



No influence of male origin on mating characteristics and queen survival in *Bombus terrestris*

Ismail Yashan BULUS¹ , and Ayhan GOSTERIT² 

¹ Department of Animal Production and Technologies, Faculty of Applied Sciences, Muş Alparslan University, Muş, Turkey

² Department of Animal Science, Faculty of Agriculture, Isparta University of Applied Sciences, Isparta, Turkey

Received 21 April 2025 – Revised 3 November 2025 – Accepted 16 December 2025

Abstract – This study was aimed at determining the mating characteristics and diapause performances of queens mated with queen-born males (QMs) and worker-born males (WMs) in *Bombus terrestris* colonies. Using laboratory-reared colonies, mating latency, copulation duration, and queen mating preferences were analyzed for both QM and WM groups. Results showed no significant differences in mating latency and copulation duration between the two male groups. However, WMs were slightly heavier than QMs during the mating process ($t = -2.02$, $P = 0.044$). Despite these weight differences, the mating success rates of QMs and WMs were comparable, with queens showing no significant preference for either group. Additionally, the survival rates of queens during diapause were unaffected by whether they mated with QMs or WMs. This research suggests that the source of males in *B. terrestris* colonies does not influence mating success or queen survival, providing valuable insights for bumblebee breeding and colony management.

***Bombus terrestris* / Mating characteristics / Worker-born males / Queen-born males / Diapause**

1. INTRODUCTION

Bumblebees are essential for crop pollination, especially in greenhouses and natural flora. There are more than 250 species of bumblebees around the world (Williams et al. 2008). Despite some variations in biological, behavioral, and ecological properties among the bumblebee species, their colony lifecycles can be described similarly (Gradish et al. 2019). For instance, *Bombus terrestris*, one of the most common bumblebee species, has an annual lifecycle. This cycle begins when the mated queen exits the diapause. After emergence, the queen starts to seek an optimum place where to lay eggs. During

this time, the queen consumes pollen and nectar, and her ovaries are ready to lay eggs. Subsequently, the queen begins to lay eggs (Goulson 2012). At this stage, she not only tends to the brood but also forages for food to sustain herself and the larvae. When the first workers emerge, the workers take on foraging and brood-caring responsibilities, while the queen focuses on egg laying. When the colony population reaches the maximum in terms of workers, the founder queen changes egg production strategies. She starts to lay haploid male eggs instead of diploid female eggs. While this happens at a switch point, on the other hand, already egg-laid diploid eggs have grown into new queens (Duchateau and Velthuis 1988). The stage when the founder queen loses her influence and superiority over the colony is the competition stage, which is also the last stage

Corresponding author: I. Y. Bulus, y.bulus@alparslan.edu.tr
Manuscript editor: Mathieu Lihoreau

of the colony life cycle. In this stage, competition for reproduction starts among the workers, especially between the queen and the workers. The fact that some of the workers start laying eggs, the behavior of eating or throwing out each other's eggs between the queen and workers, or even among the workers themselves, indicates that the colony order is disrupted (Duchateau and Velthuis 1988; Amsalem et al. 2015). The competition phase in which workers start laying eggs is also considered an indicator of the imminent end of the colony (Yeninar et al. 2000; Gosterit and Gurel 2005; Gosterit 2016). In this stage, males develop from haploid eggs laid by both queens and workers as adults. In addition, these males are indistinguishable from each other visually and can also mate with queens and fertilize. After a certain period, these abnormal changes in colony organization end with the death of the founder queen, workers, and males. Only newborn queens live.

One of the most important stages in the life cycle of *Bombus terrestris* is the mating stage. It influences both colony foundation success and pollination performance. Several factors affect mating success, including temperature, humidity, kinship, and the size and age of queens (Amin et al. 2010, 2012; Erkan et al. 2024). Another important factor is male traits, such as weight, age, and virginity (Amin et al. 2012; Gösterit 2016; Belsky et al. 2020; Zhao 2021). For instance, in *B. terrestris* males, weight influences mating and remating ability. According to previous studies, lighter males exhibit longer mating latency and longer copulation duration compared to heavier males (Amin et al. 2012; Gosterit and Gurel 2016). Specifically, heavier males experience shorter mating latency and shorter copulation duration compared to lighter males (Amin et al. 2012; Gosterit and Gurel 2016). In addition, sperm can influence the survival of fertilized *B. terrestris* queens (Korner and Schmid-Hempel 2003), as well as hibernation success, queen longevity, and fitness (Baer and Schmid-Hempel 2005).

The source of produced males are queens and workers in *B. terrestris* colonies. Although there is competition in male production between

queens and workers, queens have a domination on male production. According to previous studies, the queen produces 95% of males in *B. terrestris* colonies (Alaux et al. 2004; Lopez-Vaamonde et al. 2004). However, both queen-born males (QM) and worker-born males (WM) seem quite similar, contrary to honeybees. In colonies established by queens mated with two different groups of males, there are no differences in terms of the colony development traits such as colony initiation time, timing of the first worker's emergence, and populations of offspring (Gosterit and Bulus 2019; Zhao et al. 2021). On the other hand, WMs have smaller wings and sperm counts compared to QMs (Zhao et al. 2021).

In recent years, several studies have explored the ecological and biological significance of bumblebee males (Ostevik et al. 2010; Wolf et al. 2012; Ogilvie and Thomson 2015; Belsky et al. 2020; Zhao et al. 2021). Despite this, research on the reproductive males produced by queens and workers and their specific characteristics remains limited—particularly with regard to their impact on colony dynamics and mating behavior. Gosterit and Bulus (2019) investigated colony developmental traits in *B. terrestris* colonies founded by queens that mated with males produced by either queens (QMs) or workers (WMs). Similarly, Zhao et al. (2021) examined sperm and mating traits of *B. terrestris* males along with colony development traits.

In commercial and scientific rearing of *B. terrestris*, efforts are typically made to minimize relatedness, optimize environmental conditions for mating (e.g., temperature and humidity), and use individuals of appropriate age. However, the origin of males—whether queen- or worker-derived—is often overlooked when males are collected from colonies. Even under optimal mating conditions, mating success does not always reach expected levels, and considerable queen mortality may occur during diapause despite apparently successful mating. These factors suggest that additional biological variables, such as male origin, may contribute to variation in reproductive outcomes. Therefore, the primary aim of this study was to evaluate whether male origin (queen- or worker-derived) influences

mating performance and the diapause success of queens in *B. terrestris*.

days, respectively. The experimental design is presented in Fig. 1.

2. MATERIAL AND METHODS

2.1. Obtaining queen-born and worker-born males

In this study, laboratory-reared *Bombus terrestris* colonies were established from commercially purchased founder queens whose prior relatedness was unknown; however, mating between males and young queens from the same colony was avoided to prevent inbreeding in the following generation. As mentioned in the previous section, queen born males (QMs) and worker born males (WMs) are almost identical in appearance. To be able to easily distinguish between these males, some special techniques have to be used. The most reliable method to obtain queen born males is to use virgin queens. As this ensures, it can be guaranteed that all males develop from haploid eggs laid by the queen caste. For this reason, virgin queens were collected from *B. terrestris* colonies. These collected queens were placed in individual tubes in the diapause chamber without mating. At the end of the diapause period of about 2 months, these virgin queens were placed in groups of 10 in special rearing boxes and transferred to the bumblebee rearing room (27–28 °C, RH 55–60%). In this way, the diapaused virgin queens were allowed to lay eggs and produce males, thus obtaining QMs. Meanwhile, in order to obtain males from the eggs of workers, groups of 20 reproductive workers were put into similar boxes and transferred to the bumblebee rearing room, just like virgin queens. Thus, WMs were obtained. Both virgin queens and reproductive workers were fed ad libitum with 50 Brix sugar syrup and pollen until sexual maturity, which occurs after 7 days for queens and 12 days for males (Duvoisin et al. 1999; Amin et al. 2010). In this study, the ages of the queens and all males (QMs and WMs) used were 6–8 days and 12–14

2.2. Mating stages

All of the QMs and WMs were marked on the thorax using a queen marking pen in two different colors. After the marking process, mating was carried out using mating age queens collected from *B. terrestris* colonies reared in the laboratory. In the mating procedure, 30 virgin queens and 60 males (30 QMs + 30 WMs) were placed in the mating cage each time, and they were expected to mate. As soon as the queens and males started to mate, the time was recorded and taken into separate transparent boxes in pairs. These boxes were observed, and the mating time of each male was determined by recording the time at the end of mating (Gosterit and Gurel 2016). At this stage, the mating latency, mating choices rates of queens, and mating rates of males in two different groups were also determined. In addition, immediately after mating, the queens and males were weighed, and their weights were recorded. The mating applications were repeated 13 times using different males and queens each time. The mating cages were observed for 1 h in each mating application. The queens and males that did not mate within this period were considered non-mated.

2.3. Data analysis

The data obtained for both groups of males were analyzed using the statistical package MINITAB. Descriptive statistics were obtained for each trait, and the Shapiro–Wilk test was used to test whether the data were normally distributed. As only the mating latency data were not normally distributed, the Mann–Whitney *U* test was used to compare the groups. The remaining characteristics, such as copulation duration, queen weight, and male weight, were normally distributed, and the *t*-test was used to compare

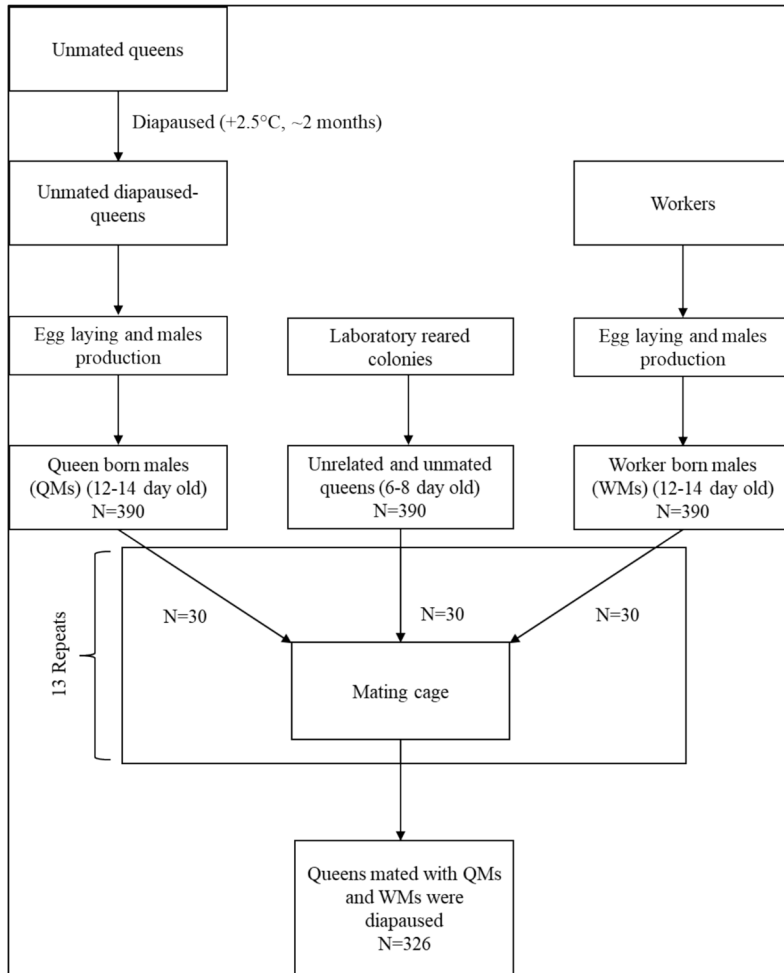


Fig. 1 Experimental design for mating trials and diapause assessment in *Bombus terrestris* (unmated queens and workers were used to produce queen-born males (QMs) and worker-born males (WMs), respectively. Unrelated unmated queens (6–8 days old) were paired with 12–14-day-old QMs or WMs in mating cages ($N=30$ per group) across 13 replicates. A total of 390 males from each group were tested. After successful mating, queens were subjected to diapause ($N=326$) to evaluate post-mating diapause survival and subsequent colony initiation.)

them. In addition, the z test was used to determine the differences between the groups in terms of the proportions obtained in the study Fig 1.

3. RESULTS

In the study conducted to test the mating latency of queens mated with queen-born males (QMs) and worker-born males (WMs), 326 pairs were mated. According to our findings, the mating latency of queens mated with QMs and WMs

was 6.82 ± 0.45 min and 7.33 ± 0.50 min, respectively (Table I, Fig. 2). There were no significant differences between the groups of QMs and WMs ($Z = -1.213$, $P = 0.225$). Accordingly, the copulation duration of queens mated with WMs was 27.44 ± 0.66 min, while the copulation duration of queens mated with QMs was 26.86 ± 0.63 min (Table II, Fig. 3). The difference between the copulation duration of queens mated with these two groups of males was not statistically significant ($t = -0.64$, $P = 0.523$). In addition, the research used two times as many males as

Table I Mating latency of queens mated with queen-born males and worker-born males

Groups	N	Mating latency (min)		
		(Mean ± S.E)	Min	Max
QMs	169	6.82 ± 0.45	1.00	29.00
WMs	157	7.33 ± 0.50	1.00	38.00
Total	326	7.07 ± 0.34	1.00	38.00

mated queens were also determined (Table V). There was no significant difference between the weights of mated queens in both experimental groups ($t = 1.05$, $P = 0.294$).

In order to determine the relationship between queen weight, male’s weight, mating latency, and copulation duration, correlations between these traits were analyzed (Table VI). According to the correlation coefficient values between the traits, there is no significant

relationship between queen weight and mated male weight, mating latency, and copulation duration. Similarly, mating latency did not affect the copulation duration of the couples. However, the results showed that there was a significant positive relationship between male weight and mating latency and a significant negative relationship between male weight and copulation duration.

Table II Copulation duration of queens mated with queen-born males and worker-born males

Groups	N	Copulation duration (min)		
		(Mean ± S.E)	Min	Max
QMs	169	26.86 ± 0.63	7.00	55.00
WMs	157	27.44 ± 0.66	9.00	55.00
Total	326	27.14 ± 0.45	7.00	55.00

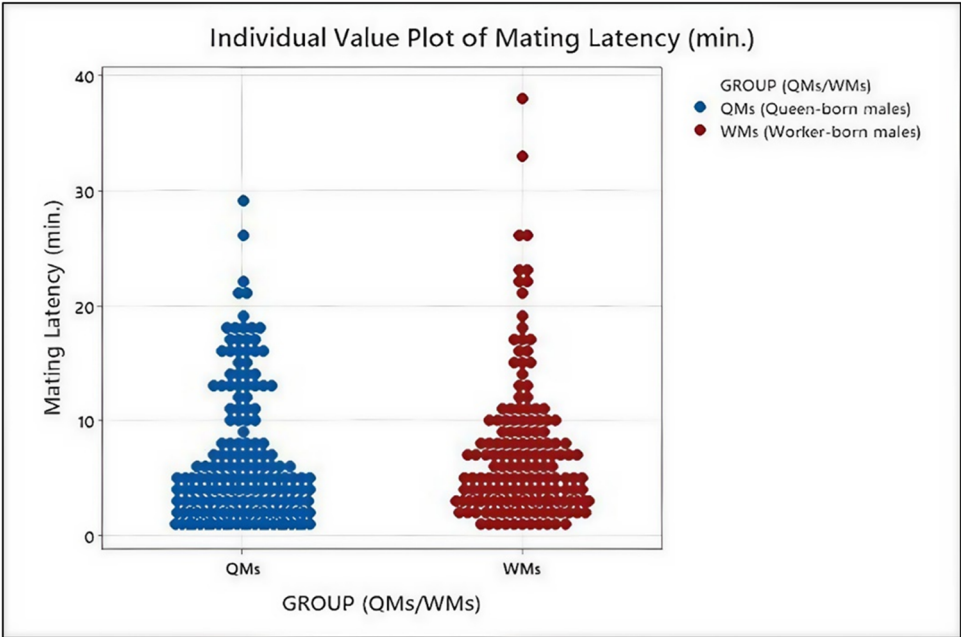


Fig. 2 Individual value plot of mating latency in *Bombus terrestris* males. (The plot shows the time elapsed before copulation initiation (mating latency, minutes) for queens paired with queen-born males (QMs; blue) and worker-born males (WMs; red). Each point represents an individual mating trial. The figure illustrates the variation and distribution of mating latency between QMs and WMs)

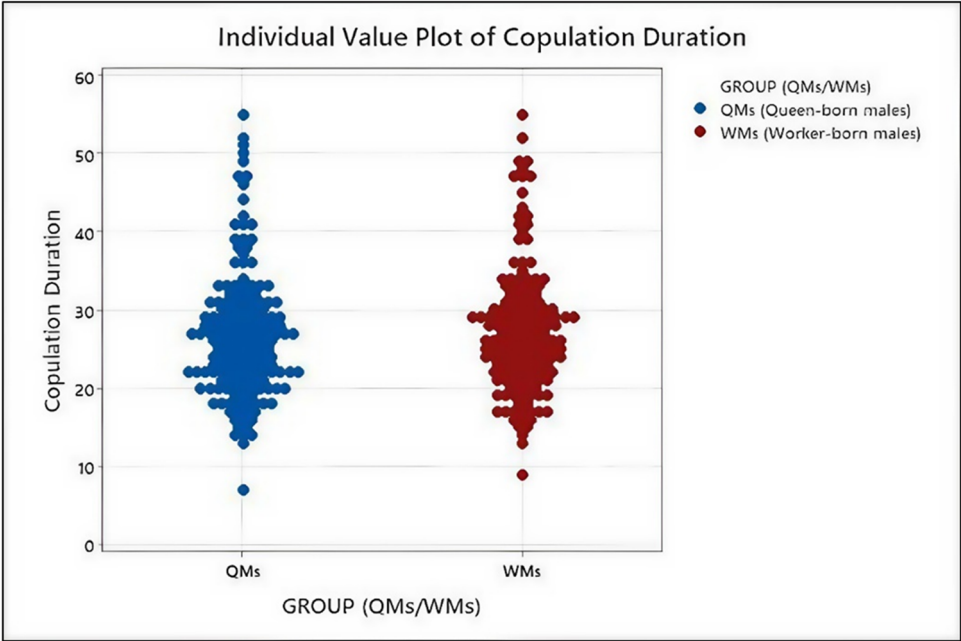


Fig. 3 Individual value plot of copulation duration of *Bombus terrestris* males (Copulation durations (minutes) are shown for queen-born males (QMs, blue) and worker-born males (WMs, red). Each point represents an individual mating event. The plot indicates the variation and distribution of copulation duration between the two male groups)

Table III The values of mate (QMs or WMs) selection of queens

Groups	Number of queens	Number of males	Mated males	Mating ratio (%)
QMs		390	169	43.33
WMs		390	157	40.25
Total	390	780	326	83.55

Table IV Mating weight of queen-born males and worker-born males

Groups	N	Weight (g)		
		(Mean ± S.E)	Min	Max
QMs	169	0.240 ± 0.003 ^b	0.137	0.369
WMs	157	0.249 ± 0.003 ^a	0.154	0.336
Total	326	0.245 ± 0.002	0.137	0.369

^{a,b}Means followed by different letters are different ($P < 0.05$)

Table V Mated queen weight with queen-born males and worker-born males

Groups	N	Weight (g)		
		(Mean ± S.E)	Min	Max
QMs	169	0.795 ± 0.008	0.440	1.053
WMs	157	0.783 ± 0.008	0.502	1.027
Total	326	0.789 ± 0.006	0.440	1.053

queens from both experimental groups in each mating. In general, the mating rate in the study was 83.58% (Table III).

According to the results, the mating weights of QMs and WMs were 0.240 ± 0.003 g and 0.249 ± 0.003 g, respectively (Table IV). There was a significant difference between the groups in terms of the weight of males during the mating period ($t = -2.02$, $P = 0.044$). Although not directly related to the performance of QMs and WMs, the mating weights of the used and

Table VI Correlation coefficients between mating performance characteristics of males and queens mated with these males

	Queen weight	Male weight	Copulation duration
Male weight	0.072 0.192		* **
Copulation duration	−0.040 0.476	−0.135 0.015	
Mating latency	−0.098 0.077	0.109 0.048	0.017 0.760

*, **, The upper value in each cell represents the correlation coefficient, and the lower value represents the *P* value

A total of 326 queens, 169 of which were mated with males produced by queens and 157 of which were mated with males produced by worker bees, were put into diapause. Of the queens in diapause, 126 surviving queens mated with QMs, and 113 surviving queens mated with WMs. At the end of the diapause period, the survival rates of the queens in the groups were 74.55% and 71.97%, respectively (Fig. 4).

4. DISCUSSION AND CONCLUSION

There are two sources of produced males in *Bombus terrestris* colonies, one from workers and one from queens. While queens and males mate randomly in nature, except for inbreeding, queens are mated with males from unrelated colonies in bumblebee mass rearing. Mating is carried out without paying attention to the resources

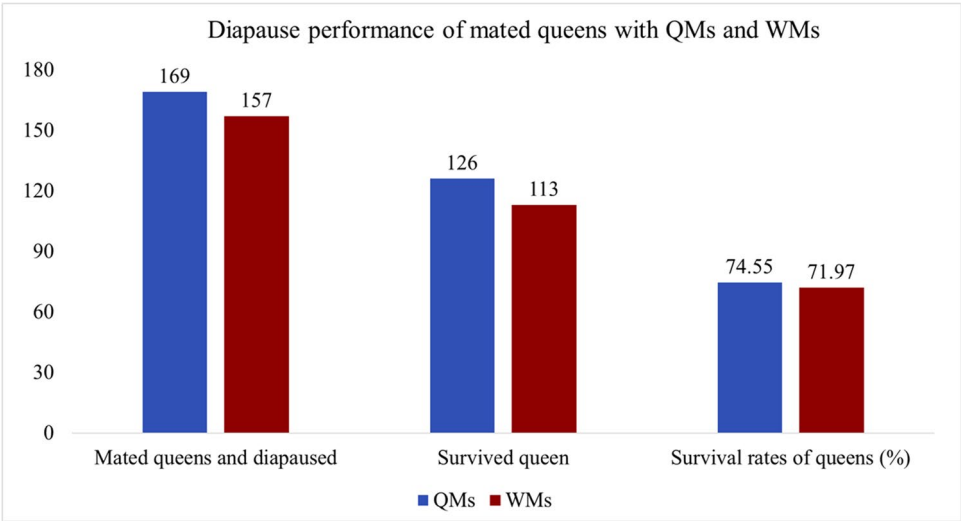


Fig. 4 Diapause performance of mated queens with queen-born males (QMs) and worker-born males (WMs) (The number of queens that mated and entered diapause (QMs: *N* = 169; WMs: *N* = 157), the number of queens that survived diapause (QMs: *N* = 126; WMs: *N* = 113), and the survival rates (%) after diapause are presented. Although queens mated with QMs showed slightly higher survival (74.55%) compared to those mated with WMs (71.97%), the overall diapause performance was similar between groups)

of males produced in these manageable colonies. However, considering that the quality of sperm can influence mortality, diapause success, and fitness of mated queens (Korner and Schmid-Hempel 2003; Baer and Schmid-Hempel 2005), it can be argued that the characteristics of the male are as important as those of the queen for future generations.

There is dimorphism in the males of *B. terrestris* (Zhao et al. 2021), although the queen-born males (QMs) and worker-born males (WMs) of bumblebees are not visually distinguishable. In honeybees, WMs are lighter than QMs, and this situation is consistent (Gencer and Firatli 2005). Conversely, there is a gap in QMs' and WMs' weights in bumblebees. In a previous study, the weight of QMs and WMs was found to be 371.07 ± 63.84 mg and 256.99 ± 68.08 mg, respectively (Zhao et al. 2021). In contrast to their study, our results have shown that the weight of WMs was heavier than QMs (0.249 ± 0.003 g and 0.240 ± 0.003 g, respectively). These weight differences between male groups may be related to emerging weight and methodological differences in the production of QMs.

According to previous studies, the mating ratio in *B. terrestris* is influenced by many factors, including age, size of males and queens, pheromones, temperature, humidity, and mating cage materials (Kwon et al. 2006; Amin et al. 2010, 2012; Imran et al. 2017). However, our results show that the source of males (QMs or WMs) does not play a role in the mating ratio, contrary to the previous study (Zhao et al. 2021). Males produced by workers or founder queens do not influence the mate choice of queens, nor does the mating ratio. In addition to the mating characteristics of QWs and WMs, the diapause performance of the queens mated with these males was determined. During diapause, queen survival is influenced by environmental factors and intrinsic traits (Beekman et al. 1998; Gosterit and Gurel 2009; Nasir et al. 2019; Woodard et al. 2019; Shi et al. 2023). In the present study, it was found that QWs and WMs mating with queens did not affect the survival rate of queens in diapause. According to Zhao et al. (2021), the

survival rate of WM-mated queens was higher than that of QM-mated queens, in contrast to our finding.

Consequently, the effects of male sources (QMs and WMs) on the mating performance of *Bombus terrestris* were tested in the present study. According to the results obtained, whether the males with which queens mate are queen-sourced or worker-sourced does not affect the mating latency, copulation duration, and mate choice of queens. Among the traits examined in the study, males from workers were found to be heavier than those from queens.

Although studies on the role of males have increased in recent years, the role of males in bumblebee colonies is still not fully understood (Rundlöf et al. 2014; Gosterit and Gurel 2016; Belsky et al. 2020; Fowler et al. 2020; Zambra et al. 2020; Jin et al. 2024). It is hoped that this study will provide insight into the mating and diapause processes of QMs and WMs produced in colonies. In addition, it is expected that the studies carried out to fill the knowledge gap on the importance and role of males will lead to important steps in improving bumblebee breeding methods, investigating the pollination behavior of plants on which bumblebees are used, and controlling diseases and pests.

AUTHOR CONTRIBUTIONS

Study conception and design were done by IYB and AG. Data collection and preparation were done by IYB. Data analysis was done by AG. The first draft of the manuscript was written by IYB and AG. All authors read and approved the final manuscript.

FUNDING

Open access funding provided by the Scientific and Technological Research Council of Türkiye (TÜBİTAK). This study was supported by the Scientific and Technological Research Council of Turkey (TUBITAK) under the Grant Number 118O457. The authors thank TUBITAK for their support.

DATA AVAILABILITY

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval No license is required to study this bee.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

REFERENCES

- Alaux C, Savarit F, Jaisson P, Hefetz A (2004) Does the queen win it all? Queen-worker conflict over male production in the bumblebee, *Bombus terrestris*. *Naturwissenschaften* 91:400–403. <https://doi.org/10.1007/s00114-004-0547-3>
- Amin MR, Than KK, Kwon YJ (2010) Mating status of bumblebees, *Bombus terrestris* (Hymenoptera: Apidae) with notes on ambient temperature, age and virginity. *Appl Entomol Zool* 5:363–367. <https://doi.org/10.1303/aez.2010.363>
- Amin MR, Bussière LF, Goulson D (2012) Effects of male age and size on mating success in the bumblebee *Bombus terrestris*. *J Insect Behav* 25:362–374. <https://doi.org/10.1007/s10905-011-9306-4>
- Amsalem E, Galbraith DA, Cnaani J, Teal PE, Grozinger CM (2015) Conservation and modification of genetic and physiological toolkits underpinning diapause in bumble bee queens. *Mol Ecol* 24:5596–5615. <https://doi.org/10.1111/mec.13410>
- Baer B, Schmid-Hempel P (2005) Sperm influences female hibernation success, survival and fitness in the bumble-bee *Bombus terrestris*. *Proc R Soc Lond B Biol Sci* 272:319–323. <https://doi.org/10.1098/rspb.2004.2958>
- Beekman M, van Stratum P, Lingeman R (1998) Diapause survival and post-diapause performance in bumblebee queens (*Bombus terrestris*). *Entomol Exp Appl* 89:207–214. <https://doi.org/10.1046/j.1570-7458.1998.00401.x>
- Belsky JE, Camp AA, Lehmann DM (2020) The importance of males to bumble bee (*Bombus* species) nest development and colony viability. *InSects* 11:506. <https://doi.org/10.3390/insects11080506>
- Duchateau MJ, Velthuis HHW (1988) Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour* 107:186–207. <https://doi.org/10.1163/156853988X00340>
- Duvoisin N, Baer B, Schmid-Hempel P (1999) Sperm transfer and male competition in a bumblebee. *Anim Behav* 58:743–749. <https://doi.org/10.1006/anbe.1999.1196>
- Erkan C, Bulus IY, Gösterit A (2024) Sexual selection against inbred mates and inbreeding effects on some mating properties in *Bombus terrestris*. *Bull Insectology* 77:1–5
- Fowler AE, Stone EC, Irwin RE, Adler LS (2020) Sunflower pollen reduces a gut pathogen in worker and queen but not male bumble bees. *Ecol Entomol* 45:1318–1326. <https://doi.org/10.1111/een.12915>
- Gencer HV, Firatli C (2005) Reproductive and morphological comparisons of drones reared in queenright and laying worker colonies. *J Apic Res* 44:163–167. <https://doi.org/10.1080/00218839.2005.11101172>
- Gosterit A (2016) Adverse effects of inbreeding on colony foundation success in bumblebees, *Bombus terrestris* (Hymenoptera: Apidae). *Appl Entomol Zool* 51:521–526. <https://doi.org/10.1007/s13355-016-0427-2>
- Gosterit A, Bulus IY (2019) Development traits of *Bombus terrestris* colonies founded by queens mated with males produced from haploid eggs of queens and reproductive workers. *Zir Fak Der* 14:104–111
- Gosterit A, Gurel F (2005) Comparison of development patterns of imported and native *Bombus terrestris* L. (Hymenoptera: Apidae) colonies in the Mediterranean coastal region. *Turk J Vet Anim Sci* 29:393–398
- Gosterit A, Gurel F (2009) Effect of different diapause regimes on survival and colony development in the bumble bee, *Bombus terrestris*. *J Apic Res* 48:279–283. <https://doi.org/10.3896/IBRA.1.48.4.08>

- Gosterit A, Gurel F (2016) Male remating and its influences on queen colony foundation success in the bumblebee, *Bombus terrestris*. *Apidologie* 47:828–834. <https://doi.org/10.1007/s13592-016-0438-6>
- Goulson D (2012) Bumblebees: Behavior, Ecology and Conservation. 2nd ed. Oxford, UK
- Gradish AE, van der Steen J, Scott-Dupree CD, Cabrera AR, Cutler GC et al (2019) Comparison of pesticide exposure in honey bees (Hymenoptera: Apidae) and bumble bees (Hymenoptera: Apidae): implications for risk assessments. *Environ Entomol* 48:12–21. <https://doi.org/10.1093/ee/nvy168>
- Imran M, Ahmad M, Naeem M, Nasir MF, Bodlah I, Nasir M, Sheikh UAA (2017) Effect of different types of boxes on rearing of bumble bee, *Bombus terrestris*. *Pak J Zool* 49:169–174. <https://doi.org/10.17582/journal.pjz/2017.49.1.169.174>
- Jin XF, Ye ZM, He YD, Yang CF et al (2024) Intraspecific and interspecific resource partitioning between bumblebee workers and males related to nectar quantity and quality. *Insect Sci*. <https://doi.org/10.1111/1744-7917.13425>
- Korner P, Schmid-Hempel P (2003) Effects of sperm on female longevity in the bumble-bee *Bombus terrestris* L. *Proc R Soc Lond B Biol Sci* 270:227–229. <https://doi.org/10.1098/rsbl.2003.0039>
- Kwon YJ, Amin MR, Suh SJ (2006) Mating propensity of *Bombus terrestris* reared in different photoperiodic regimes. *Apidologie* 37:679–686. <https://doi.org/10.1051/apido:2006047>
- Lopez-Vaamonde C, Koning JW, Brown RM, Jordan WC, Bourke AF (2004) Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature* 430:557–560. <https://doi.org/10.1038/nature02769>
- Nasir M, Saeed S, Ahmad M, Aziz MA (2019) Effect of different diapause conditions on *Bombus terrestris* colony characteristics. *Pak J Zool* 51. <https://doi.org/10.17582/journal.pjz/2019.51.4.1273.1280>
- Ogilvie JE, Thomson JD (2015) Male bumble bees are important pollinators of a late-blooming plant. *Arthropod-Plant Interact* 9:205–213. <https://doi.org/10.1007/s11829-015-9368-x>
- Ostevik K, Manson J, Thomson J (2010) Pollination potential of male bumble bees (*Bombus impatiens*): movement patterns and pollen-transfer efficiency. *J Pollinat Ecol* 2:21–26. [https://doi.org/10.26786/1920-7603\(2010\)3](https://doi.org/10.26786/1920-7603(2010)3)
- Rundlöf M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol Conserv* 172:138–145. <https://doi.org/10.1016/j.biocon.2014.02.027>
- Shi M, Guo Y, Dong K, Wu J, Huang J (2023) A review of factors influencing diapause in bumble bee queens. *Insect Soc* 70:157–165. <https://doi.org/10.1007/s00040-023-00903-w>
- Williams PH, Cameron SA, Hines HM, Cederberg B, Rasmont P (2008) A simplified subgeneric classification of the bumblebees (genus *Bombus*). *Apidologie* 39:46–74. <https://doi.org/10.1051/apido:2007052>
- Wolf S, Toev T, Moritz RL, Moritz RF (2012) Spatial and temporal dynamics of the male effective population size in bumblebees (Hymenoptera: Apidae). *Popul Ecol* 54:115–124. <https://doi.org/10.1007/s10144-011-0285-2>
- Woodard SH, Duennes MA, Watrous KM, Jha S (2019) Diet and nutritional status during early adult life have immediate and persistent effects on queen bumble bees. *Conserv Physiol* 7. <https://doi.org/10.1093/conphys/coz048>
- Yeninar H, Duchateau MJ, Kaftanoglu O, Velthuis H (2000) Colony developmental patterns in different local populations of the Turkish bumble bee, *Bombus terrestris dalmatinus*. *J Apic Res* 39:107–116. <https://doi.org/10.1080/00218839.2000.11101030>
- Zambra E, Martinet B, Brasero N, Michez D, Rasmont P (2020) Hyperthermic stress resistance of bumblebee males: test case of Belgian species. *Apidologie* 51:911–920. <https://doi.org/10.1007/s13592-020-00771-4>
- Zhao H, Liu Y, Zhang H, Breeze TD, An J (2021) Worker-born males are smaller but have similar reproduction ability to queen-born males in bumblebees. *Insects* 12. <https://doi.org/10.3390/insects12111008>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.