

An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae)

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Abstract. *Bombus terrestris* is one of the most abundant bumblebee species in the West-Palaearctic. Its widespread domestication results in the movement of many colonies. The aim of this paper is to describe the 9 subspecies currently recognised and to list some of their most obvious characteristics. *Bombus terrestris* is not declining anywhere, on the contrary, its synanthropic spread through domestication may be expected. However, its autumn and winter populations rely on a restricted choice of flowers so they may be threatened locally by scrub clearance and the destruction of their favourite autumnal flowers.

Résumé. *Bombus terrestris* est une des espèces de bourdons les plus abondantes dans la région ouest-paléarctique. Son utilisation généralisée sous forme domestique entraîne des déplacements fréquents de très grands nombres de colonies. Le but de cet article est de présenter les 9 sous-espèces actuellement reconnues et de souligner certaines de leurs caractéristiques les plus notables. *Bombus terrestris* n'est en régression nulle part. Au contraire, du fait de sa domestication, on doit s'attendre à son expansion synanthropique. Toutefois, comme ses populations d'automne et d'hiver dépendent d'un choix très étroit de fleurs, celles-ci peuvent être localement menacées par le débroussaillage et la destruction de ses fleurs automnales favorites.

Keywords: Bumblebees, domestication, pollination, interbreeding, phenology.

Bombus terrestris (L. 1758) is one of the most abundant and widespread bumblebee species in the West Palaearctic. In 1988, the rearing had started in Belgium and in the Netherlands with *Bombus terrestris terrestris* collected locally. It is now widely domesticated and large numbers of colonies from different subspecies are transported from country to country (Velthuis 2002). This leads to more and more mixing between populations (Ings *et al.* 2005a).

Bombus terrestris includes several well differentiated subspecies. The most recent comprehensive papers about the *Bombus terrestris* subspecies are from Krüger (1951, 1954, 1956, 1958).

The aim of this paper is to describe the subspecies currently recognised among *Bombus terrestris* (L.), to give their main synonyms and to list some of their most obvious characteristics.

The *Bombus terrestris* (L.) subspecies

The most useful keys to identify *Bombus terrestris* characters are from Løken (1973) and Amiet (1996). A comprehensive comparison of the species with the near

Palaearctic *Bombus lucorum* (L. 1761), *B. cryptarum* (Fabricius 1785) and *B. magnus* (Vogt 1911), can be found in Rasmont (1984) and Rasmont *et al.* (1986).

In addition to the synonyms given here, Krüger (1951, 1954, 1956, 1958) used more than 90 names for infrasubspecific colour forms. These are not listed here.

We can recognize the following nine morphological subspecies in *Bombus terrestris*.

Ssp. terrestris (L.)

Apis terrestris L. 1758:578; lectotype ♀ Linnean Society London, Rasmont 1988. The lectotype designated by Day (1979) among the Linne's syntype do not fit with the most common interpretation of the species. A decision of the International Commission of Zoological Nomenclature now stabilizes this most common interpretation (Løken *et al.* 1994).

=*Bombus terrestris holsaticus* Krüger 1954:284; locus typicus: N. Germany. Type Zoölogische Museum Amsterdam, revised by PR.

Colour patterns. Fig. 1H. Collar narrow, yellow often mixed with black hairs, sometimes missing; fore margin of T2 yellow; hind margin of T3, T4, T5 and side of T6 white or whitish (T = Tergite); black elsewhere; corbicular cuticle and setae black. **Range:** continental Europe, N. of the 45th parallel.

Ssp. africanus Krüger 1956

Bombus terrestris africanus Krüger 1956:91; locus typicus: N. Algeria. Type Zoölogische Museum Amsterdam, revised by PR.

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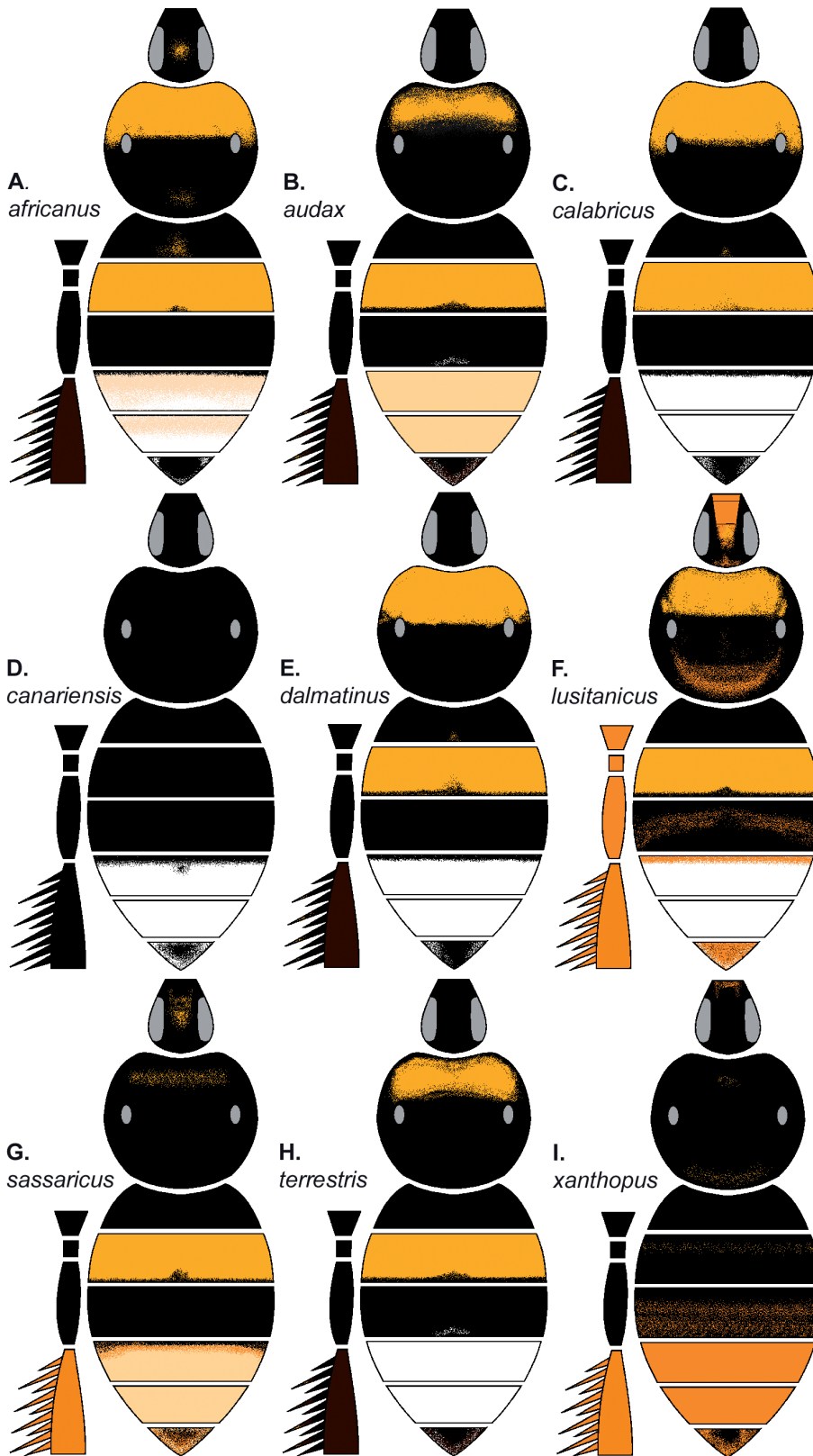


Figure 1

Schematic colouration of *Bombus terrestris* (L.) queens. **A**, ssp. *africanus* Krüger; **B**, ssp. *audax* (Harris); **C**, ssp. *calabricus* Krüger; **D**, ssp. *canariensis* Pérez; **E**, ssp. *dalmatinus* Dalla Torre; **F**, ssp. *lusitanicus* Krüger; **G**, ssp. *sassaricus* Tournier 1890; **H**, ssp. *terrestris* (L.) sensu stricto; **I**, ssp. *xanthopus* Kriechbaumer. For each ssp. the right-hand diagram shows the coat color; the left hand diagram represents a hind leg (coxa, trochanter, femur, tibia, corbicular bristles)

Colour patterns. Fig. 1A. Vertex with a few yellow hairs, more abundant in males; collar very wide, yellow never mixed with black; T2 yellow; hind margin of T3, T4, T5 and side of T6 white or whitish; black elsewhere; corbicular cuticle and setae black. **Range:** N. Africa.

Ssp. audax (Harris 1780)

Apis audax Harris 1780:130 nec 1780:137; locus typicus: England. Not revised.

Colour patterns. Fig. 1B. Collar narrow, yellow, often mixed with black; fore margin of T2 yellow; T4, T5 and side of T6 light reddish in queens, white in workers and males; black elsewhere; corbicular cuticle and setae black. **Range:** British Islands.

Ssp. calabricus Krüger 1958

Bombus terrestris calabricus Krüger 1958:328; locus typicus: "Calabrien". Type Zoölogische Museum Amsterdam, revised by PR.

Colour patterns. Fig. 1C. Collar yellow, very wide, extending below the tegula, very low on the mesopleuron; T2 yellow; T4, T5 and side of T6 white; black elsewhere; corbicular cuticle and setae black. **Range:** S. Italy, Sicily.

Ssp. canariensis Pérez 1895

Bombus terrestris var. *canariensis* Pérez 1895:191. Locus typicus: "Canaria et Tenerife". Type Erlandsson 1979:189; revised by PR.

=*Bombus (Bombus) schmidtii* Pittioni 1938b:253; locus typicus: "auf Blumen des botanischen Gartens in Orotava auf der Insel Tenerife - Kanarische Inseln". Not revised.

Colour patterns. Fig. 1D. T4 and T5 white, T6 mostly white, black elsewhere; corbicular cuticle and setae black. Coat shaggy. **Range:** only bumblebee on the Canary Islands (Gran Canaria, La Gomera, El Hierro, La Palma, Tenerife).

Ssp. dalmatinus Dalla Torre 1882

Bombus terrestris Dalmatinus Dalla Torre 1882:26; locus typicus: "Mittelmeerküsten: Fiume, Livorno, Sizilien, Spalato, Ragusa, Athen, Amasia und Elizabethpol". Not revised.

=*Bombus terrestris lucoformis* Krüger 1956:87; locus typicus: Anatolie. Type Zoölogische Museum Amsterdam, revised by PR. See Aytekin et al. (2003)

=*Bombus terrestris uralicola* Krüger 1956:89; locus typicus: Orenburg. Lectotype ♀ Zoölogische Museum Amsterdam, revised, present designation; labels: 1) manuscript "Orenburg"; 2) printed on red paper "TYPE"; 3) printed "collectie C. et O. Vogt, Acq.1960"; 4) manuscript "B. terrestris prope nigro apicalis"; 5) typed on white paper with a red border "Rasmont det. 1996 *Bombus terrestris uralicola* Krüger, 1956:89 LECTOTYPUS femelle"; 6) printed "Rasmont det.1996, *Bombus (Bombus) terrestris uralicola* Krüger B1108". Paralectotype ♂, labels: 1) manuscript "Orenburg"; 2) printed "collectie C. et O. Vogt, Acq.1960"; 3) printed with a red border "Rasmont det. 1996 *Bombus terrestris uralicola* Krüger, 1956:89 PARALECTOTYPUS"; 4) printed "Rasmont det.1996, *Bombus (Bombus) terrestris uralicola* Krüger B1108"; **syn. nov.**

Colour patterns. Fig. 1E. Collar yellow never mixed with black, wide but never extending below the tegula; fore margin of T2 yellow; T4, T5 and side of T6 white; black elsewhere; corbicular cuticle and setae black. **Range:** farthest S.E. France, N. Italian and Balkanic Peninsulas and surrounding regions,

Anatolia, Transcaucasia, Caucasus, N. Iran, S. Ural, Alai, Altai.

Ssp. lusitanicus Krüger 1956

Bombus terrestris lusitanicus Krüger 1956:78; locus typicus: Portugal. Type Zoölogische Museum Amsterdam, revised by PR.

=*Bombus terrestris balearicus* Krüger 1956:78; locus typicus: Mallorca. Type Zoölogische Museum Amsterdam, revised by PR.

=*Bombus terrestris ferrugineus* auct. nec Schmiedeknecht (*ferrugineus* Schmiedeknecht 1878:359 is only an infrasubspecific form). Not revised.

=*Bombus terrestris pyrenaicus* Krüger 1958:328; locus typicus: Pyrenees. Type Zoölogische Museum Amsterdam, revised by PR.

=*Bombus maderensis* Erlandsson 1979:191; locus typicus: "Madeira, Funchal"; Type Naturhistoriska Riksmuseet Stockholm, revised by Rasmont et al. 1986.

Colour patterns. Fig. 1F. Collar yellow of variable size, most often wide but not extending below the tegula; often some reddish hairs on the scutellum; fore margin of T2 yellow; hind margin of T3, T4, T5 and side of T6 white; black elsewhere, though more or less reddish (occasionally, all the black coat may turn reddish); cuticle and legs setae most often entirely reddish. **Range:** S.W. France, Iberian Peninsula, Balearic Islands, Madeira. There may be an intergradation between *ssp. terrestris* and *lusitanicus*, in a cline extending from S. France to central Germany, the hybrid being the form *ferrugineus* Schmiedeknecht.

Ssp. sassaricus Tournier 1890

Bombus sassaricus Tournier 1890:223. Not revised.

Colour patterns. Fig. 1G. Some yellow hairs on the vertex; collar missing or restricted to a few yellow hairs; T2 with a narrow yellow stripe; T4 to T6 off-white; black elsewhere, though more or less reddish (in some cases, all the black coat may turn reddish); cuticle and legs setae entirely reddish. **Range:** Sardinia.

Ssp. xanthopus Kriechbaumer 1870

Bombus xanthopus Kriechbaumer 1870:157. Locus typicus: "Corsica".

Type Zoologische Staatssammlung München, revised by PR.

Colour patterns. Fig. 1I. Collar missing or restricted to a few yellow hairs; T4 to T6 reddish to red; black elsewhere, mixed with reddish hairs on the ventral side; cuticle and legs setae entirely reddish. **Range:** Corsica, Capraia Island, Elba Island.

Discussion

Geographical range

In its original distribution, *Bombus terrestris* is the only bumblebee species with a Mediterranean-centred area. It occurs in all the countries around the Mediterranean sea except in Egypt (fig. 2). It is not restricted to this region, however: to the north, it extends to the latitude of Helsinki and east, to the Altai (Pekkarinen & Kaarnama 1994) but it is absent from the high alpine level, the deserts and the arid, subdesertic steppes.

Bombus terrestris has been introduced as a pollinator in (for example) New-Zealand (ssp. *audax*; Hopkins 1914; Dumbleton 1949; Gurr 1964; MacFarlane & Gurr 1995; Goulson & Hanley 2004), Tasmania (ssp. *audax*; Semmens *et al.* 1993; Buttermore 1997; Hingston *et al.* 2001), Chile (ssp. *audax*; Ruz & Herrera 2001; Ruz 2002) and Japan (ssp. *terrestris* and ssp. *dalmatinus*; Matsumura *et al.* 2004; Inari *et al.* 2005; Nagamitsu *et al.* 2007). Its range tends to expand quickly, reaching adjacent countries such as Argentina (Torretta *et al.* 2006), and competing with native pollinators (Dafni & Shmida 1996; Dafni 1998; Hingston & McQuillan 1998, 1999; Hergstrom *et al.* 2002; Matsumura *et al.* 2004; Hingston 2005, 2006; Inoue *et al.* 2007). It is now clear that, contrary to the fears expressed by Özbek (1993), *Bombus terrestris* is not a threatened species but, instead, a more or less invasive one.

Phenology

Whereas, in N. Europe, the phenology of *Bombus*

terrestris is similar to that of other bumblebee species, the same is not true in the Mediterranean regions, where colony foundation may occur in autumn and winter. Duhayon & Rasmont (1993) described the particular life-cycle of this species in the Maure Mts (S.E. France). In this region, queens enter a summer diapause by mid-July, with the midsummer heat. They emerge in late-September, with the first heavy autumn rains (fig. 3). Except for this two-and-a-half months diapause, *B. terrestris* is active all year round with at least two generations. The same phenology has been described in Corsica (Ferton 1901; Rasmont & Adamski 1996) and in Sardinia (Krausse 1910a, 1910b). In S.W. Turkey, it seems that *B. terrestris* shows only one winter generation, without a spring or summer generation (Yeninar *et al.* 2000; Gürel *et al.* 2008).

According to Ricciardelli d'Albore (1986), this winter activity occurs only at lower altitudes. Over 500 m, the phenology of *B. terrestris* is identical to that of other bumblebees. The same phenological shift occurs

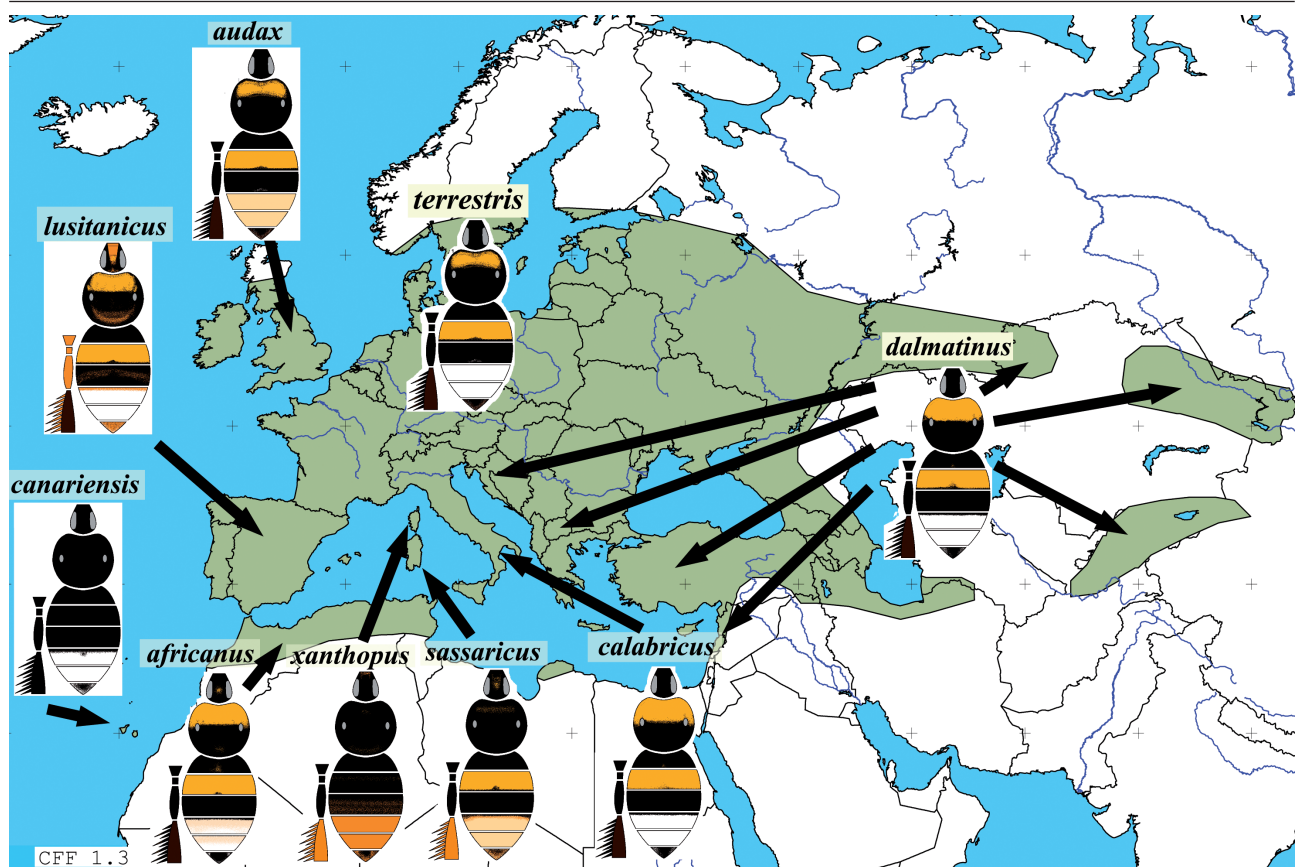


Figure 2
Distribution of *Bombus terrestris* (L.)

from the Mediterranean regions to temperate climates, where the phenology of *B. terrestris* is similar to that of other bumblebee species, i.e. active from March till August (fig. 4).

This ability of *Bombus terrestris* to fit to eco-climatic conditions through phenology variations is a key to the success of its domestication (Velthuis 2002).

Flower preferences

Bombus terrestris is a highly polylectic bumblebee, collecting from hundreds of different flower species. For France and Belgium, Rasmont (1988) lists 309 flower species. In Poland, Ruskowski (1971) lists 570 flower species. This latter author, however, pooled data for *B. terrestris* and *B. lucorum* and did not recognise *B. magnus* and *B. cryptarum*. For Corsica, Rasmont & Adamski (1996) state that “*Bombus terrestris* seems to exploit any available floral resource”. In Turkey, Özbek (1997) mentions 62 favourite plant taxa, among which *Vitex agnus-castus* L. is the late-summer forage-resource for the entire Aegean region. In Anatolia, the authors themselves observed 29 visited plant species (Rasmont & Flagthier 1996).

Most of the plant species mentioned above flower in spring or summer. In the Mediterranean regions, *B. terrestris* has to rely on a much narrower choice for its autumn generation. In this season, *Arbutus unedo* L. becomes the most important and, in many places, the only resource. It is likely that, without this plant, *B. terrestris* would not be able to have an autumn generation. This relationship may be even more specific: Rasmont *et al.* (2005) have stressed that the pollen of *Arbutus* flowers has a sterol content that matches the metabolic needs of *B. terrestris*.

The ruderal *Salpichroa origanifolia* (Lam.) Baillon, originating from S. America, is currently invading waste ground in the western Mediterranean, providing additional forage during autumn and winter (Rasmont 1999). Where this plant thrives, it supports huge populations of *B. terrestris*. As *Arbutus unedo* is often destroyed to prevent forest fires, *Salpichroa origanifolia* could locally be the only remaining autumn foraging plant, as it is the case in the Hyères surroundings (France, Var; pers. obs.).

In the Canary Islands, another imported ruderal plant: *Ipomoea purpurea* Roth fulfils the same role for *canariensis* (Rasmont 1999).

Subspecies status

Bombus terrestris has evolved into well differentiated subspecies. Some of the insular ones are so distinct that they have been described as true species: *canariensis* in the Canary Is., *xanthopus* in Corsica and *sassaricus* in

Sardinia. Other subspecies are less clearly differentiated: *audax* in the British Is., *lusitanicus* in the Iberian Peninsula and *africanus* in N. Africa. Some subspecies are hardly distinct from the nominal *terrestris* from N. Europe: *calabricus*, from Italy and Sicily and *dalmatinus* from the Balkans, the Urals and Asia.

Subspecies differ not only in coat colours but also in physiological features, such as the conditions for diapause (De Jonghe 1986a,b), visual capabilities (Chittka *et al.* 2004) and susceptibility to nosema (De Jonghe 1986a). Behavioural traits also differ markedly: *canariensis*, *xanthopus* and *sassaricus* are more aggressive, *sassaricus*, *lusitanicus* and *dalmatinus* form larger colonies, *canariensis* and *sassaricus* are the quickest nectar gatherers (Chittka *et al.* 2004; Ings *et al.* 2005b;

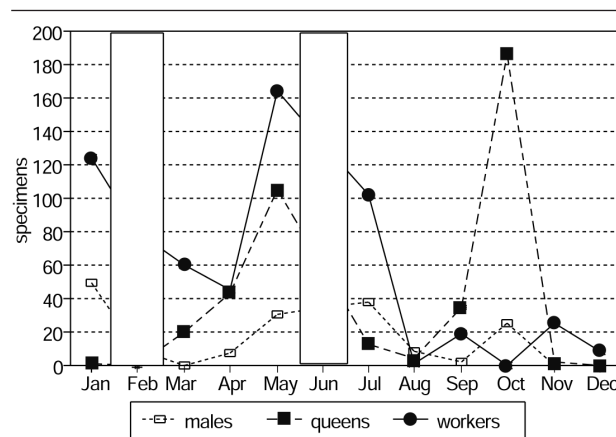


Figure 3

Phenology of *Bombus terrestris* (L.) in the S.E. of France. After Duhayon & Rasmont (1993). Data for February and June are too few to be introduced in the graph (white boxes).

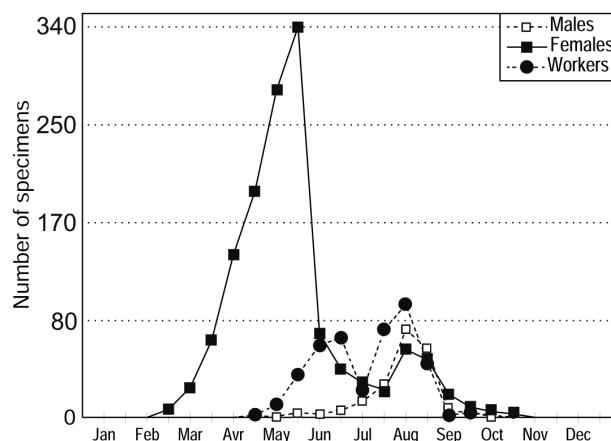


Figure 4

Phenology of *Bombus terrestris* (L.) in Belgium and N. France. Data from the Banque de Données Fauniques de Gembloux et Mons (Belgium), data set used by Rasmont *et al.* 1993. Original.

Velthuis & van Doorn 2006 and numerous personal observations). It is therefore understandable that some subspecies have been domesticated more often than others (Velthuis 2002; Velthuis & van Doorn 2006). The most widely reared subspecies is nowadays *dalmatinus*. Some other subspecies are reared in small number, as it is the case of *canariensis*. A huge number of *sassaricus* colonies have been produced until 1998 but this subspecies is now completely abandoned. The bumblebees breeders also gave up with the ssp. *xanthopus* and the ssp. *lusitanicus*.

Some specimens of these insular or peninsular subspecies have escaped from greenhouses and may nowadays be encountered in horticultural surroundings throughout Europe (e.g. Ortiz-Sanchez 1992, 1993; Ornos 1996 and personal observations). Some authors fear that they may interbreed with, or even supplant the local subspecies (Ings *et al.* 2005a, b; 2006; Velthuis & van Doorn 2006).

Even if the insular taxa *xanthopus* (from Corsica), *sassaricus* (from Sardinia) and *canariensis* (from the Canary Island) look very different, Estoup *et al.* (1996) show that their genetic variability overlaps that of *B. terrestris* (L.). However, Widmer *et al.* (1998) quote that *canariensis* is genetically quite distant from all the others subspecies, while van den Eijnde & de Ruijter (2000) show that it interbreeds easily in the lab with the ssp. *terrestris* from the Netherlands. Erlandsson (1979) describes *maderensis* as a good species endemic from the island of Madeira and Widmer *et al.* (1998) find that it is also genetically quite distant from continental populations, however, it is not morphologically different from the Iberian subspecies *lusitanicus* and we conserve here *maderensis* as a simple synonym.

B. terrestris is far less polymorphic in the oriental part of its distribution. There are no perceptible differences between the populations from the S.E. France, Balkan, Asia Minor, the Ural and the mountains of central Asia: they all belong to the subspecies *dalmatinus*. Even detailed molecular or morphometric studies are unable to draw a clear distinction between some of the taxa formerly recognized by Krüger, as *lucoformis* Krüger (Aytekin *et al.* 2003). However, Widmer *et al.* (1998) show that the populations from Crete are clearly differentiated by their DNA from other *dalmatinus* strains.

The variability of N. African populations is poorly known and needs further investigation.

As far as we know, all these taxa are able to interbreed in experimental conditions (De Jonghe 1986a, b; van den Eijnde & de Ruijter 2000; ; Velthuis *et al.* 2002; Ings *et al.* 2005a). Some interbreeding could also occur in natural conditions (Rasmont & Adamski 1996; Rasmont & Quaranta 1997). However, it seems that at least some of these subspecies are able to

distinguish between themselves and others as they do not copulate freely but show a significant preference for a consubspecific mate (Ings *et al.* 2005a).

Conservation status

To conclude, *Bombus terrestris* is not declining anywhere. On the contrary, it is likely to be widely spread by domestication, leading to some interbreeding between the currently known subspecies. However, it is of concern that its autumn and winter populations rely on a narrow choice of flowers. These populations may be locally endangered by scrub clearance or the destruction of their favourite autumnal flowers.

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