Apidologie (2021) 52:792–800
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DOI: 10.1007/s13592-021-00865-7

Original article

Assessing of reproductive performance of commercial *Bombus terrestris dalmatinus* colonies in different conditions and some practical ways to mitigation of its invasive risk

Fehmi GUREL, Rahman SAKLI

Department of Animal Science, Akdeniz University, 07058, Antalya, Turkey

Received 10 November 2020 – Revised 14 March 2021 – Accepted 18 April 2021

Abstract – To better understand the potential establishment and spread of *B. t. dalmatinus*, we compared reproductive outputs of 45 commercially produced *B. t. dalmatinus* colonies, containing one queen and 50 workers in their natural habitat, greenhouse, and laboratory conditions. The total number of adult gynes and gyne pupae produced per colony was significantly higher in the laboratory colonies (100.90 ± 46.20) than in the field colonies (63.70 ± 44.70) and greenhouse colonies (28.47 ± 12.39), respectively. Although laboratory colonies significantly produced more gynes, reproductive abilities of greenhouse and field colonies show that commercial movement of bumblebee colonies for pollination could have serious impacts on natural ecosystems notably for pollination of open field crops. The nest entrance of all colonies was restricted by fitting with a queen excluder. All vents of the greenhouses were suitably covered with nets. Colonies were removed from the greenhouses about 6 weeks after initial placement. Following these measures, we prevented 266 gynes from escaping from 15 hives in 2.3 ha area of tomato greenhouse. To be 100% effective, we strongly recommend that these measures should be implemented together.

Bombus terrestris **/ gyne production / invasion / measures**

1. INTRODUCTION

Bumblebees are ecologically and economically important pollinators and consist of approximately 250 known species (Williams 1998; Michener 2000). Five bumblebee species (*B. terrestris*, *B. lucorum*, *B. ignitus*, *B. impatiens*, and *B. occidentalis*) are currently used as commercially produced pollinators worldwide. *Bombus terrestris* L. (native to Eurasia and North Africa) is the most widely used species (Velthuis and van Doorn 2006). Each year, more than two million commercially produced *B. terrestris* colonies have been used in at least 60 countries, some of which are outside of their native range including in China, Korea, Japan, Mexico, and Chile (Graystock et al. 2016). Although several subspecies of *B. terrestris* were used in the early years of commercial rearing, today *Bombus terrestris dalmatinus* (native to South East Europe, especially Balkan Peninsula and Turkey) has become the main commercialized subspecies due to the suitable characteristics for mass rearing such as the large size of workers and high success rate of colonies. *Bombus terrestris terrestris* (native to Northern Europe) is also currently produced by some companies (Lecocq et al. 2016; Chandler et al. 2019).

B. terrestris is an annual, eusocial insect and shows great ecological flexibility, particularly in terms of diapause responses (Estoup et al. 1996;

Corresponding author: F. Gurel, fgurel@akdeniz.edu.tr
Handling editor: David Tarpy

Dafni 1998). In cooler climates, mated queens emerge from hibernation in late winter or spring and found new colonies. Towards the end of the colony cycle in late summer, sexuals (gynes and males) are produced. Gynes and males leave the colony to find mates. The old queen, workers, and males die, and the newly mated queens go into diapause as foundresses the following spring (Alford 1975; Goulson 2003; Chandler et al. 2019). However, in warmer climates such as Mediterranean coastal region, queens aestivate during the warm dry summer rather than hibernating, and colonies are active throughout the winter (Gurel et al. 2008). Several authors have also observed bivoltinism (two colony cycles per year) in some *B. terrestris* populations (Douglas 1973; Buttermore 1997; Rasmont et al. 2008).

After a large number of colonies were introduced around the globe, it was recognized that commercially produced *B. terrestris* (mainly *B. t. dalmatinus*) colonies have become established and spread in the wild of both native and non-native regions. Invasions occur when reproductive queens escape. The queens are capable of founding new colonies and producing a high number of reproductives (Dafni et al. 2010; Goulson 2010). Additionally, commercial *B. terrestris* colonies produce more gynes and are better competitors than the local conspecific populations (Gosterit and Gurel 2005; Ings et al. 2006). Some other invasive traits of *B. terrestris* are early seasonal emergence, generalist foraging preference, high adaptability under adverse climatic conditions in various habitats, and regulation of life cycle in a year in newly colonized area (Dafni et al. 2010). The invasion of this species has caused some negative ecological effects including the introduction of non-native bumblebee species, subspecies, the introduction of novel or more virulent pests and parasites, and competition with native pollinators for floral resources and nest sites (Evans 2017). Since mass rearing of *B. terrestris* started in the late 1980s, many studies have shown that commercial greenhouse *B. terrestris* populations have become established and spread outside their native range in many countries such as Australia (Tasmania), Japan, Chile, and Argentina (Buttermore 1997; Goka 2010; Montalva et al. 2011; Morales et al. 2013). Previous studies also suggest that gene introgression from non-native bumblebee species (Kondo et al. 2009), subspecies, or non-local genotypes (Goulson 2010; Kraus et al. 2011) had occurred and pathogens had spilled over from commercial greenhouse *B. terrestris* populations to wild bumblebee populations (Colla et al. 2006).

Although there are examples of establishment in the wild originating from commercial colonies, the scale of risk is difficult to assess due to lack of information on the rate of queen production of colonies placed in greenhouses and fields. To date, experimental studies have investigated colony growth and reproductive production of commercial *B. terrestris* in different habitats (Inoue et al. 2010; Parmentier et al. 2014) and compared colony growth and reproductive success between native and commercial *B. terrestris* colonies under field conditions (Ings et al. 2006) and laboratory conditions (Gosterit and Gurel 2005). For a more precise risk assessment, data on reproductive success of commercial colonies held in very different environments would be needed. In this study, to better understand the potential establishment and spread of *B. t. dalmatinus*, the main subspecies used by bumblebee rearing industry, we compared reproductive outputs (focusing on the numbers of gynes and gyne pupae produced) of commercial *B. t. dalmatinus* colonies, containing one queen and 50 workers in their natural habitat, greenhouse, and laboratory conditions. We also evaluated the usefulness of measures to mitigate invasive risk posed by commercial bumblebees.

2. MATERIALS AND METHODS

In this study, forty-five colonies of *B. terrestris dalmatinus* were obtained from a commercial supplier. Prior to the experiment, we checked all colonies and counted numbers of workers in the colonies. All nests were weighed (without the sugar solution reservoir and outer cardboard box). At the beginning of the experiment, all colonies (about 8 weeks old) contained one queen and approximately 50 workers and had not yet produced any adult gynes and males and gyne and male pupae. The nest entrance of all colonies was restricted by fitting with a queen excluder device

to keep gynes in the nest. The colonies were randomly allocated to one of three treatments, laboratory, greenhouse, or field. Fifteen colonies per treatment were established in place on 14 March 2020. In the laboratory colonies, some colony parameters such as number of adult bees, founding queen status (alive or dead), timing of the first gyne emergence, and gyne and gyne pupae status (present or absent) were monitored three times a week. In the field colonies, 3 weeks after the colonies were placed in the field, the nest entrances of all colonies were entirely closed at nightfall, and colonies were then transferred to laboratory two times a week. After the same observations, the colonies were returned to field and placed on exactly the same spot where they had been before. The laboratory and field treatments were terminated for each colony when either a great number of males and gynes had emerged and founding queen had died or when moribund, defined as less than 10 workers remaining and the color of the combs become dark brown. The laboratory and field treatments were terminated on day 35.33 ± 3.56 (lasted about 5 weeks) and on day 63.47 ± 2.87 (lasted about 9 weeks), respectively. In the greenhouse colonies, to prevent the escape of any gynes in colonies, we did not make any observations within the nests during the experiment**.** Therefore, it was not possible to determine the timing of the first gyne emergence for greenhouse colonies. The end date of the greenhouse treatment was considered by observing foragers entering with pollen. Four weeks after the colonies were placed in the greenhouse, each colony was monitored for a 15-min period (between 09:00 and 12:00 h) two times a week. Colonies were removed from the greenhouse when less than 10 workers carrying pollen were seen for a 15-min period. Greenhouse treatment was terminated on day 42.20 ± 3.10 (lasted about 6 weeks).

At the end of the each treatment, colonies were re-weighed and then placed in a −20°C freezer to kill and keep the nest until dissection. Each nest was dissected, and the following parameters were recorded: total number of gynes, total number of gyne pupae, colony life time under treatment conditions, colony weight change, and timing of the first gyne emergence (except for greenhouse colonies). Viable gyne larvae were not recorded in any of the nests. Unfortunately, for experimental reasons, it was not possible to precisely determine total number of workers and males produced in the field and greenhouse colonies because inevitably some males escaped from the nests and some workers died in the field and greenhouse colonies. We had no information concerning the number of dying and escaping individuals in these colonies.

2.1. Colony treatments

In the laboratory treatment, all colonies were fed ad libitum with the same sugar syrup solution (50%, w/w) and frozen fresh pollen collected from honeybee colonies and maintained under standard rearing conditions (26°C, 60% relative humidity and constant darkness). In the greenhouse treatment, colonies with syrup solution reservoir were placed in six commercial beefsteak tomato greenhouses (covered with plastic and glass approximately 50/50 %, a total of 2.3 ha area, six to seven colonies per ha) in Antalya, Turkey (latitude: 36° 99′ 73N, longitude: 30° 77′ 68E, altitude: 60 m above sea level). All vents of the greenhouses were suitably covered with nets. This locality was roughly 30 km from the Akdeniz University campus area and situated in the Mediterranean coastal line. In the field treatment, colonies were placed in two field sites, situated in the Akdeniz University campus area, in Antalya, Turkey (latitude: 36° 89′ 37N, longitude: 30° 64′ 71E, altitude: 50 m above sea level). Each of these two sites, consisting of seven or eight colonies, was located at least 2 km apart to enhance foraging activity. Colonies were also placed at least 2 m apart to reduce the accidental movements between nests. This campus area consisted of 360 ha of land including mostly evergreen sclerophyllous trees and shrubs, such as maquis and garrigue (Ünal and Gökçeoğlu 2003) and had a typical Mediterranean climate with long, hot, dry summers and rainy warm winters (Figure S1). There were also a number of ornamental and medicinal plants and citrus and acacia trees that were visited by bumblebees during the field treatment period. We selected this field area because native *B. t. dalmatinus* populations were observed in this habitat before the use of commercial

B. terrestris colonies in Turkey (Özbek 1997). We also determined the placement date of colonies in field in accordance with the life cycle stage of native *B. t. dalmatinus* populations in this region (Gurel et al. 2008). Unlike native *B. t. dalmatinus* nests, all nest boxes were covered with plastic and placed on metal stands in a shaded area to protect them from rain, predators, direct sunlight, and ground moisture. The sugar solution reservoirs of colonies were removed from the hives before placing the colonies in the field.

2.2. Statistical analysis

Prior to statistical analyses, all raw data were tested for normality and homogeneity of variances using the Shapiro-Wilk test. Data for the colony weight change, the colony life time, and the total number of adult gynes and gyne pupae produced per colony (normally distributed) were analyzed using a one-way ANOVA followed by Tukey's post hoc tests. Data for the number of gynes produced by colonies and the number of gyne pupae produced by colonies (non-normally distributed) were analyzed using non-parametric Kruskal-Wallis H test followed by the Mann-Whitney U test. All analyses were carried out in the statistical software package SPSS (version 12.01). Data were reported as mean and standard deviation (SD). The timing of first gyne emergence was calculated as the time in days between the colony placement (the beginning of experiment) and the date of the emergence of the first gyne in the colony.

3. RESULTS

Significant differences between treatments were found in the number of gynes, the number of gyne pupae, and the total number of adult gynes and gyne pupae (Table I). The mean number of gynes produced by colonies in the laboratory treatment was 60.27 ± 37.05, whereas in field and greenhouse treatments, it was only 25.00 ± 31.01 and 17.73 ± 8.02, respectively (Kruskal-Wallis Test: Chi-Square = 15.94, df=2, P<0.0001). Laboratory colonies also produced significantly more gyne pupae (40.60 ± 15.44) than in the greenhouse colonies (10.73 ± 9.32) (Kruskal-Wallis Test: Chi-Square = 22.66, df=2, P<0.0001). Similarly, the total number of adult gynes and gyne pupae produced per colony was significantly higher in the laboratory colonies (100.90±46.20) than in the field colonies (63.70 ± 44.70) and greenhouse colonies (28.47 ± 12.39), respectively (Table I) (one-way ANOVA, df=2, F value= 13.74, P<0.001).

As expected, there were no differences in colony weight between treatments at the beginning of the experiment. But at the end of the experiment, significant differences between treatments were found in the colony weight (one-way ANOVA, df=2, F value= 45.21, P<0.001). On average, colonies gained 786.40 ± 138.10 g in weight in the laboratory treatment, 487.50 ± 217.60 g in field treatment, and 254.60 ± 65.30 g in the greenhouse treatment (Fig. 1). Due to males escaping from the nests and workers dying outside the nests, this is not an estimate of true weight changes in the field colonies and greenhouse colonies. Interestingly, colony weight in greenhouse treatment was 52 % lighter than those in the field treatment. The highest colony life time under treatment conditions was found in the field colonies (lasted 63.47 ± 2.87 days) followed by greenhouse colonies (lasted 42.20 ± 3.10 days) and laboratory colonies (lasted 35.33 ± 3.56 days) (one-way ANOVA, df=2, F value= 317.09, P<0.001) (Fig. 2). The mean timing of the first gyne emergence was observed at the nests in field colonies and laboratory colonies on days 48 (n=10) and 27 (n=15), respectively. Although reproductive output varied substantially between colonies both within and between treatments, all colonies produced males and gyne pupae. While all laboratory and greenhouse colonies produced adult gynes, in the field colonies, 10 of the 15 colonies produced adult gynes at the end of the experiment.

4. DISCUSSION

Our results clearly show that there were significant differences in the number of gyne and gyne pupae between treatments (laboratory, field, and greenhouse). Similarly previous studies showed that gyne production in bumblebees can be highly variable (ranged from 0 to 304) between colonies

Table I. The number of gynes and gyne pupae in laboratory, field, and greenhouse colonies

Colony traits	Laboratory			Field			Greenhouse		
	N	Mean ± SD	Min–max	*N*	Mean ± SD	Min–max	*N*	Mean ± SD	Min–max
Number of gynes	15	60.3 ± 37.0[a]	13–125	10	25.0 ± 31.0[b]	0–101	15	17.7 ± 8.0[b]	7–35
Number of gyne pupae	15	40.6 ± 15.4[a]	15–60	15	38.7 ± 22.3[a]	10–70	15	10.7 ± 9.3[b]	2–40
Total number of gyne and gyne pupae	15	100.9 ± 46.2[a]	45–185	15	63.7 ± 44.7[b]	11–147	15	28.5 ± 12.4[c]	12–61

Means that do not share a letter are significantly different ($p < 0.05$) based on Mann-Whitney *U* and Tukey's post hoc tests

and affected by many factors such the food quality and quantity, the diapauses conditions, the worker/larva ratio, the climate conditions, and genetic factors (Duchateau and Velthuis 1988; Beekman and van Stratum 2000; Duchateau et al. 2004; Gosterit and Gurel 2005; Hingston et al. 2006; Holland and Bourke 2015). Indeed, gyne production requires greater resource investment than male and worker production and should depend on the continuous supply of proteins and carbohydrates (Duchateau and Velthuis 1988; Goulson et al. 2002; Requier et al. 2020). In the laboratory, all colonies were fed ad libitum (unlimited) with pollen and sugar solution. Therefore, it is not surprising that laboratory colonies in our experiments produced the highest number of gyne and gyne pupae (Table I). But in field colonies, workers must forage for pollen and nectar as well as feeding and tending the larvae. Our field results also show that the cost of foraging and

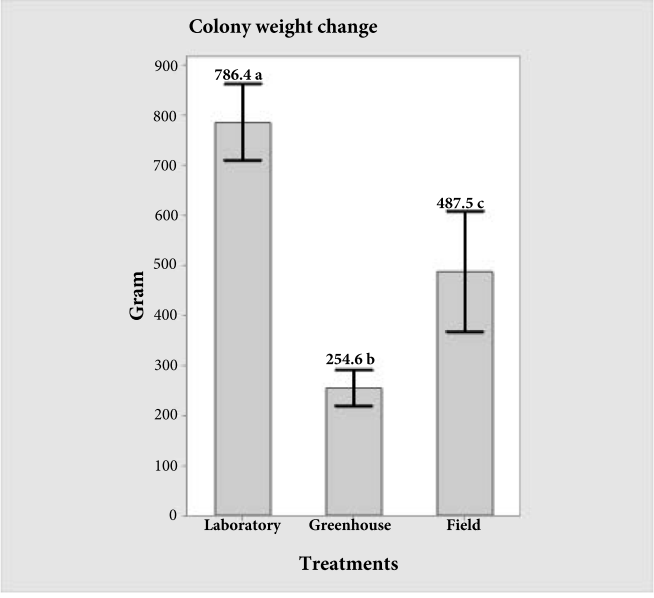


Figure 1 Mean change in weight of bumblebee colonies placed in laboratory, field, and greenhouse. Letters above bars indicate significant differences between treatments based on Tukey's post hoc test ($p < 0.05$).

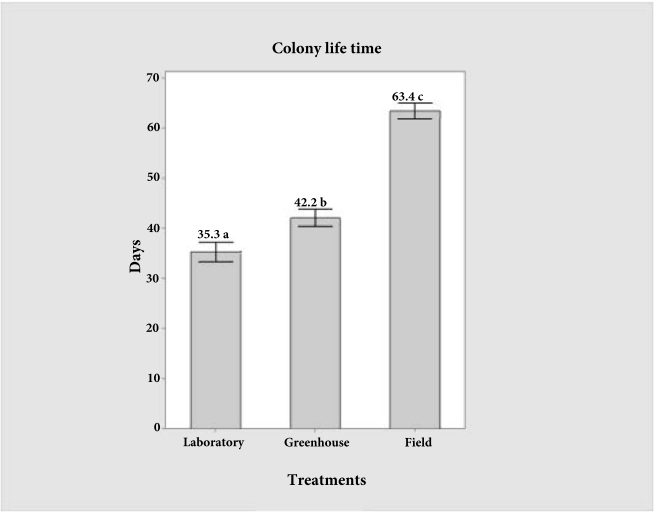


Figure 2 Comparison of the colony life time between three different treatments. Letters above bars indicate significant differences between treatments based on Tukey's post hoc test ($p < 0.05$).

foraging tradeoff has an impact on queen production. As a result, in this study, we determine the potentials of gyne production of commercially produced *B. t. dalmatinus* colonies placed in the favorable natural habitat and greenhouse conditions. Interestingly considering all the parameters examined in this study, results show that variations among greenhouse colonies were lower than in the laboratory and field colonies. For example, the number of gynes produced varied from 13 to 125 in the laboratory colonies, 0 to 101 in the field colonies, and 7 to 35 in the greenhouse colonies (Table I). The low variations in greenhouse colonies in our experiment could be explained by availability of limited amount of pollen and a single pollen source.

Our results also show that greenhouse and field colonies produce large numbers of queens and pose a potential ecological risk. Unfortunately, we currently have very limited knowledge on what proportion of commercial *B. t. dalmatinus* queens has established colonies outside greenhouses and how does this vary according to locations and seasons. Bumblebee queens released from commercial colonies face with a range of stress factors in the field that can reduce their establishment and survival. For example, availability of food, nest sites or hibernation/aestivation sites, as well as parasites and climatic conditions play important roles (Holland and Bourke 2015; Baron et al. 2017; Requier et al. 2020). Moreover, habitat loss, pollution, pesticides, predators, and climate change (very high and low temperatures, flooding) have had some negative effects not only on *B. terrestris* but also on all bee species (Williams and Osborne 2009). Under field conditions, colony foundation and early colony growth are also a critical phase where high levels of colony mortality are observed (Baer and Schmid-Hempel 2003). Previous study also shows that bumblebee populations may be limited by availability of nest sites or hibernation/aestivation sites rather than forage (Goulson et al. 2002). Indeed, abundance of native *B. t. dalmatinus* populations varies greatly in similar climatic and food availability conditions in the Mediterranean region (F. Gurel, personal observations).

Although escaping gynes have to cope with many factors to established colonies, considering the large quantities of colonies used over the last two decades, it seems that some colonies may develop outside the greenhouses (Goka 2010; Montalva et al. 2011; Morales et al. 2013). Because of their ability to effectively pollinate a diversity of flowering plants, commercial bumblebee colonies provide pollination services for both

greenhouse and open field crops. We also know very little about the risks posed by using commercial bumblebee colonies for the pollination of open field crops. Therefore, because of the complexity of ecosystems, further studies will be necessary to determine the establishment and reproductive ability of the introduced bumblebees in different conditions and in different seasons. The regulations and restrictions on the use of commercially produced bumblebee colonies focus largely on non-native species or subspecies. However, most important possible undesirable effects of commercial bumblebees are transmission of parasites or pathogens to native organisms and competition with native bees for floral resources and nest sites (Goulson 2003). Using native species or subspecies may not reduce these risks. In addition, it is difficult to distinguish commercial strains and subspecies because of morphological similarities. Hence, more holistic approaches including native subspecies are required.

In general, measures such as covering greenhouse vents and doors with nets, fitting of a mechanical restriction (queen excluder) in the hive entrance to keep gynes in the nest, and disposing of old nests (at the end of their functional foraging life, usually 6 weeks later) to restrict the escape of males and gynes are recommended to reduce the spread of commercially produced bumblebees (Ings et al. 2006; Koide et al. 2008; Goka 2010; Evans 2017). In this study, following these measures, we prevented 266 gynes from escaping from 15 hives in 2.3 ha greenhouse tomato areas. To be 100% effective, we strongly recommend that these measures should be implemented together. Regardless of the origin of the commercial produced colonies, to minimize the environmental risks, the disposal of all used colonies (no later than 6–7 weeks after initial placement) should be strictly implemented by bumblebee suppliers, the queen excluders should be compulsory on all bumblebee boxes used for both greenhouse and open field pollination, and the use of screens on greenhouses should be mandatory. Considering the many benefits of bumblebees, these precautions would be the most viable option. In comparison to greenhouse, under open field conditions, commercial bumble bee colonies carry greater environmental risks such as competition with native pollinators, transmission of parasites or pathogens, and hybridization. Therefore in using commercial bumble bee colonies for field pollination, more effective measures and management strategies for risk mitigation are needed.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-021-00865-7.

ACKNOWLEDGEMENTS

We would like to thank Yakup Efendi for supplying the bumblebee colonies used in this study and two anonymous referees for their valuable comments on this manuscript.

Availability of data and material All data generated or analyzed during this study are included in this published article.

Code availability Not applicable.

AUTHOR CONTRIBUTION

FG designed the experiments. FG and RS performed the laboratory, field and greenhouse work, and data analyses. FG wrote the manuscript. Both authors read and approved the final manuscript.

FUNDING

This research was supported by the Scientific Research Projects Coordination Unit of Akdeniz University, Project Number: FYL-2020-5227.

DECLARATIONS

Ethics approval Not applicable.
Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

Évaluation de la performance reproductive de colonies commerciales de *Bombus terrestris dalmatinus* dans différentes conditions et quelques conseils pratiques pour atténuer leur risque d'invasion.

***Bombus terrestris* / production de jeunes reines / invasion / mesures.**

Eine Methode zur Erfassung der Reproduktionsleistung von kommerziellen *Bombus terrestris dalmatinus* Kolonien unter unterschiedlichen Bedingungen und einige praktische Hinweise um ihr Invasionsrisiko zu mindern.

***Bombus terrestris* / Produktion von Jungköniginnenn / Invasion / Massnahmen.**

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