Conclusion: Based on the information provided and summarized above, TSSC considers that while potentially invasive, the ecological effects of this process on unlisted native species and ecological communities are not clearly defined or easily predicted, and that there are few quantitative data on actual or potential impacts. The information is considered insufficient to determine whether the threatening process meets this criterion at this time.

B. Could the threatening process cause a native species or an ecological community to become eligible to be listed in another category representing a higher degree of endangerment?

Conclusion: TSSC considers that, based on the information provided and summarized above, the potential for this process to cause the Swift Parrot, Helmeted Honeyeater or Regent Honeyeater to become eligible for listing in a category representing a higher degree of endangerment, is not sufficiently known, nor easily predicted. The information is considered insufficient to determine whether the threatening process meets this criterion at this time.

C. Does the threatening process adversely affect two or more listed threatened species (other than conservation dependent species) or two or more listed threatened ecological communities?

Conclusion: Based on the evidence provided and summarized above, TSSC considers that, although the process may be adversely affecting the listed Swift Parrot, there is, as yet, no evidence of an effect; the process is not currently adversely affecting the Helmeted Honeyeater or the Regent Honeyeater; the threatening process is not adversely affecting at least two listed threatened species and is therefore not eligible under this criterion.

In reaching these conclusions, it added finally that ‘The Committee regards the introduction of any exotic species as a potential environmental risk, noting that in Tasmania, the bumblebee has become widespread in both modified and natural systems. However, on the data available, insufficient impact has been detected, and therefore the Committee recommends that the threatening process cannot be listed at this time. The Committee urges that extreme caution be shown in considering any proposal to introduce this species to the mainland. In taking this position, it highlights the concern that many native species are dependent on native pollinators, so it could potentially be a threat in the future’.

The Federal Threatened Species Scientific Committee declined to list *B. terrestris* as a Key Threatening Process in 2001 because of insufficient evidence

*The AHGA supports the need for a precautionary approach, but after further review and an extensive literature search, strongly believes there is no evidence in past or present history of *B. terrestris* to indicate that it is likely to become a pest on mainland Australia, or will impact negatively on native plants or pollinators, even without the safeguards that will be put in place regarding usage and selected subspecies.*

Conclusion

A nomination by those opposed to *B. terrestris* importation to the mainland was submitted to the DEH in 2001 to have *B. terrestris* declared a Key Threatening Process under the *Environment Protection and Biodiversity Conservation Act 1999*. The nomination was rejected on the basis that there was insufficient evidence to make such a determination at that time. In reviewing current available information (2008), we can find no evidence to suggest that this decision should be revised.

8.2. State risk assessments

New South Wales The New South Wales Scientific Committee, established by the *Threatened Species Conservation Act 1995*, made a determination in February 2004 to support a proposal to list the Introduction of the Large Earth Bumblebee, *Bombus terrestris* (L), as a Key Threatening Process in Schedule 3 of the *Act* (http://www.nationalparks.nsw.gov.au/npws.nsf/Content/Bombus_terrestris_ktp_declaration). The intent of this identification as a Key Threatening Process is to focus on issues of importance in conservation of biodiversity. The determination was made on the basis of very limited information (only six references were quoted). Reasons for the listing were given as a possible increase in the abundance and distribution of weed species, including Scotch broom, foxglove and Solanaceae, and disruption of pollination of native plant species.

By a curious process of extrapolation, the anticipated increase in Scotch broom on the Barrington Tops (already covering 10,000 ha without the aid of bumblebees, see discussion on Scotch broom in Section 7.1) will apparently endanger the native plant *Epacris hamiltonii*, the Bathurst Copper, *Paralucia spinifera*, the Ben Halls Gap National Park Sphagnum Moss Cool Temperate Rainforest Endangered Ecological Community, and the vulnerable terrestrial orchid, *Chiloglottis platyptera*. Scotch broom was not listed as a Weed of National Significance, nor as a Key Threatening Process in New South Wales, until very recently (http://www.nationalparks.nsw.gov.au/npws.nsf/Content/scotch_broom_ktp). In this listing, the NSW Scientific Committee mentions the main pollinators of Scotch broom as honeybees and *B. terrestris*, with the latter a more effective pollinator, but the three references cited in support of this claim are misrepresentations. The first study, Simpson *et al.* (2005), investigated only honeybees at Barrington Tops, NSW. The second, Parker (1997), investigated bee pollinators in California, where little pollination occurred and visitation rates by bumblebees (not *B. terrestris*) were very low. The third,

Stout (2000), was carried out in the UK, where visitation rates by *B. terrestris* were low, seed set was not determined, and honeybees were virtually absent, courtesy of the Varroa mite. A submission was made to the NSW Scientific Committee 8 January 2008 on this matter, while it was still open for public consultation, but no acknowledgement has been received, nor the inaccuracies corrected. It remains our opinion that the risk assessment efforts on these determinations have not been well-considered nor fully researched and should not be prejudicial to further determinations.

The NSW Government recently erected a Threatened Species Website (<http://www.threatenedspecies.environment.nsw.gov.au/index.aspx>), which outlines four threat abatement strategies to tackle this process. We support the removal of unauthorised or accidental arrivals of *B. terrestris*, but regret that the Department has not fully investigated the evidence available and reassessed its position on bumblebees. If they had, they could not possibly have sustained this recommendation.

Victoria The introduction and spread of the large earth bumblebee *Bombus terrestris* into Victorian terrestrial environments was listed in September 2000 as a potentially threatening process under the *Victorian Flora and Fauna Guarantee Act 1988* (FFGA) (<http://www.dpi.vic.gov.au>). The following recommendation was made:

‘Bumble bees may compete with nectarivorous birds (honeyeaters e.g. Regent Honeyeater and Helmeted Honeyeater), specialized parrots (lorikeets and the endangered Swift Parrot *Lathamus discolor*), some native mammals (Pygmy-possum and Sugar Glider) and endemic bees, thus reducing the reproductive output of these native flower-loving fauna.’

Only two references are quoted, with no supporting evidence. The FFGA provides for listing of a Threatening Process, with delisting a possibility. A follow-up Action Statement has apparently not been made. We hope that the Department will reconsider its position after reviewing the wealth of information available in this document.

The Departments of Agriculture/Primary Industries in WA and QLD have fact sheets that reiterate the same misinformation about *B. terrestris* being a serious pest that stings repeatedly, but regrettably fail to mention the minimal risks of this occurring.

Summary of Section 8

The States of Victoria and New South Wales enacted legislation in 2000 and 2004, respectively, declaring the introduction of the large earth bumblebee, *B. terrestris*, a threatening process in their States. The decisions were largely based on unsubstantiated claims which we believe were overly influenced by individuals or interest groups limited in their understanding and knowledge of the behaviour, ecology and biology of *B. terrestris*. These claims have been challenged in this report. In contrast, a similar nomination to the DEH in 2001 under the *Environment Protection and Biodiversity Conservation Act 1999* was rejected by the Threatened Species Scientific Committee on the basis of insufficient evidence for a determination.

9. COMMONWEALTH, STATE AND TERRITORY LEGISLATIVE CONTROLS ON THE SPECIES

General measures to control non-native incursions or introductions into Australia are outlined by Maynard *et al.* (2004) and by Animal Health Australia (2004).

9.1. Commonwealth The Terms of Reference addressed in this document are part of the process of an application by the AHGA to the Department of Environment, Water, Heritage and the Arts for import of live *Bombus terrestris* into mainland Australia. In order to amend the list of specimens suitable for live import, it is necessary to comply with the Federal *Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act)*, specifically, guidelines under Subdivision B - Assessments relating to the amendments of the list of specimens suitable for import, subsections 303 EC, ED, EE, EJ and EF (<http://scaleplus.law.gov.au/html/pasteact/3/3295/1/PA005470.htm>).

9.2. State *Bombus terrestris* is listed as a Key Threatening Process in Schedule 3 of the *NSW Threatened Species Conservation Act 1995*, and as a Potentially Threatening Process under the *Victorian Flora and Fauna Guarantee Act 1988* (see Section 8.2). These determinations follow intensive lobbying by certain parties on the basis of very limited research and much totally-biased conjecture, the rebuttal of which is addressed elsewhere in this document.

Summary of Section 9

Under Federal legislation, as an alien species, *B. terrestris* is presently excluded from importation into mainland Australia until an amendment is made to the approval list. Victoria and NSW currently have *B. terrestris* listed as a Key Threatening Process, a decision which should logically be reversed as it was made only on the basis of unsubstantiated conjecture.

10. CONDITIONS OR RESTRICTIONS THAT COULD BE APPLIED TO THE IMPORT OF THE SPECIES TO REDUCE ANY POTENTIAL FOR NEGATIVE ENVIRONMENTAL IMPACTS

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The AHGA strongly believes that there is no evidence that significant negative impacts would occur should *B. terrestris* succeed in establishing on the mainland. Potential negative effects are so far all based on conjecture, whereas positive impacts are well documented and substantial. However, in the current climate of risk-aversion relating to non-native introductions, and to allay public concerns, the AHGA recognizes the need to negate perceived risk, however small. We believe that the conditions and restrictions detailed in Section 1.4, and summarised here, could be applied to the import of *B. terrestris* to achieve this:

10.1. Usage

1. *Bombus terrestris* would only be permitted to be used in approved secure greenhouse production facilities, and *not* released into the broader environment.
2. Approved secure greenhouses would be those suitably screened at all vents to prevent escape of any bumblebees, and to have an annex at all entry points with positive air pressure.
3. Hives would be acquired only from an approved commercial company with expertise in rearing and with appropriate technology.
4. Hives would be fitted with a queen excluder device, such as is used for *B. impatiens* shipped to western North America. The fitting of a queen excluder device was a condition of moving *B. impatiens* to western States (Velthuis & van Doorn 2004a). This practice is believed to have been required, at least in Canada, when hives were originally produced and shipped in from Europe, and it has been retained. The device prevents exit of any queens, which are potential breeding stock, and is considered 99.9% effective (Richard Ward, Managing Director, Biobest, Canada, pers. comm. to M. Steiner 2005). *Bombus impatiens* is naturally confined to the east of the Rocky Mountains, but the indigenous western species, *B. occidentalis*, is unsuitable for mass rearing. Movement of *B. occidentalis* and *B. impatiens* in the USA is regulated under the Plant Protection Act (2000), which allows import of these species from Canada, and transfer anywhere in the USA within 48 States (Winter *et al.* 2006). APHIS permits similar movement (http://www.aphis.usda.gov/plant_health/permits/organism/bees.shtml).
5. Hives require no maintenance by the grower, but would be fitted with a tamper-proof metal strap. All hives would be required to be destroyed in an approved manner at the end of their functional life (usually 4-8 weeks). In a large one hectare greenhouse, the number of hives to be disposed of each week should be no more than three.

10.2. Source

1. The source of the nuclear stock of bumblebees would most likely be Tasmania. However, the genetic composition of the Tasmanian bumblebee is very restricted and it is not known what impact this may have on the success of a commercial venture. Until this is known, an option of New Zealand stock or an insemination program to widen the genetic base might be required. In both these geographic areas, only the subspecies *Bombus terrestris audax* is present. This is a temperate subspecies naturally associated with temperate climates and it is not found in hot climates, nor is it known to aestivate. Risk of feral establishment on the mainland is thus minimal in the unlikely event that all other safeguards fail. The Tasmanian population is free of all important pathogens and parasites.
2. Notwithstanding, nuclear breeding stock and any additional breeding stock required would be certified free of known pathogens and parasites. While most large commercial companies overseas now produce their own breeding stock and rarely source from the wild, other smaller operations do not. Thus, it will periodically be necessary to add to and replace stock in the Australian context for the foreseeable future. When this is required, any feral material will be kept in isolation in an approved quarantine unit and reared through at least two generations to evaluate any inherent pests, parasites and pathogens.
3. The production unit would be sited in Tasmania, or, if permitted, an area of the mainland where the climate would not support establishment of feral populations. A facility on the mainland should be permitted to ship secure hives into Tasmania, conversely, if the facility is sited in Tasmania, regular shipments of secure hives to the mainland will be necessary, as will a secure holding building.
4. The facility will be built as a secure system, comprising a queen-rearing facility, a commercial production facility and packing rooms.
5. The entrance to the hive, in which the queen excluder is situated, will be sealed within the packing unit before being put into a delivery truck.
6. Regulations would apply to greenhouse operations using bumblebees. This might include pre-approval, training, and inspection on an agreed basis as a condition of receipt, instructions for safe disposal of hives, and penalties for non-compliance.

Breeding stock of B. terrestris will be examined and certified free of known pathogens and parasites before shipment to growers

10.3. Disease-free status

To allay any concerns regarding cross-infection with honeybees and native bees, shipments will be certified free of named pathogens, parasites and nest commensals. A similar scheme exists for bumblebees going from New Zealand to importing countries such as China (<http://www.biosecurity.govt.nz/exports/animals/bees/omars/bmblebee.prc.htm>). Before leaving New Zealand, bees must comply with any specific import requirements of the receiving country, which generally include certification by an official veterinarian that tracheal mite (*Acarapis woodi*), Asian mite (*Tropilaelaps clareae*), and European foulbrood (*Melissococcus pluton*), do not occur in New Zealand, and that the honeybee diseases American foulbrood (*Paenibacillus larvae larvae*), Varroa mite (*Varroa destructor*), and Nosema disease (*Nosema apis*) are not diseases of bumblebees in New Zealand. Similarly, the Commission of the European Union requires health certification for the importation of both honeybees and bumblebees from certain third countries, requiring freedom from small hive beetle (*Aethina tumida*), and *Tropilaelaps* mite. It states that there is no evidence that *Tropilaelaps* mite can infest colonies of bumblebees, and the hive beetle has only been shown to infest bumblebee colonies under experimental conditions. The importation of bumblebees into EU countries is authorized for small consignments bred and reared under environmentally controlled conditions within

recognized establishments (queen plus 200 workers), with a recognition that bumblebees still need to be sourced from the wild (queen plus 20 attendants, queens only to be retained) (<http://www.the-apa.co.uk/Legislation/Archive/eurlx2003712.html>; <http://www.defra.gov.uk/hort/Bees/Intertrade/index.htm>; <http://beebase.csl.gov.uk/pdfs/importingbees.pdf>).

Information on parasites, pathogens and predators of *B. terrestris* is contained in the original submission (Goodwin & Steiner 1997 URL: <http://www.tmag.tas.gov.au/workshop/append2.html>) and in many other publications (Alford 1975; Lipa & Triggiani 1992; De Wael *et al.* 1993; Macfarlane *et al.* 1995; van der Steen 2000; Schmid-Hempel 2001; Goulson 2003b; Fries & Brown 2004; O'Connor 2005; Benton 2006). *Bombus terrestris* nest associates are specific to the genus *Bombus* and have not been recorded crossing over to honeybees or to any other entomological species (Whitfield & Cameron 1993; Griffiths, pers. comm. 2005). Likewise, the physical conditions, strict quarantine and production rules of a reputable commercial operation preclude the development of these agents. Also, and most importantly, known species appear to be host specific. Those of concern to bumblebees are primarily parasites such as *Crithidia bombi* (protozoan), *Locustacarus buchneri* (mite), *Nosema bombi* (protozoan), *Apicystis bombi* (protozoan) and *Sphaerularia bombi* (nematode). Brief details of these and other important bee pests are given below. While some people have argued that because we know very little about native bee diseases, we cannot preclude that they might be affected by *Bombus* diseases, this is extremely unlikely, given the unrelatedness of the species and their different lifestyles, and the lack of such associations across the range of other countries where native bees and *Bombus* co-exist.

Parasites and pathogens associated with bumblebees:

1. *Apicystis bombi*, a neogregarine protozoan, can destroy the fat body and severely reduce colony reproduction (Durrer & Schmid-Hempel 1995). It is not found in New Zealand or Tasmania.
2. *Crithidia bombi* is a trypanosome protozoan parasite inhabiting the gut of bumblebees; it can be mild or severely infect *Bombus* colonies, particularly queens in hibernation (Schmid-Hempel 2001). It does not occur in New Zealand or Tasmania. It may act against late diapausing queens where it occurs, limiting or delaying colony founding. It has not been recorded from honeybees or other bees. Increased incidence in wild bumblebees in the vicinity of commercial greenhouses in Canada was reported (Colla *et al.* 2006). Further information can be found in Imhoof & Schmid-Hempel (1999), Schmid-Hempel & Reber Funk (2004), Otterstatter *et al.* (2005), Gegear *et al.* (2005, 2006), Yourth & Schmid-Hempel (2006) and Otterstatter & Thomson (2006, 2007).
3. *Kuzinia laevis* (Astigmata, Acari). Hergstrom *et al.* (2002), expressed concern at finding large populations of this mite in feral Tasmanian colonies of *B. terrestris*. It was also the only commensal noted by Allen *et al.* (2007) in Tasmania. It is a pollen feeder, living on the spilt pollen in feral nests (Chmielewski 1971). The second stage in its life history is specially adapted morphologically to attach itself to a bee and thus be transported out of the hive, ideally upon a new queen. Transfer on flowers apparently does not occur with this mite species (Schwarz & Huck 1997). It requires a living environment in which the relative humidity must be at least 70% to survive (Chmielewski 1991). The physical conditions inside a commercial production unit are such that *Kuzinia* cannot survive. Finally, a feral colony failure due to *K. laevis* has never been recorded (D. Griffiths, pers. comm. 2005).
4. *Locustacarus buchneri*, the tracheal mite, is an internal mite parasite of some 18

Bombus species across Europe, Asia and North America (http://insects.umz.lsa.umich.edu/beemites/Species_Accounts/Podapolipidae.htm). It also occurs in feral *Bombus* nests in New Zealand (Macfarlane 1975; Donovan 1980), but not in Tasmania (Allen *et al.* 2007). This mite was found in commercial stocks of *B. terrestris* imported into Japan from both Belgium and Holland (Goka *et al.* 2000) a few years ago. It is not reported from other bees. Additional information on tracheal mite is reported in Otterstatter & Whidden (2004), Otterstatter *et al.* (2005) and Yoneda *et al.* (2007b).

5. *Nosema bombi* (protozoan) causes a chronic disease of variable impact in bumblebees. When commercial production first began, there was concern that there could be a transfer, either way, of *Nosema* between 'nurse' honeybees, employed to service young laying *B. terrestris* queens, and their charges. However, it was shown that the *Nosema* found in these two species were separate entities, namely, *Nosema bombi* and *Nosema apis*, each being host specific (Fantham & Porter 1914; van den Eijnde 2000). *Nosema bombi* can cross-infect other *Bombus* species, but this is not a concern in Australia, as it has no native *Bombus*. It is widespread and common, including in New Zealand, but absent from Tasmania (Allen *et al.* 2007). It is not present in properly maintained insectaries (pers. comm. D. Griffiths 2005; S. Steinberg 2005). *Bombus occidentalis* from eastern North America was particularly susceptible to *Nosema bombi*, perhaps a European strain, and commercial rearing had to be abandoned. Additional information is reported in McIvor & Malone (1995), Imhoof & Schmid-Hempel (1998, 1999), Colla *et al.* (2006), and Klee *et al.* (2006). A European Union project begun in 2003 has already made significant progress in identifying and characterizing *Nosema* in Europe (EU-AgriNet project Pollinator Parasites <http://www.entom.slu.se/res/Bumble%20Bee/index.htm>) finding only one species, *Nosema bombi*, across all *Bombus* spp., but with some variants. A rapid, PCR-based diagnostic tool-kit has been developed to determine microsporidium presence and prevalence.
6. *Sphaerularia bombi* is the only known parasitic nematode in bumblebees. It does not infect other bees. It is present in restricted areas in New Zealand but not in Tasmania (Macfarlane & Griffin 1990; Allen *et al.* 2007). Higher infestation rates lead to disorientation of the queen, sterilisation and lack of colony founding (Alford 1975; Goulson 2003a; Benton 2006).

A certificate of freedom from parasites and pathogens of honeybees may be required by importing countries for bee stock, thus the common ones are listed.

Parasites and pathogens of honeybees These may include:

1. *Acarapis woodi*, the honeybee tracheal mite, is a serious pest of honeybees, not present in Australia or New Zealand. It is not associated with bumblebees (<http://maarec.cas.psu.edu/PDFs/Tracheal/pdf>).
2. *Aethina tumida*, the small hive beetle, is a nest commensal that was detected in Australia in 2002 in NSW and is now widespread in honeybees. It is not yet in New Zealand or Tasmania. It has not been found in bumblebee colonies except under experimental conditions (Stanghellini *et al.* 2000) and recently in very close proximity to heavily infested honeybee hives (Spiewok & Neumann 2006). It should be easily detectable in commercial rearing facilities. It has never been found in commercial stock. The annual nature of bumblebee colonies should break the life cycle in nature.
3. *Braula coeca*, the bee louse, is a commensalate wingless fly found in honeybee

colonies. It occurs in Tasmania and many other parts of the world (<http://creatures.ifas.ufl.edu/misc/bees/beelouse.htm>). It is not associated with bumblebees. Animal Health Australia (2004) lists bumblebees as a possible vector of this fly in their Ausvetplan (2006), which is misleading as it has never been found in association with them.

4. *Tropilaelaps acarina* is a mite parasitic on honeybees. It has not been found infesting bumblebee colonies.
5. *Varroa destructor* is an ectoparasitic mite specific to species in the genus *Apis*. It does not attack bumblebees. *Varroa jacobsoni* was originally thought to be the same species, but it has been determined that they are separate species and that only *V. destructor* attacks *Apis mellifera* (Anderson & Trueman 2000; <http://www.en.wikipedia.org/wiki/Varroa>). *Varroa destructor* is thought to have originated from *Apis cerana*, a species of honeybee resistant to it, and to have been carried into Brazil and then North America by infected *Apis mellifera* colonies from Japan. There is more than one strain of *V. destructor*, with the Korea strain predominating and present in New Zealand (Zhang 2000). There is some hope of breeding honeybees for resistance to *Varroa*.

Bumblebees are not a vector of Varroa mite or the parasitic fly Braula coeca-both can only live on honeybees

Thus information supplied to honeybee producers in Australia suggesting that *B. terrestris* is a carrier of *Varroa* is incorrect. To explode an often quoted myth, it cannot exist either in commercial or feral colonies of *B. terrestris*. In the days when the UK was free from *Varroa*, in order to import bumblebee hives from Holland, the British government required that trials be conducted to determine survival possibilities in bumblebees (D. Griffiths, pers. comm. 2005). It was determined that *Varroa* is unable to survive on bumblebees. More importantly, of all the thousands of commercial and feral hives that have subsequently been examined, *Varroa* has never been discovered. The occasional publication reporting its presence in the nest of a species other than *Apis mellifera* is due to the misidentification of the much smaller, but look-alike, phoretic stage of astigmatid mites (D. Griffiths, pers. comm. 2005). In Florida *Varroa* has been recorded as being carried phoretically on the bodies of flower-feeding insects such as syrphid flies and on scarab beetles, and also on *B. pennsylvanicus* (<http://www.padi.gov.au/viewPest.aspx?id=387>). Kevan *et al.* (1990) and Pettis *et al.* (2003) both report finding *Varroa* on cut flowers imported into the USA. These were no doubt deposited there accidentally by honeybees and attach themselves to any visitors. This no more makes *B. terrestris* a carrier of *Varroa* than someone bringing home a bunch of flowers. Transfer between honeybees in the hive is a much more likely avenue of movement.

Varroa is being linked to spread of honeybee viruses (<http://www.chdphd.co/PhD/>; Cameron *et al.* 2005; Yue & Genersch 2005; Genersch *et al.* 2006; Tentcheva *et al.* 2004, 2006; Gauthier *et al.* 2007), including Israeli acute paralysis virus, a possible contributor to colony collapse disorder in the USA (Cox-Foster *et al.* 2007). Analytical techniques for virus testing have greatly improved in recent years. With the recent injection of research dollars into colony collapse disorder, detection and identification of viruses in bees is on the horizon.

Varroa destructor was detected in New Zealand on the North Island in 2000 (Biosecurity New Zealand website: <http://www.biosecurity.govt.nz/pests-diseases/animals/varroa/guidelines/control-of-varroa-guide.pdf>). This reference also states that *Varroa* can only reproduce on honeybee brood. The mite was found near Nelson on the South Island in June, 2006 (<http://www.biosecurity.govt.nz/pests-diseases/animals/varroa.htm>). It is not yet present in Australia. Australia probably cannot avoid *Varroa*, it can only delay its arrival (Cunningham *et al.* 2002).

In general, far fewer pathogens and parasites are reported from *Bombus* spp. than from honeybees. The major diseases of honeybees, such as *Varroa* and *Acarapis*, bacterial foulbroods, honeybee viral sac broods, and fungi (*Ascosphaera*) have no widespread or common equivalents in bumblebees. Those shared with honeybees and *Bombus* are the bacteria-like *Spiroplasma apis* and *S. melliferum* (USA, pathogenicity to bumblebees not known), and the acute bee paralysis virus (USA, New Zealand). Deformed wing virus, a honeybee pathogen not known in Australia or New Zealand (Europe, Asia, South Africa), was recently found in Europe in bumblebee colonies close to honeybee hives and a commercial bumblebee facility using honeybees to stimulate queen oviposition (Genersch *et al.* 2006).

The development of appropriate protocols for detection and maintenance of freedom from pests and diseases of honeybees and bumblebees would be undertaken by Biosecurity Australia, and involve consultation with the Australian honeybee industry, Australian apicultural scientists and State Departments of Primary Industry, with input from commercial bumblebee operations.

Summary of Section 10

The AHGA proposes several restrictions that could be imposed on the importation of *B. terrestris* into mainland Australia that would see *B. terrestris* present a negligible risk to the environment, while providing enormous benefits to the greenhouse industry and a stimulus to State and regional development. These include use of the temperate subspecies *B. t. audax*, a secure production facility, certified healthy stock, a specially-designed hive fitted with a queen-excluder device, and netting over vents. To present negligible risk, restrictions are outlined which could be placed on greenhouse facilities wishing to use bumblebee technology.

11. OVERALL ANALYSIS OF THE POTENTIAL IMPACTS OF IMPORTING THE SPECIES

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11.1. Proposed import A proposal has been presented for the safe importation of the bumblebee *B. terrestris* onto mainland Australia within secure hives, for the sole purpose of pollination of greenhouse crops, primarily tomatoes. These are described in detail in Sections 1 and 10. The secure production unit could be sited in either Tasmania, or, if permitted, on the Australian mainland. Given that all hives will be secured, fitted with a queen excluder device, and destroyed before new queens are produced, and that all greenhouses will be screened and monitored, the chances of an escape of newly mated queens into the environment, followed by successful survival and overwintering, is minimal. The AHGA believes that on this basis alone, the benefits in improved pollination efficiency, estimated as at least A\$40 million cash benefit per annum, are substantial. The disincentive to invest in greenhouse tomatoes, because of outdated technology and reduced yields, is *costing* Australia a great deal more than this. Bumblebees are used globally in 40,000 ha of tomato crops, with annual world-wide sales exceeding 1 million hives in 2004 (Velthuis & van Doorn 2006). The greenhouse area presently suitable (with stated modifications) for use of bumblebees in Australia is estimated at 200-250 ha. At current estimates of approximately 50 colonies/ha/annum for a single crop, this amounts to 10,000-12,500 colonies/annum.

11.2. Potential establishment of feral colonies Through the controlled process of importation that has been outlined in this document, the establishment of feral colonies of bumblebees is not expected. Similarly, should bumblebees arrive inadvertently by boat or other means of ingress, information contained in this document regarding climatic and other limitations on establishment would suggest that survival will be transient and limited, and may assist in taking a reasoned approach to its management. It would be contrary to the interests of greenhouse producers to have feral bumblebees on the mainland which might carry unknown pests and pathogens, therefore full support would be given to containment and elimination procedures deemed necessary. Procedures already developed for *Apis cerana*, the Asian honeybee, may be applicable (Ausvetplan Edition 3, 2006, Animal Health Australia (2004)).

The AHGA has gone to some considerable effort to examine the potential problems that might arise should *B. terrestris*, despite all safeguards, escape into the environment on the mainland. The AHGA includes many environmentalists amongst its members and is a responsible and professional organization. It no more wishes to cause environmental problems in Australia than the population at large, no matter the unarguable economic benefits of *B. terrestris* as a pollinator. In assessing all the available evidence, for each of the Terms of Reference, we can find no *prima facie* case for accepting accusations of negative effects on the environment; no negative impact on native plants, birds, bees, or spread of weeds has been demonstrated. The species is widespread in its considerable natural range and causes no problems; rather, it is considered an important and beneficial pollinator and considerable effort is underway to increase numbers. Similarly, no harm

has been reported in New Zealand, where four species were imported over a century ago for forage pollination, amid similar claims at the time of dire consequences. They are being reared commercially there for both greenhouse and field crop pollination. A parasite-free strain has successfully established in Tasmania since 1992, and despite several years of research, convincing claims of negative effect remain to be shown. Both Tasmania and New Zealand present ideal climates in many areas for proliferation and spread of this temperate subspecies of bumblebee. They have indeed done just that, but no harm has eventuated. Only the southern and coastal extremes of mainland Australia might present a suitable climate for establishment and persistence. Drought, high summer temperature maxima, and other restrictions may preclude this, but it is difficult to predict with absolute certainty. Even if establishment did occur, the weight of evidence presented is for no measurable environmental impact. New Zealand provides considerable evidence that no harm is likely from presence of bumblebees in Australia. If the same subspecies is used, which is not known to aestivate under hot dry conditions, then a restricted potential distribution in the southern coastal areas can be confidently predicted, with a similar propensity to be far more abundant in settled areas than in native bush, because of well-established floral preferences for introduced plants.

There are good reasons for not introducing an alien pollinator under some circumstances. These are where a) native, closely related bumblebee species are already present, possibly leading to resource overlap and competitive displacement of a native species, b) there is a risk of introducing pests, parasites and pathogens which might affect native bumblebees or honeybees, c) it is aggressive and a danger to public health, d) it is likely to displace native anthophiles or change plant characteristics through abundance and/or aggressive behaviour. None of these pertains to the situation with the proposed import of *B. terrestris* into Australia. Alien leafcutter bees were introduced into SA and NSW from New Zealand and Canada in very large numbers until 2005, without incident. Honeybees are also alien and their presence in native bush contentious, but they are indispensable to the alien crops we grow to feed ourselves. Would we choose to do without them? We export our native bees to countries where they do not exist, and raise no questions.

A small core of people vociferously opposed to bumblebees has succeeded in creating the public perception of a super bee with no redeeming characters, a pest akin to rabbits, cane toads, foxes, European wasps and other vermin. Nothing could be further from the truth. Regrettably, many opponents of the introduction have unquestioningly accepted evocative statements based on sensationalist, unscientific statements and shaky or preliminary data, which are aimed primarily at galvanising public opinion against bumblebees. The AHGA acknowledges that this concerted campaign over many years has been very successful, and frustrating to try to counteract. Apart from supportive articles in *Practical Hydroponics & Greenhouses Magazine* (Issue 77, July/August 2004), the considerable number of press articles, website presentations and scientific publications relative to this issue fail to present a fair and balanced perspective on the issue. Newspapers and websites have largely ignored requests to present a contrasting viewpoint. The Horticultural Industry in Australia would benefit greatly from a managed, specialist pollinator which can be produced on demand, and their use would greatly assist with both a home-based and an export industry, in promoting biological pest management and in substantially reducing pesticide residues. These are very tangible benefits, and it is why more than 40 other countries around the world rapidly adopted this technology. While several countries are endeavouring to commercialise their own bumblebee species or strains, none has stopped using bumblebees. The enormous growth in the greenhouse industry in developed and developing countries in recent years has been a direct result of

The considerable number of articles, website presentations and scientific publications emanating from Australia have failed to present a fair and balanced view of bumblebees

bumblebee availability. We would therefore request that the information presented in this document be thoroughly reviewed in an impartial manner before any final decision is made.

Australia is too dependent on a single pollinator for its exotic crops, and should not close the door on alternatives without good cause

In reviewing this application, it is also very important to consider the far-reaching effects that loss of Australia's main crop pollinator, the honeybee, might have on agricultural productivity in Australia (Cunningham *et al.* 2002; Williams 2002). *Varroa* mite has had a devastating effect on honeybees in North America and many other countries, including New Zealand, since the early 1990's. Australia is perceived to be at high risk of importing *Varroa*, and its honeybees already carry viruses suspected of being transmitted by *Varroa* and which may be linked to colony collapse disorder (Tentcheva *et al.* 2004, 2006; Yue & Genersch 2005; Cox-Foster *et al.* 2007). A biosecurity plan to safeguard the honeybee industry is being developed (RIRDC, Pollination Australia Workshop, 2008), but it is focussed only on protecting honeybees. What is Plan B if this fails? Dependence on a single pollinator which can be wiped out in less than a year is fraught with danger. Money and effort has gone into developing alternative pollinators among both native and introduced bees in North America, including several species of bumblebees (Allen-Wardell *et al.* 1998; Cane & Tepedino 2001). Australia also needs to consider alternative pollinators.

The major causes of loss of biodiversity in Australia are man-made, through land-clearing, grazing activities, fire and use of pesticides. Bumblebees will add little or nothing to their combined impact

A diversity of pollinators with varying characteristics is essential to reduce our reliance on one primary pollinator (Westerkamp & Gottsberger 2000). In North America, mass production of native bees to replace honeybees has been attempted but has also had its problems, and use is very limited. There is still a large pollinator deficit in countries where *Varroa* has decimated honeybees. Japan is still importing and evaluating non-native bees, despite the campaign against use of imported bumblebees (<http://www.agnet.org/library/tb/167>). There is no guarantee and little likelihood that native bee species in Australia will adequately pollinate all the introduced crops on which we depend.

Following pressure from a strong environmental lobby, managed hives of honeybees have been banned from National Parks in Queensland and Northern Territory, and their use restricted in New South Wales, Victoria, Tasmania and Western Australia (Reeves & Cutler 2005, <http://www.thecie.com.au/publication.asp?PID=102>). Feral honeybees were declared a Key Threatening Process by State governments in both New South Wales and Victoria in 2002. Meanwhile, we do little to prevent massive loss of native habitat through land clearing, grazing and fire, and we promote the use of pesticides, which are by far the major contributors to loss of biodiversity in Australia, and against which any contribution that honeybees and bumblebees might make pales in comparison. This is not the direct concern of the AHGA, but reflects a similar disturbing mindset, of not seeing the bigger picture. These decisions may come back to haunt us in the future, because we will always be dependent on agriculture for survival in the foreseeable future.

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APPENDIX I

CLIMEX[®] MODELS TO PREDICT THE POTENTIAL NATURALISED
RANGE OF THE EUROPEAN BUMBLEBEE *BOMBUS TERRESTRIS* (L.)
IN AUSTRALIA (A. McCLAY 2005).

Report prepared for the
Australian Hydroponic and Greenhouse Association

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SUMMARY

The European bumble bee *Bombus terrestris* is a widely distributed species that occurs over most of Europe except the far north, parts of North Africa, and in Asia east to Kazakhstan, northern Iran, and Afghanistan. It includes a number of geographically separate subspecies, of which *audax* is restricted to the British Isles. *Bombus terrestris* ssp. *audax* has also become established in New Zealand and Tasmania. Two models were developed to predict the potential geographic range of the European bumble bee *Bombus terrestris* ssp. *audax* in mainland Australia. The models used the CLIMEX v2 program, which estimates the climatic requirements and tolerances of a species by a process of fitting parameters to its known distribution. The first model assumed that the climatic adaptations of subspecies *audax* are similar to those of *Bombus terrestris* as a whole, while the second assumed that *audax* is narrowly specialized to the climatic conditions of the British Isles. Under the first model the potential range of *B. terrestris* in Australia includes almost all of Victoria, south-eastern coastal areas of South Australia, the eastern half of New South Wales, coastal areas of southern Queensland, higher elevation areas near the coast in northern Queensland, and coastal areas of Western Australia from Eyre to Geraldton. Under the second model the potential range of *B. terrestris* ssp. *audax* would be coastal Victoria, parts of the coast of new South Wales north almost to Sydney, higher elevation areas of eastern Victoria and southern New South Wales, and some areas around the Armidale area of New South Wales. As the second model is based on the unproven assumption that *B. terrestris audax* is an extreme climatic specialist, the predictions from this model should be considered as an absolute minimum estimate of the potential range of this subspecies in Australia. It should be expected that *B. terrestris audax* would be able to establish in broader areas of Australia, possibly approaching the limits predicted from the model for *B. terrestris* as a whole.

1. Introduction

1.1. Background

The European bumble bee *Bombus terrestris* (L.) has been proposed for introduction into mainland Australia for pollination of tomatoes and other greenhouse crops. One factor that must be considered in the review of this proposal is the potential for establishment of feral populations of *B. terrestris* as a result of possible escape of fertile queens from greenhouse operations, and the possible ecological consequences of such establishment. The models described in this report were developed, at the request of the Australian Hydroponic and Greenhouse Association, to attempt to predict the potential geographic range of *B. terrestris* in mainland Australia on the basis of its climatic tolerances and requirements. *Bombus terrestris* is a widespread species consisting of a number of geographically separate subspecies within its native range. Several of these have been used as greenhouse crop pollinators. However, the subspecies most likely to be used as a pollinator in mainland Australia is *B. terrestris* ssp. *audax* (Harris), native to the British Isles. This subspecies was introduced to New Zealand, where it is now widely established, and has now also become established in Tasmania.

1.2. CLIMEX

The models were developed using CLIMEX (version 2), a program that allows the user to estimate the potential geographic distribution and seasonal abundance of a species in relation to climate (Sutherst *et al.* 2004). CLIMEX models consist of a set of growth parameters that define the preferred ranges of temperature and moisture conditions that allow population growth of a species during a favourable season, and a set of stress parameters that define its ability to survive unfavourable seasons. Additional parameters can be used to define conditions required to induce and terminate diapause, and to specify the number of degree-days needed to complete a single generation. The suitability of a particular location for a given species is estimated by a series of indices based on meteorological data for that location and the CLIMEX parameters for that species. CLIMEX includes an extensive worldwide meteorological database for use in these calculations. The environmental index (EI) gives an overall assessment of how well adapted a species is to a given climate. Locations with an EI above 30 represent very favourable climates for the species, while values close to 0 indicate marginal or unfavourable conditions. The program allows maps of EI and other indices to be plotted, thus giving an indication of the potential geographic range of the species.

CLIMEX parameters are primarily estimated by an iterative process of adjustment until the predicted range matches the known geographic range of the species. Information from experimental studies of temperature and moisture effects on the species, diapause requirements, etc., may also be used when available.

The fundamental assumption of CLIMEX is that species' ranges are limited by their responses to climatic factors. Other factors, such as geographic barriers, habitat types, natural enemies (parasites, pathogens, etc.), the need for particular hosts or food plants, or soil conditions, may also be important in limiting the range of some species. Thus a favourable CLIMEX index does not automatically mean that a species can survive in a particular location, and other factors affecting its potential establishment should also be considered.

1.3. Distribution of *Bombus terrestris*

1.3.1. Native range of *B. terrestris sensu lato*

The species *Bombus terrestris* as a whole, including all its subspecies, is referred to taxonomically as *B. terrestris sensu lato* (Latin for 'in a broad sense'). The native range of *B. terrestris sensu lato* is summarized in *Figure 1*. The sources from which the distribution is estimated are discussed here.

The most detailed listing of the distribution of *B. terrestris* is given by Løken (1973) as follows: "Europe (British Isles; from Portugal, Spain, Mediterranean Islands, Greece throughout the continent up to Denmark, Southern Scandinavia, Poland; in European USSR north to districts of Minsk, Bryansk, Moscow, Penzensk, Kuibyshev) – Canary Islands – Algeria –Tunisia –Turkey – Caucasus – Transcaucasus – Southern Ural – northern and eastern Kazakhstan – Turkestan". [Note that the old term 'Turkestan' refers to a large area of Central Asia including the modern republics of Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan as well as parts of Kazakhstan, Afghanistan, Iran, and western China. Thus, records from Turkestan could refer to anywhere in this area. From the reference to 'northern and eastern Kazakhstan', I have assumed that *B. terrestris* is found in the steppe, forest and mountain areas of the country but not the southern semi desert and desert areas.]

The distribution in western Europe is well known from numerous records and the range boundaries here are fairly accurate. *B. terrestris* is well recorded from most of Europe (e.g. Rasmont 1983, 1984; Williams 1986; Herrera 1990; Maciel Correia 1991; Pekkarinen and Teräs 1993; Intoppa *et al.* 1995; Estoup *et al.* 1996; Dimitrov 1997; Widmer *et al.* 1998; Calabuig 2000; Pawlikowski 2001; Mänd *et al.* 2002; Quaranta *et al.* 2004). It occurs throughout the British Isles except the outer Scottish islands (Williams 1982) but has only recently spread into northern Scotland (Macdonald 2001). It was not present in Finland according to Løken (1973), Pekkarinen *et al.* (1981), and Pekkarinen and Teräs (1993) but was reported as a new arrival around Helsinki by Pekkarinen and Kaarnama (1994). In Lithuania *B. terrestris* comprised 10.3% of *Bombus* individuals trapped in funnel traps (Ostrauskas and Monsevicius 2002), while in Estonia it occurs at a low frequency, 0.65% of total *Bombus* individuals (Mänd *et al.* 2002).

There are fewer records from the southern and eastern extremes of the species' range in North Africa, Russia, and central Asia, so the boundaries in those directions are more tentative. In Turkey, *B. terrestris* occurs throughout most of the country but was not recorded from southeast Anatolia by Özbek (1997). Reinig (1971) reports it throughout the country except in the Armenian highlands (eastern Turkey). It was reported as a common pollinator of sunflower at Kahraman Mara° (Aslan 2003). In Morocco the subspecies *africanus* is found throughout the country north of the ridge of the Atlas Mountains (map from data by P. Rasmont at <http://zoologie.umh.ac.be/marocbiodiv/fiche.asp?ID=2108&CarteID=180>). There are also definite records from eastern Kazakhstan (edge of the Altai Mountains: Rasmont, pers. comm. To D. Griffiths), northern Iran (Mazandarn province, Alborz mountains, Gorgan) (Baker 1996), Afghanistan (one record) (Williams 2004), Kyrgyzstan (record in Apoidea collection of Siberian Zoological Museum, Novosibirsk, see <http://szmn.sbras.ru/Hymenop/Apoidea.htm>), northern Israel (Ne'eman and Dafni 1999), and Algeria (Atlas Mountains: P. Rasmont, pers. comm. to D. Griffiths).

Well-surveyed areas in which *B. terrestris* is not found include Iceland (Prÿs-Jones *et al.* 1981), Kashmir (Williams 1991), and most of northern Scandinavia (Løken 1973; Pekkarinen *et al.* 1981).

1.3.2. Distribution of subspecies

A tentative distribution list for some of the subspecies of *B. terrestris* is as follows (D. Griffiths, pers. comm., and see map at *Figure 2*):

British Isles	<i>Bombus terrestris audax</i>
North west continental Europe	<i>Bombus terrestris terrestris</i>
Spain	<i>Bombus terrestris ferrugineus</i>
Spain - south & Portugal	<i>Bombus terrestris lusitanicus</i>
Southeast Europe	<i>Bombus terrestris dalmatinus</i>
Sardinia	<i>Bombus terrestris sassaricus</i>
Corsica and Elba	<i>Bombus terrestris xanthopus</i>
North Africa	<i>Bombus terrestris africanus</i>
Madeira	<i>Bombus terrestris maderensis</i>

Populations from the Canary Islands have been considered as a separate species, *B. canariensis* Erlandson, or as a subspecies of *B. terrestris* (Estoup *et al.* 1996; Widmer *et al.* 1998; Williams 1998).

1.3.3. Areas of introduction of *Bombus terrestris*

Bombus terrestris audax was introduced from England into New Zealand as a pollinator and established in 1885. It now occurs in all areas of the North and South islands, up to elevations of 2,500 m in the Mount Cook region and in areas of annual rainfall from 339 to over 10,000 mm (Macfarlane & Gurr 1995). It was first observed in Tasmania in 1992. Its means of introduction there is unknown but it has now spread to occupy most of the state (Stout & Goulson 2001; Hingston *et al.* 2002).

Bombus terrestris (subspecies not stated) is reported to be well established in Japan (Matsumura *et al.* 2004; Nakajima *et al.* 2004; Inari *et al.* 2005). A series of maps at the website of the Japanese Society of Conservation Ecology documents the apparent spread of *B. terrestris* from the first observations in Hokkaido in 1996 throughout most of the main islands by 2004

(http://www003.upp.so-net.ne.jp/consecol/english/maruhana/maruhana_info_eng.html).

Ruz and Herrera (2001) and postings on the Bombus-L mailing list also indicate that *B. terrestris* (subspecies not stated) is established in Chile (around Santiago).

2. Objectives

For this study the development of two CLIMEX models was requested, one for *B. terrestris sensu lato* (i.e., for the whole species including all its subspecies), and one for *B. terrestris ssp. audax*. Because of the differences in how these models were derived, it is better to consider them as being alternative models for *B. terrestris ssp. audax*: one based on the hypothesis that this subspecies shares the same range of climatic requirements and tolerances as the whole species, and one based on the hypothesis that it is specifically adapted to a narrow range of climates resembling those of its native range.

3. Methods

3.1. General approach

3.1.1. Model for *B. terrestris sensu lato*

As mentioned previously, *B. terrestris* is a widespread species consisting of a number of geographically separated subspecies. These species are mainly differentiated by colouration and morphology, and little information is available on differences in their climatic requirements or responses to environmental conditions. Studies of genetic markers in mainland European populations of *B. terrestris* show very little genetic differentiation between them, although island subspecies populations have diversified more (Estoup *et al.* 1996; Widmer *et al.* 1998). This however, does not imply that local populations or subspecies are not adapted to local climates in their areas. Peat *et al.* (2005) found that Greek populations of *B. terrestris* had shorter thoracic setae than British populations, suggesting they were adapted to enhance heat loss in warm climates. There is some evidence from studies cited in Estoup *et al.* (1996) that variation between populations in length of diapause is under genetic control, although there is also a strong environmental component in the determination of diapause.

For the purposes of the first CLIMEX model, however, it was assumed that *B. terrestris sensu lato* is a single unit with a wide range of climatic adaptability that allows it to survive throughout its whole native range from North Africa to southern Scandinavia and from Ireland to eastern Kazakhstan. Under this assumption any particular population, such as *B. terrestris audax*, shares the same range of climatic tolerances as the species as a whole, and could thus establish in any climate where any other *B. terrestris* population can survive. Parameters for this CLIMEX model were adjusted until the predicted range of *B. terrestris* matched its observed distribution in the native range.

3.1.2. Model for *B. terrestris ssp. audax*

In order to develop a model for *B. terrestris ssp. audax*, it was necessary to make a different set of assumptions. Because *audax* is an island subspecies in its native range, its distribution is primarily limited by geographic barriers (the North Sea and English Channel) and not by climate. It is possible that occasional individuals of *audax* cross this barrier into mainland Europe, but their genetic material would likely be diluted out by cross breeding with the mainland subspecies, and thus *audax* would not be able to establish permanent populations there.

Since the distribution of *audax* is not limited by climate in its native range, it is not possible to use the normal approach based on matching the observed distribution to fit parameters for a CLIMEX model for this subspecies. Instead, an indirect approach was used. Starting from the model for *B. terrestris sensu lato*, the upper temperature limits were reduced, lower moisture limits increased, and the cold, heat and dry stress parameters were increased until the resulting predicted distribution was restricted as far as possible to the British Isles and other areas (New Zealand and Tasmania) where this species is known to be established. This model thus represents the assumption that *B. terrestris ssp. audax* is a narrow climatic specialist, restricted to climates closely resembling those of its native range in Britain. It is important to point out that there is no direct evidence for this assumption. Thus, this model is not intended as a realistic representation of the climatic requirements of *B. terrestris ssp. audax*, but predicts a minimal range of climates within which the subspecies should definitely be able to

establish.

3.2. Parameter value selection

Initial parameter values were selected based on the ‘temperate template’ provided with CLIMEX (Sutherst *et al.* 2004) and published values for species with similar distributions, e.g. *Meligethes viridescens* (Mason *et al.* 2003), *Oulema melanopus* (Olfert *et al.* 2004), and *Leptinotarsa decemlineata* (Sutherst *et al.* 2004). There is relatively little experimental data available for *B. terrestris* that would assist in setting parameter values. Corbet *et al.* (1993) found a threshold temperature for foraging activity of *B. terrestris* and *B. lucorum* of around 6°C. In southern England *B. terrestris* is the earliest bumble bee species to emerge from hibernation: queens appeared March 7 – March 25 at air temperatures of about 10 – 12°C (Alford 1969). Workers begin fanning to control nest temperature at about 28°C (Weidenmuller 2004): nest temperatures above 30°C impair brood development (Vogt 1986), quoted in Weidenmuller (2004). Development times from egg to adult for workers is 22 days, for males 26 days, and for queens 30 days (Duchateau & Velthuis 1988), quoted in Beekman *et al.* (1998). However, as the first broods reared are workers, which do not reproduce, from a life-history perspective the relevant generation time is the time from colony foundation to the appearance of reproductive adults (queens and males). Degree-day totals in CLIMEX were adjusted so that a single generation would occur along the northern end of the range, with two or more generations in areas with longer favourable seasons.

In Mediterranean and Aegean coastal regions queens have a summer diapause (aestivation) emerging in September – November, while in inland areas and in Europe they have a winter diapause (hibernation) emerging in February – March (Gösterit and Gürel 2005). Genetic and environmental factors controlling diapause, however, have not been well studied. Colonies founded from queens of aestivating populations of subspecies *sassaricus* and *dalmatinus* produced young queens which hibernated when transferred to environmental conditions of the Netherlands, suggesting considerable flexibility in diapause responses (Duchateau, cited in Estoup *et al.* 1996).

3.3. CLIMEX modelling procedures

Parameter fitting for the *B. terrestris sensu lato* model was done using a subset of the world station data provided with CLIMEX v.2, including all stations between latitude 20°N and 75°N and between longitude 30°W and 90°E, which covers the whole native range of *B. terrestris*. Results were then validated by examining the predicted distribution in other areas where *B. terrestris* is established (Japan, New Zealand, Tasmania, and Chile). When parameter values had been finalized, a map of the predicted distribution in Australia was generated. Final maps for the report were generated using the 0.5° grid climatic data from the Climatic Research Unit, Norwich, as supplied with CLIMEX.

Parameter fitting for the *B. terrestris audax* model was done using the station data for Europe, New Zealand and Tasmania, which includes all areas where *B. terrestris audax* occurs as a native or established exotic species. When parameter values had been finalized, a map of its predicted distribution in Australia was generated using the 0.5° grid climatic data.

4. Results

Parameters for the two models are given in *Table 1*. No diapause parameters were used in

either model, as there is little experimental information on the cues required to induce or terminate diapause in *B. terrestris*. It was found possible to match the observed range without their use. The interaction stresses available in CLIMEX (cold-wet, hot-dry etc.) were also not used.

4.1. Native range of *B. terrestris sensu lato*

The predicted distribution for *B. terrestris sensu lato* in Europe, North Africa and adjacent areas of Asia from this model is shown in *Figure 3*. This matches the known native range shown in *Figure 1* reasonably well. According to the model, distribution at the northern edge of the range is limited by lack of sufficient degree-days to complete a generation. Cold stress during overwintering did appear to limit the distribution – increasing the rate of cold stress accumulation beyond the value used had the effect of excluding it from northern and eastern Kazakhstan, areas that are reported to be within its distribution. Heat and drought tolerances were adjusted to fit the known southern limits of the distribution. Coastal areas of Egypt and Libya, where *B. terrestris* does not occur, are not much hotter than areas of southern Italy and Algeria that are within its range, but are much dryer. Drought tolerances and stress rates were thus adjusted to exclude *B. terrestris* from the former areas. The predicted distribution was less sensitive to heat stress. A slight heat stress accumulation above 30°C was used to exclude areas of Iraq, Iran, and Turkmenistan that otherwise would have been predicted to be marginally suitable. Higher heat stress rates would have excluded *B. terrestris* from areas of Turkey and Greece that are known to be within its range. *B. terrestris* occurs in areas with annual precipitation up to 2,000 mm in northwestern England, so no wet stress parameters were used in the model.

The same set of parameters predicted that all of New Zealand, Tasmania, and Japan, as well as Chile between approximately 33°S and 42°S, would be climatically suitable for *B. terrestris sensu lato* (data not shown). The model is thus consistent with the areas in which *B. terrestris sensu lato* is known to have become established as an exotic.

4.2. Native range of *B. terrestris ssp. audax*

The predicted potential distribution of *B. terrestris ssp. audax* in Europe according to the model is shown in *Figure 4*. With these parameters, *audax* would be restricted to the British Isles and adjacent coastal areas of northwestern Europe. It was not possible with realistic parameter values to restrict the predicted range any further than this. The same parameter values predict that virtually the whole of New Zealand and Tasmania would be suitable for *audax* (*Figure 5*), in agreement with observations. With these parameters, some locations in eastern central Tasmania have some degree of drought stress for *audax*, while some high-altitude areas in western Tasmania have insufficient degree-days for a full generation. *B. terrestris ssp. audax* has been reported from all these areas (Stout and Goulson 2000; Hingston *et al.* 2002). Thus it seems unlikely that it would be realistic to restrict the climatic range of *B. t. audax* any further than is indicated by this model.

4.3. Predicted range of *B. terrestris sensu lato* in Australia

The predicted range of *B. terrestris sensu lato* in Australia according to this model is shown in *Figure 6*. Areas predicted to be suitable include almost all of Victoria, south-eastern coastal areas of South Australia, the eastern half of New South Wales, coastal areas of southern Queensland, higher elevation areas near the coast in northern Queensland, and coastal areas of Western Australia from Eyre to Geraldton.

4.4. Predicted range of *B. terrestris audax* in Australia

The predicted range of *B. terrestris audax* in Australia according to this model is shown in *Figure 7*. Areas predicted to be suitable are coastal Victoria, parts of the coast of New South Wales north almost to Sydney, higher elevation areas of eastern Victoria and southern New South Wales, and some areas around the Armidale area of New South Wales.

5. Discussion

The model for *B. terrestris sensu lato* fits the observed distribution of the species in its native and introduced ranges fairly well. Some refinement may still be necessary to the parameters affecting the cold extremes of its range, as the model appears to slightly underestimate the northern extent of *B. terrestris* in the British Isles and overestimate it in Scandinavia. The model also suggests that *B. terrestris* may be excluded by cold conditions from high elevation areas of western Tasmania (*Figure 5*), where it has in fact been recorded (Hingston *et al.* 2002). However, any such adjustments would be unlikely to affect the predicted range in mainland Australia, where *B. terrestris* is not likely to be significantly limited by cold conditions.

The predicted potential range of *B. terrestris* in Australia under this model (*Figure 6*) is quite extensive. This is not surprising, given the wide geographic and climatic range of the species in its native range. There is some uncertainty regarding the northern boundaries, as climates in this area do not correspond to any that occur along the southern native range limits of *B. terrestris*. Along its southern limits in North Africa and Asia, *B. terrestris* experiences hot, dry conditions, whereas coastal New South Wales and Queensland are high rainfall areas. Hot, moist conditions may make *B. terrestris* more vulnerable to pathogens; this would be an example of ‘hot-wet’ stress interaction in CLIMEX terms. The northern extent may also be limited by failure to meet conditions necessary for diapause, if this requires a cool winter season. Because of the lack of quantitative data on diapause requirements, it was not possible to incorporate these in the models. These factors may limit the northward potential distribution of *B. terrestris* in comparison with the predictions of this model, but it is not possible to say by how much.

The potential range predicted for *B. t. audax* under the second model is much more restricted (*Figure 7*). However, it must be kept in mind that this represents an absolute minimum predicted range for this subspecies in Australia. Even if *B. t. audax* is highly specialized to climates resembling those of its native range in Britain, it would still be expected to be able to establish throughout this area. There is no direct evidence that the climatic requirements of *B. t. audax* are in fact as specialized as is assumed for this model. Thus, it should be expected that even this subspecies could establish in broader areas of Australia, possibly approaching the limits of the potential distribution of *B. terrestris sensu lato* shown in *Figure 6*.

It should also be remembered that if other subspecies of *B. terrestris*, particularly southern European ones such as *dalmatinus* or *ferrugineus*, were to be introduced, the narrow model for *B. t. audax* is not relevant in predicting their potential range. These subspecies should be presumed able to establish throughout most of the range predicted in *Figure 6*.

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Table 1 Parameters of CLIMEX models for *Bombus terrestris sensu lato* and *Bombus terrestris audax*.

CLIMEX parameters	<i>Bombus terrestris</i> <i>lato</i>	<i>sensu</i> <i>Bombus terrestris</i> <i>audax</i>
Temperature Index		
Limiting low temperature DV0	8	8
Lower optimal temperature DV1	12	12
Upper optimal temperature DV2	27	21
Limiting high temperature DV3	30	24
Moisture Index		
Limiting low moisture SM0	0.1	0.3
Lower optimal moisture SM1	0.15	0.5
Upper optimal moisture SM2	1.8	1.8
Limiting high moisture SM3	2.5	2.5
Light Index	not used	not used
Diapause Index	not used	not used
Cold Stress		
Cold Stress Temp. Threshold (Average TTCSA)	-5	0
Cold Stress Temp. Rate (Average) THCS	-0.0002	-0.01
Heat Stress		
Heat Stress Temperature Threshold TTH	30	24
Heat Stress Temperature Rate THHS	0.0025	0.01
Dry Stress		
Dry Stress Threshold SMDS	0.1	0.3
Dry Stress Rate HDS	-0.04	-0.01
Wet Stress	not used	not used
Cold-Dry Stress	not used	not used
Cold-Wet Stress	not used	not used
Hot-Dry Stress	not used	not used
Hot-Wet Stress	not used	not used
Degree-days per Generation	815	815

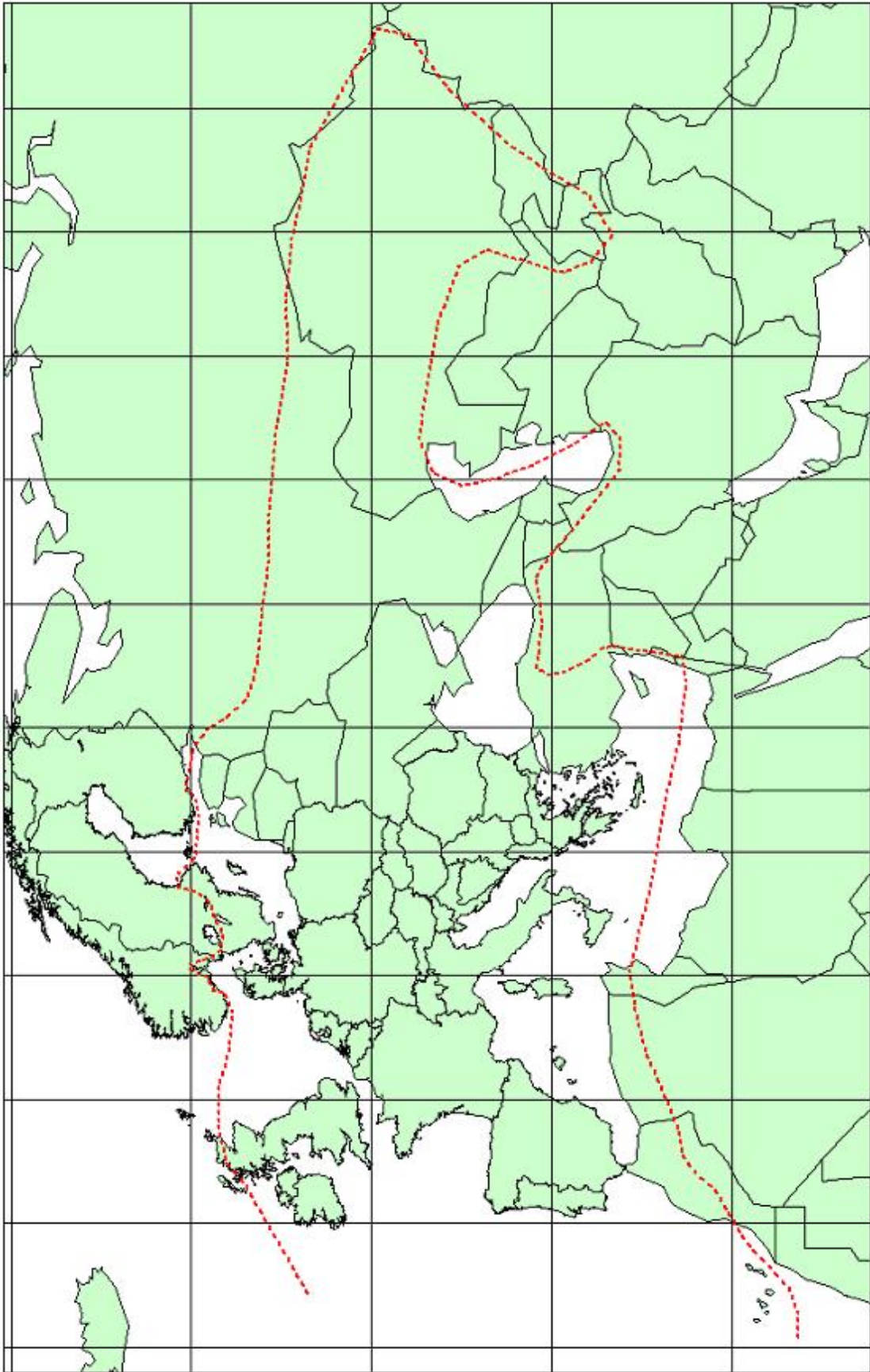


Figure 1. Approximate native range of *Bombus terrestris*, including all subspecies. From sources listed in text.

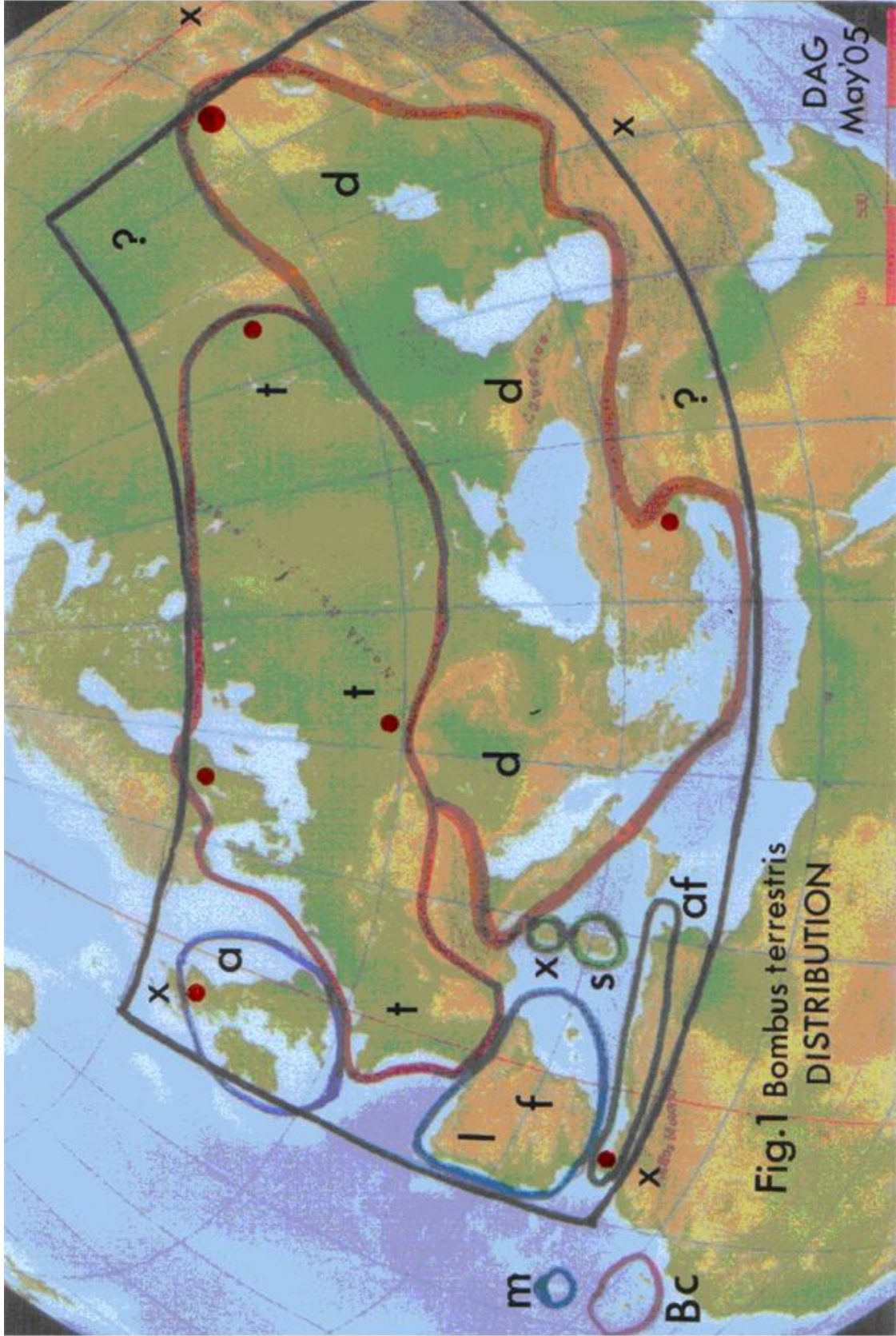


Figure 2. Distribution of subspecies of *Bombus terrestris* in Europe (map provided by D. Griffiths).
 Subspecies indicated by letters: a – *audax*, af – *africanus*, d – *dalmatinus*, f – *ferrugineus*, l – *lusitanicus*, s – *sassaricus*,
 t – *terrestris*, x – *xanthopus*; Bc – *Bombus canariensis*; x (outside range boundaries) – no records of *B. terrestris*.

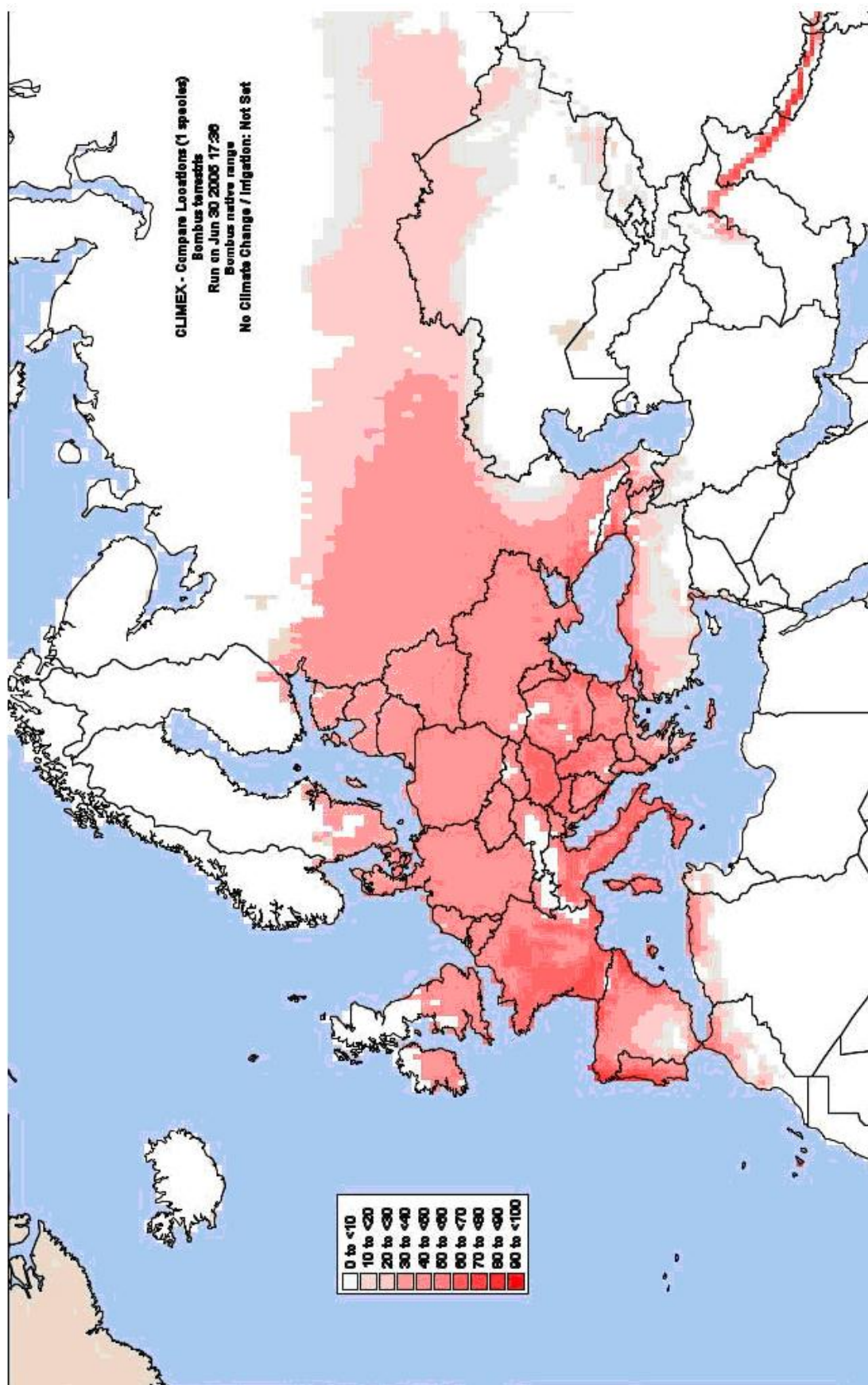


Figure 3. Predicted distribution of *Bombus terrestris sensu lato* in Europe and adjacent regions according to the CLIMEX model parameters in Table 1.

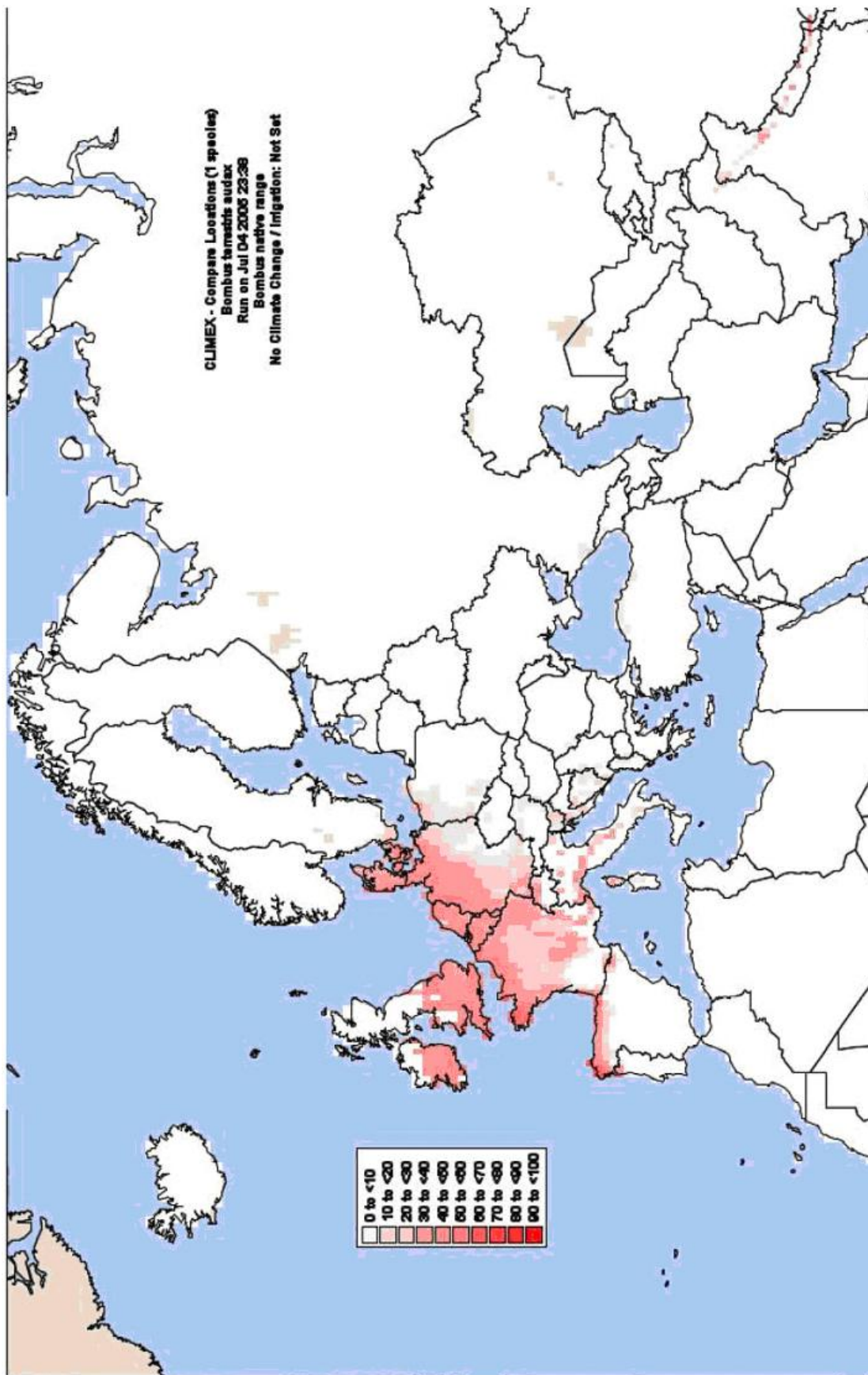


Figure 4. Predicted distribution of *Bombus terrestris* ssp. *audax* in Europe and adjacent regions according to the CLIMEX model parameters in Table 1.

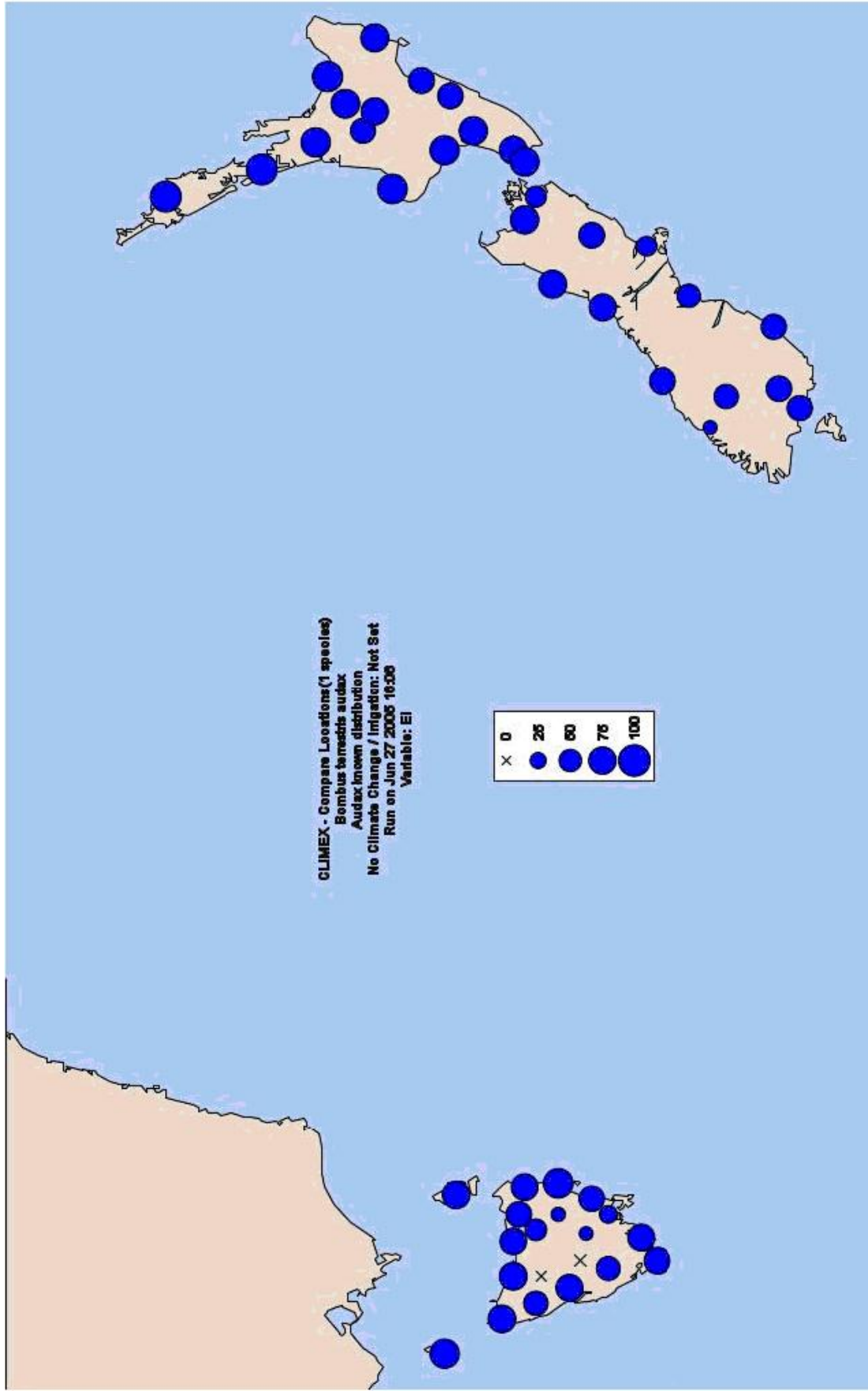


Figure 5. Predicted distribution of *Bombus terrestris* ssp. *audax* in New Zealand and Tasmania according to the CLIMEX model parameters in Table 1.

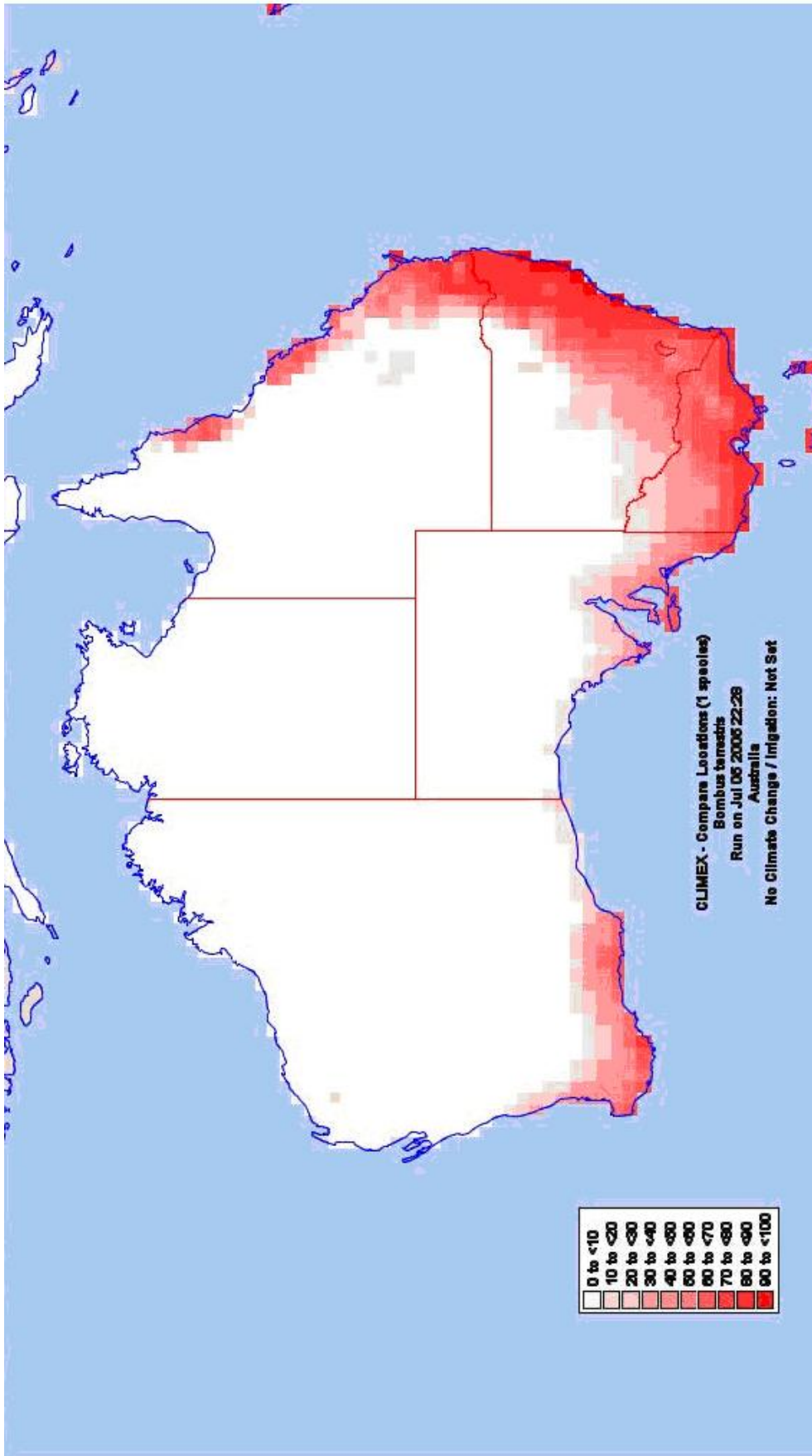


Figure 6. Predicted distribution of *Bombus terrestris sensu lato* in Australia according to the CLIMEX model parameters in Table 1.

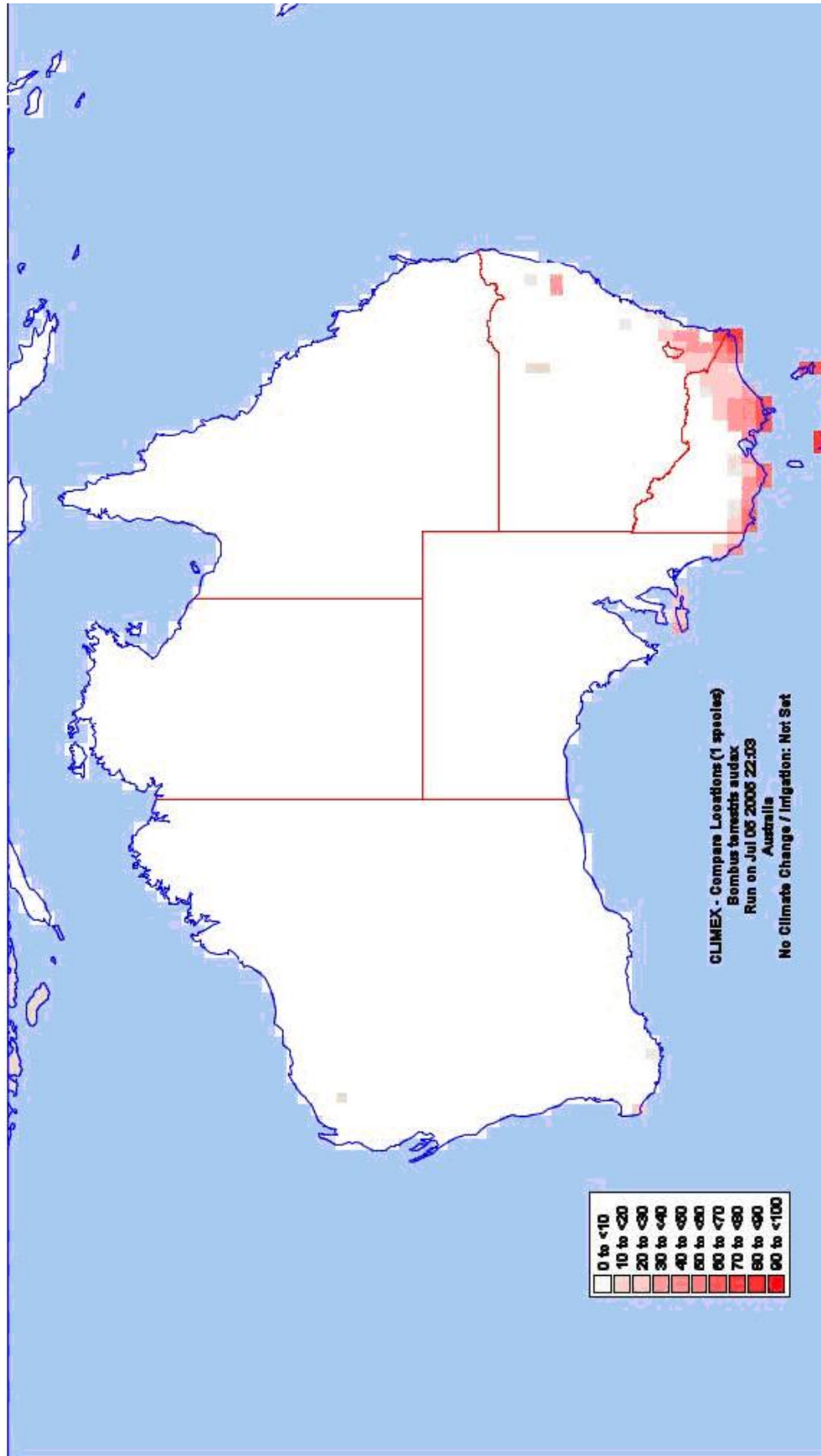


Figure 7. Predicted distribution of *Bombus terrestris* ssp. *audax* in Australia according to the CLIMEX model parameters in Table 1.

APPENDIX II

INFLUENCE OF LONG TERM GEOGRAPHIC ISOLATION, AND A COOL TEMPERATE CLIMATE, RELATIVE TO THE DEVELOPMENT OF GENETIC ISOLATION IN THE SUBSPECIES *Bombus terrestris audax*

D. A. GRIFFITHS

Two separate CLIMEX models were prepared for *B. terrestris*, one from climatic data in the natural range of *B. terrestris audax* in the UK, to which was added data from New Zealand and Tasmania, and the other for the species as a whole, which includes all 11 subspecies (Appendix I). Because we disagree with some of the assumptions of the consultant about the genotype of *B. t. audax* and thus the relevance of one of the models to this subspecies, this matter is further discussed here.

Because *B. t. audax* is already present in Tasmania and New Zealand and is relatively pest and pathogen-free, this is the subspecies of most interest for commercial development. The CLIMEX models were developed to provide some indication of where climate alone might limit feral establishment on mainland Australia. The extent of establishment cannot be predicted with certainty, as hard data are not available as to its physiological abilities to withstand hot dry conditions. We do know that in its isolated natural habitat of the British Isles it is exposed to a cool moist climate, with some indications that distribution is skewed towards the wetter western regions. Certainly it has not in its history been exposed to hot, dry climatic conditions for long periods. Indeed, complete isolation accompanied by a cool temperate climate occurred over 7,000 years ago when the North Sea broke through to form the English Channel (Williams 1986). Inevitably, when an organism is exposed to such long periods of isolation, prevailing selective pressures will trigger genetic drift within its genotype. Indeed, isolation *per se* is recognized as a very important building block in the evolutionary progression of species formation.

Worthington (1940) concluded that:

‘empirically, isolation does favour differentiation and may well be seen in island forms which have diverged in isolation while their counterparts on the mainland have remained constant.’

Julian Huxley (1940) remarked that:

‘in the first place it is clear that isolation is the essential factor in bringing about taxonomic divergence.’

Moreover, pertinent to the *B. t. audax* issue, Kingdon (1990) in his classic work entitled ‘Island Africa’ maintained that:

‘it is widely accepted that within this endemic isolation the main selective pressure to which these island forms are subjected is climate.’

These views, put forward by eminent systematists, are reflected in the fact that *Bombus* taxonomists can separate all 11 subspecies on the basis of morphological characters, principally body colour and banding. For example, Peat *et al.* (2005) distinguished differences in thoracic setal lengths between Greek populations of *B. t. terrestris* and British populations of *B. t. audax*. They considered that such differences were a possible selection to deal with hotter temperatures, which conversely means that the thicker pile on the abdomen of *B. t. audax* may be an adaptation to deal with colder temperatures. Further, Widmer *et al.* (1998) established through molecular studies that within nine subspecies they could distinguish six different haplotypes. The *B. t. audax* haplotype was unique within the group, distinguishing this subspecies from both continental European and Mediterranean forms. Thus, *B. t. audax* is different from all other subspecies within the genus *Bombus*.

Differences in physiological traits have so far not been studied, but it can be argued that a prediction which suggests *B. t. audax* has evolved a genotype biased towards living in a cool, moist temperate climate is a reasonable assumption to make. To support this statement, we know that the only successful establishment outside the British Isles has been its colonisation of New Zealand, where it was introduced nearly 130 years ago, and more recently of Tasmania, where it was first recorded 16 years ago, and Hokkaido Island in Japan, of similar introduction period. These are the only sites of successful establishment of *B. t. audax*, and both fit climatologically with conditions prevailing in its unique natural habitat, the British Isles.

To assess possible establishment of an alien species in areas outside its natural range, predictive climatic modelling programs have been developed. Arguably, the best of such modelling programs is CLIMEX (Sutherst *et al.* 2004). Alex McClay, commissioned by AHGA, used CLIMEX version 2 to predict climatically suitable areas for *B. terrestris* on mainland Australia (Appendix I). In McClay's own words:

‘It allows the user to estimate potential geographic and seasonal abundance of a species in relation to climate. The fundamental assumption of CLIMEX is that any species’ range is limited by its response to climatic factors.’

McClay produced two models, one based on *Bombus terrestris s. l.*, in which he included the climatic parameters of all known subspecies, and a second model based on *B. t. audax* alone. For his first model, he assumed that the climatic parameters for *B. t. audax* and those embracing the whole of the species *B. terrestris* are the same. In other words, he is assuming that the 11 subspecies, ranging in geographic location from the southern tip of Scandinavia down to the Atlas mountains and across southern Asia to the eastern borders of Kazakhstan, share a common genotype. Or, at least, each has a genotype in which that part of the genome associated with climatic tolerances is the same or very similar for every subspecies, regardless of their different isolated origins, or has broad adaptive abilities. Not surprisingly, the predicted range for the ‘whole species’ and by extrapolation, *B. t. audax*, potentially covers a large area of the Australian mainland (Figure 6, Appendix I), namely, all of Victoria, south-eastern coastal areas of South Australia, the eastern half of New South Wales, coastal areas of southern Queensland, higher elevation areas near the coast in northern Queensland, and certain coastal areas of Western Australia.

Conversely, using the parameters found in the native habitat of *B. t. audax*, along with those of New Zealand and Tasmania, the predicted establishment area is much more restricted (Figure 7, Appendix I). The area includes coastal Victoria, parts of the coast of New South Wales north almost to Sydney, higher elevation areas of eastern Victoria and southern New South Wales.

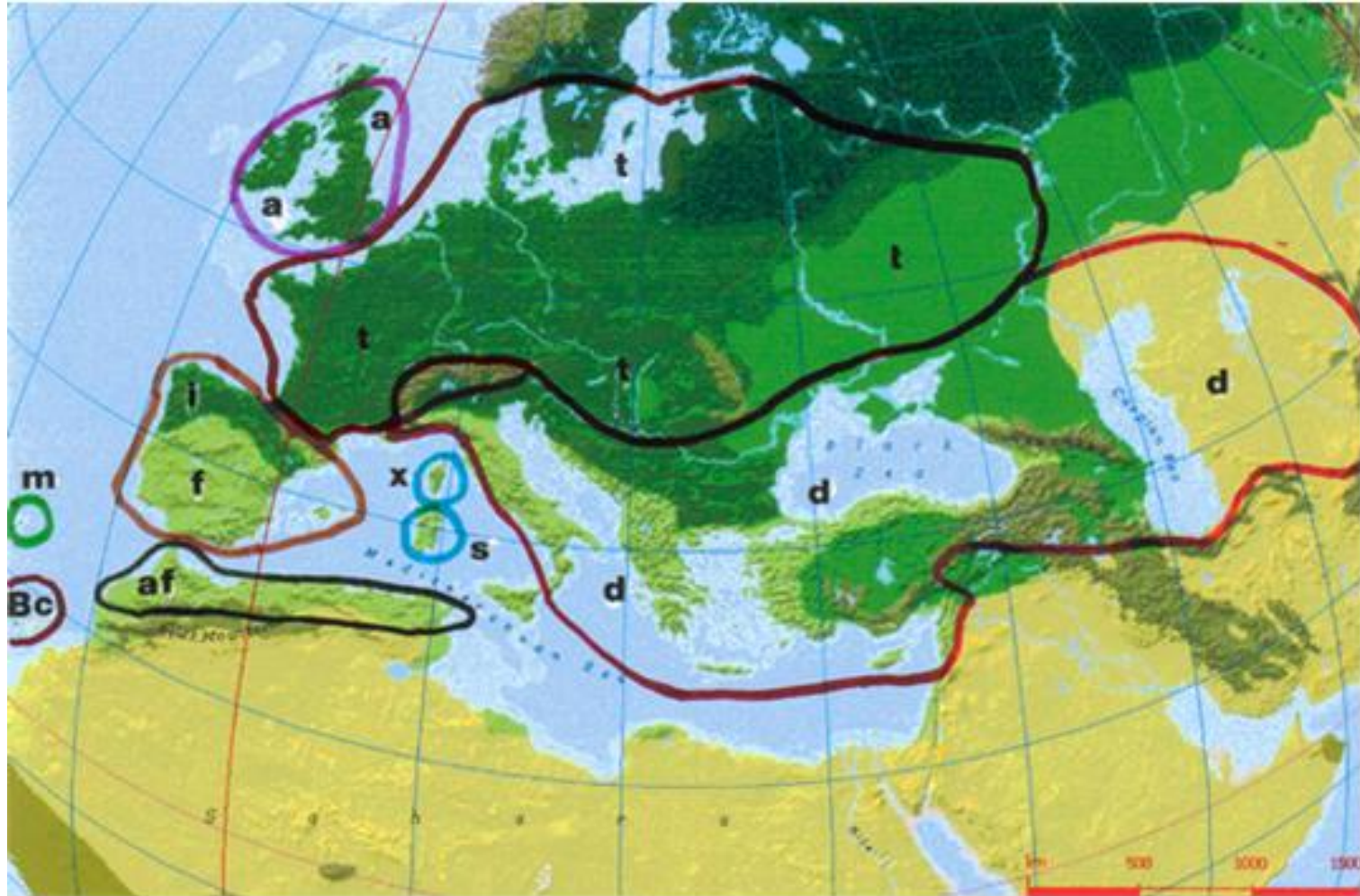


Figure 1. Probable boundaries of 10 of the subspecies of *B. terrestris*. Legend: subspecies of *B. terrestris*; a, *audax*; t, *terrestris*; l, *lusitanicus*; f, *ferrugineus*; d, *dalmatinus*; x, *xanthopus*; s, *sassaricus*; af, *africanus*; m, *maderensis*; Bc, *canariensis* (compiled by D. Griffiths, 2005).

In the penultimate paragraph of his discussion McClay states that:

‘It must be kept in mind that this [model 2] represents an absolute minimum predicted range for this [audax] subspecies in Australia. Even if *B. t. audax* is highly specialised to climates resembling those of its native range in Britain, it would still be expected to be able to establish throughout this area [model 2 range]. There is no direct evidence that the climatic requirements of *B. t. audax* are in fact as specialised as is assumed for this model. Thus, it should be expected that even this subspecies could establish in broader areas of Australia, possibly approaching the limits of the potential distribution of *B. terrestris s. l.* shown in *Figure 6*.’

This statement, based as it is on a presumptive model, appears also to stem from a limited knowledge of species concepts and species definitions (Mayr 1957). On the basis of the views of the eminent systematists expressed above, from personal knowledge and experience of studying speciation, and on the evidence of dissimilarities between *Bombus* subspecies genomes, even if they are limited, McClay’s first model is considered of limited relevance for assessing the establishment range of *B. t. audax* over the Australian mainland. It is not intended to introduce *Bombus terrestris sensu lato* to the mainland, only one of its subspecies which may or may not, but probably does not, share the same proclivities for hot/dry climates as say *B. t. africanus*, or *B. t. dalmatinus*. The island isolation enjoyed by *B. t. audax* over thousands of years cannot be dismissed as of no relevance except as a geographical barrier. As a systematist, I do not believe that McClay’s ‘broad band’ predictions for *B. terrestris sensu lato* can be applied to *B. t. audax*, given its long-term isolation in a climate not native to Australia, plus the inferences from morphology and molecular evidence that this subspecies differs from all the others (D. Griffiths, pers. comm. 2005). *Bombus t. audax* and *B. t. terrestris* are the only two subspecies confined to the colder northern regions of Europe (*Figure 1*). The southern ranges of both do not extend below latitude 45°N. The remaining nine subspecies existing below this line experience the hotter, drier conditions as defined by the presence of Mediterranean scrub vegetation (pale green colour outlining the northern shore of the Mediterranean sea), whilst in the extreme eastern part of its range *B. t. dalmatinus* is exposed to even hotter temperatures east of the Caspian sea. It does not seem reasonable to base predictive assumptions for *B. t. audax* upon heat/stress parameters experienced by these ‘southern’ subspecies. Thus we consider that only the second CLIMEX model specific to *B. t. audax* is relevant.

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APPENDIX III

LIFE CYCLE RELATIVE TO *B. TERRESTRIS* SUBSPECIES AND THEIR ABILITY TO ESTABLISH ON THE MAINLAND

Life cycle Information is taken from Sladen (1912), Cumber (1949, 1954), Alford (1975), Donovan & Wier (1978), Prÿs-Jones & Corbet (1991), Duchateau & Velthuis (1992); Goulson 2003; Benton 2006; <http://www.bio-bee.com/english/bombus/live.htm> and <http://www.bumblebee.org/>. Bumblebee colony castes comprise a queen (reproductive females, 20-23 mm long), workers (non-reproductive females, 11-17 mm long, may lay haploid eggs in the absence of a queen), and males (14-16 mm long) (*Figure 1*). The colony sequence is a single queen, then workers, and if a working brood is built up, but not on every occasion, males and new queens. The old queen, workers and males then die out, leaving the new queens to hibernate and renew the cycle.

A queen bumblebee emerging from a long hibernation in early spring must first forage for food for herself to replenish her strength and to build up her ovaries. There is a high mortality rate of new queens (Donovan & Wier 1978; Barron *et al.* 2000; Hergstrom *et al.* 2002; Goulson 2003a). After a few weeks, she begins searching for a suitable nest site, often in a disused rodent nest. The nesting material in the burrow is formed into a small chamber; pollen is collected, and with wax forms a base for the first egg mass. The queen also constructs a wax cup (the honey pot) which she fills with honey to act as her food supply while hatching her first brood of eggs. Depending upon the length and food abundance of the season, there are three separate broods (Duchateau & Velthuis 1992). The first eggs are few in number (~10). They hatch into larvae, are fed and nurtured by the queen and mature, pupate and emerge as the first workers in about three weeks. The second brood is larger (~35), and is looked after by the first generation; the new workers emerge in 3-4 weeks. Workers take over the foraging duties while the queen continues egg-laying. She will never again leave the nest. Subsequent nest size and number of reproductives produced is innately highly variable but again reflects food availability over an extended period and general health (Donovan & Wier 1978; Goulson *et al.* 2002; Goulson 2003a; Duchateau 2004; Duchateau *et al.* 2004; Hergstrom *et al.* 2002). A sequence of flowers for 12-15 weeks and a minimum nest size are needed to rear queens (Sladen 1912; Macfarlane, pers. comm. to S. Goodwin 1997). The food resources must be continuous during spring, summer and autumn, because, unlike honeybees, bumblebees only have enough food reserves in the hive to last the colony for a few days (Pelletier 2003). Only 15.5% of nests were found to have completed their developmental cycle in New Zealand, with very few queens producing reproductive nests (Donovan & Wier 1978). As Tasmanian data also show, nest size is not only variable, but those in unsuitable habitats will fail to produce any new queens (Hergstrom *et al.* 2002).

The life span of the queen from first oviposition ranges from 12-24 weeks (18 weeks on average). The life expectancy of an adult forager worker bee is about three weeks, so it has a total life cycle of seven weeks (Alford 1975). Those worker bees on nest duty only will live longer.

New queens and drones (males) are not produced until later in the cycle, in the third brood. Production of the third brood ends after ~ 2 months. Prior to this end point,

the queen may switch from laying diploid eggs into haploid eggs which become males. The earlier this process occurs, the more new queens are then produced. If this process is delayed too long, no new queens will be produced. The whole process is complex and control of the switch point to haploid egg production in the third brood and thus queen production or worker production is critical to commercial rearing. Some aspects are therefore not in the public domain. A uniform nest size and production of large numbers of workers is rare in nature, but sought after by commercial producers. It is not in the companies' interest for the hive to switch into early queen production.

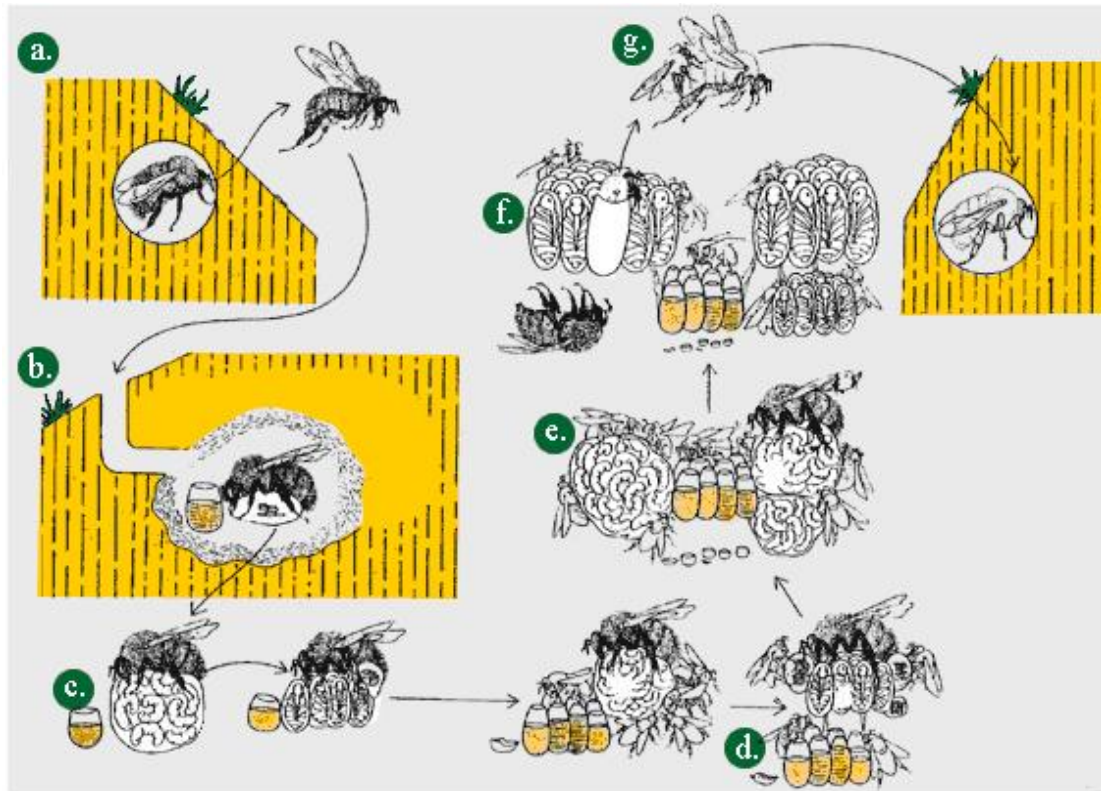


Figure 1. Life-cycle of *Bombus terrestris*. Reproduced with permission from the website of Bio-Bee Biological Systems, Israel.

(<http://www.bio-bee.com/english/bombus/live.htm>)

- a.** In springtime, the mated queen leaves her hibernation harborage and seeks out a nest site.
- b.** In the nest, the queen builds a thimble-shaped beeswax honey pot in which she stores nectar. Nearby she forms a lump of field-collected pollen, excavates a depression in it and lays one or more eggs in the depression, covering it with wax.
- c.** The eggs hatch and the larvae feed on their bed of pollen. As they grow, the queen opens the wax covering and adds more pollen and nectar. She perches on the brood clump, incubating the larvae to speed their development. The larvae mature and each spins a cocoon of silk in which it pupates and completes development into an adult.
- d.** After the new workers emerge, their empty cocoons are used as storage pots for honey or pollen. More pollen lumps with eggs are deposited alongside or on top of the old ones, and thus the irregular comb grows. Eventually there are enough worker bees to do the foraging and housekeeping tasks. The queen concentrates on laying eggs. The colony peaks to a few hundred individuals.
- e.** The colony switches from producing female workers to producing males and new queens, some time in mid- to late summer.
- f.** The males leave the nest a few days after emerging. The new queens mate with the males. The old queen dies before winter.
- g.** The new mated queens leave the nest and seek out a suitable overwintering site where they will stay

throughout winter.

The new queen must build up her fat body and fill her honey stomach to survive the hibernation period. She then leaves the nest to mate with males waiting in the vicinity, prior to dispersing to seek an individual hibernation site (Sladen 1912; Alford 1975). Age of queens at time of mating is usually 5-12 days old, ideally 7 days under long-day conditions; that of males 4-20 days old (Tasei *et al.* 1998; Sauter *et al.* 2001; Kwon *et al.* 2006a). Queens below a weight of 0.6g prior to diapause do not survive diapause (Beekman *et al.* 1998). If queens are produced early in summer, a few may found another colony to produce a second generation, but this is rare (Donovan & Wier 1978; Prÿs-Jones & Corbet 1991; Hergstrom *et al.* 2002). Hibernation sites in temperate countries are often beneath moss or leaf litter in moist sites under trees, on banks sloped to avoid arousal too early in spring (Pouvreau 1970; Alford 1969, 1975). Here the young queen stays in a diapause condition until the soil in spring reaches the required temperature to induce emergence. Dispersal may occur at this time to find forage and a nesting site. Spring migrations over large distances are reported in their natural range (Philip 1957; Estoup *et al.* 1996. This may occur even over large expanses of water (Mikkola 1984; Vepsäläinen & Savolainen 2000). It is these post-diapausing dispersing queens that are often observed in more remote areas.

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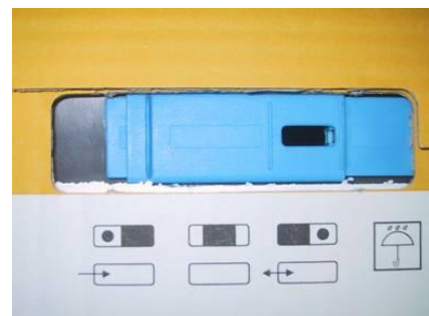
APPENDIX IV

EXAMPLE OF A COMMERCIAL *B. TERRESTRIS* HIVE FITTED WITH A QUEEN EXCLUDER DEVICE

Pictured below is the ‘total system hive’ developed by the commercial company Bunting Brinkman Bees, BV, Tilburg, Holland. This hive is used in tomato greenhouses in many countries of the world. The ‘total’ refers to the fact that the hive cover is sealed before leaving the dispatch section of the production unit, and remains so for all of its life. On dispatch it contains a supply of pollen to support the colony during transportation, together with a supply of nectar sufficient to feed the colony for all of its pollinating life. This is needed since the tomato flower does not produce nectar. During transportation, the entrance to the hive, the black rectangle just below the lid, is sealed, as shown in the first diagram below the entrance. After installation in the greenhouse, the hive can be opened in two ways: when the yellow tab is moved to the far right (lower of the three diagrams) worker bees can enter and leave on foraging expeditions. The structure and diameter of the entrance tunnel is such that it will exclude the exit of queen bees. It has been accepted by the USA, APHIS (Quarantine) authorities, as suitable for this purpose. When the tab is moved to the left (middle diagram), the entrance tube, which tapers internally, allows worker bees to enter but not exit. This position allows the grower to retain the population inside the hive, for removal when the hive completes its working life. At this time the population can be humanely killed by placing the hive in a cold store, or a small chamber filled with CO₂, after which it can be incinerated.



Commercial bumblebee hive



Example of a queen excluder device