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Long-lived winter honey bees show unexpectedly high levels of flight activity compared to short-lived summer bees

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Abstract – In temperate regions, the overwintering success of honey bee colonies, *Apis mellifera*, depends on the last generations of long-lived bees emerging in autumn, known as winter bees. While the physiological qualities of winter bees and their extended lifespan are well documented, yet literature on their flight activity performance is scarce. Here we studied the flight activity of long-lived winter honey bees and compared their performance with short-lived bees. Using radio frequency identification (RFID), we automatically monitored the number of flights, the total flight duration and the lifespan of 523 honey bees that emerged over the course of a year, including short-lived bees from spring, summer and autumn, and long-lived winter bees. We found that flight activity performance of short-lived bees decreased progressively from spring to autumn for both the number of flights and the total flight duration. Furthermore, we confirm that only a fraction of the bees emerging before winter are long-lived winter bees, with a lifespan of 143.5 ± 23.5 days (mean \pm SD). With an average of 37.5 ± 44.2 flights and 12.7 ± 15.5 h of flight, we found that long-lived winter bees were substantially more active than summer and autumn short-lived bees, but performed similar activity than spring short-lived bees. We also found that a small proportion of long-lived winter bees participate in the vast majority of the flight activity of the colony. Our results suggest that the extended lifespan of long-lived winter bees does not affect their flight activity performance, probably explained by their physiological qualities.

Apis mellifera / Winter bees / Life history traits / Flight activity performance / RFID

1. INTRODUCTION

In temperate regions, the western honey bee, *Apis mellifera*, spends the winter – a cold, resource-poor period critical to colony survival (Gray et al. 2023; Steinhauer et al. 2021; Switanek et al. 2017)– confined to its nest until spring. Colony survival depends on the last generations of long-lived worker bees that emerge in autumn, called "winter bees" (Winston 1991). Winter bees have an extended lifespan of 130 days on average (maximum of 304 days, Southwick 1991), instead of 30 days for

spring, summer and autumn workers (referred to as "short-lived bees") (Fukuda and Sekiguchi 1966; Sakagami and Fukuda 1968). This long life of winter bees is related to specific physiology (Döke et al. 2015; Fluri et al. 1982; Mattila et al. 2001). Long-lived winter bees have higher levels of protein and fat, but lower levels of juvenile hormone, known to be involved in foraging activity (Fluri et al. 1982; Shehata et al. 1981). Particular importance is attributed to the high level of vitellogenin, a glycoprotein known to increase lifespan by functioning in oxidative stress defense, immunity, behavioral control, and fat body development (Amdam et al. 2012; Fluri et al. 1982; Smedal et al. 2009). The transition from short-lived bees to

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long-lived bees is progressive, starting around 3 to 4 months before winter (late August in the Northern Hemisphere) (Mattila et al. 2001). In fact, only a part of the cohorts emerging in autumn will survive until spring and their proportion rises as winter approaches (Mattila et al. 2001). However, despite the knowledge about the longevity and physiology of the winter bees, little is known about their flight activity performance (i.e., the quantity and duration of activities outside the hive).

Flight activities allow worker bees to collect the resources the colony needs, such as water, resin (to create propolis), nectar, and pollen, which is the protein source with which the brood is fed (Winston 1991). In their entire life, short-lived bees perform about 30 flights for a total duration of 5.5 h in average (Barascou et al. 2022; Colin et al. 2022; Requier et al. 2020). The flight activity performances of worker bees vary throughout the year with the seasons (Requier et al. 2020), environmental conditions (Colin et al. 2022; Rodet and Henry 2014), the condition and needs of colonies (Rodet and Henry 2014), or the presence and load of pathogens (Bordier et al. 2018; Dosselli et al. 2016; Wells et al. 2016). However, knowledge on flight activity performance is limited to short-lived bees, although this activity performed by long-lived winter bees may be critical for colony survival (Seeley and Visscher 1985). It is assumed that underperforming long-lived winter bees would not support the growth of the colony in spring, leading to a post-winter collapse known as "spring dwindle" (Betti et al. 2016). The knowledge gap regarding the role of under-performing bees in spring dwindle is likely the result of challenges in monitoring the flight activity of bees over long periods of time and during winter. Nevertheless, recent advances in electronic applications offer the opportunity to automatically track the flight activity of bees in real field conditions, for example by using bee counters and Radio Frequency Identification (RFID) to monitor honey bee behavior during the summer (Klein et al. 2019; Requier et al. 2020; Tenczar et al. 2014).

In this study, we aimed to assess the flight activity performance of long-lived winter bees and to compare it with short-lived bees that emerged over the course of a year. We carried out automated monitoring of honey bees using RFID, in order to measure their lifespan and two metrics of flight activity performance, i.e. the number of flights and the total flight duration. We equipped bees in spring, summer and autumn to monitor the flight activity performance of short-lived bees, and we compared with long-lived winter bees (i.e., the fraction of the bees equipped before winter and surviving until spring; Mattila et al. 2001). We also tested whether long-lived bees performed most of their flight activity at the beginning of winter, at the end, or both. Finally, we investigated how flight activity was divided among long-lived winter bees to test whether a small proportion of bees perform a large majority of the flight activity of the colony, as is known for short-lived summer bees (Klein et al. 2019; Tenczar et al. 2014).

2. MATERIAL AND METHODS

2.1. RFID monitoring

This study was conducted at the CNRS (Centre National de Recherche Scientifique) of Gif-sur-Yvette, southwest of Paris, in France (48°42'11"N–2°8'45"E). The area is located in a sub-urban mixed landscape context of villages and forests with a temperate oceanic climate. Two honey bee colonies, *Apis mellifera*, were used for the study. The colonies had half-sister queens of the "Buckfast" type and were placed in 10-frame Dadant hives. The two hives were equipped with 8 RFID readers (MAJA, 13.56 MHz, Microsensus, GmbH, Erfurt, Germany) placed at the colony entrance. The RFID readers were organized with two lines of four readers in order to distinguish between bee entrances and exits (Requier et al. 2020). Each reader records the identity, date, and time (in seconds) of RFID tags that pass through the reader.

We equipped a total of 523 newly emerged worker bees (1-day-old) with RFID tags

(mic3-TAG 16k, Microsensys, GmbH, Erfurt, Germany). One day before tagging the bees, we collected frames with capped brood ready to emerge without adult bees and placed the frame in an incubator at 34°C overnight. We captured the newly emerged worker bees the following day and fixed the RFID tags on their thorax using dental cement (TempoSIL®; Coltène/Whaledent s.a.r.l.). The RFID tags weighs about 3 mg, representing ~3% of the body mass of a worker honey bee (Winston 1991). Former studies assumed that the tag would not interfere with the lifespan and flight activity performance of honey bees (Barascou et al. 2022; Prado et al. 2020, 2019; Requier et al. 2020; Streit et al. 2003), as worker bees can carry loads of pollen representing 20% of their body mass, or nectar representing 35% of their body mass and up to 80% (Winston 1991).

In 2021, in order to cover spring, summer and autumn, and in view of emergence constraints, we carried out six sessions of bee tagging, during spring on May 21st (n=90) and June 11th (n=88), during summer on July 2nd (n=89, hereafter referred to as July-A), July 23rd (n=80, hereafter referred to as July-B), and August 13th (n=84), and during autumn on October 22nd (n=92). All newly emerged bees came from two donor hives with half-sister queens of the "Buckfast" type and from the same apiary. Once tagged, the bees were introduced into the RFID-equipped hives using an introduction cage with the door sealed with sugar to delay the exit of the tagged bees. This allows them to take in the scent of the hive and improve their acceptance. The cohorts of spring and summer were introduced in one colony, and the cohort of autumn (i.e. October) was introduced in the two colonies (n=46 in the two colonies).

2.2. Measuring lifespan and flight activity performance

The lifespan and flight activity performance of all bees were recorded using the RFID system. Lifespan (LSP) was measured in days as the difference between the emergence date and last record date, assuming that bees die outside the hive, or were taken out of the hive by other workers if they

died inside (Requier et al. 2020). The metrics of flight activity performance were calculated after removing flight activities lower than 2 s (potentially linked to an individual staying under the readers) and higher than 120 min (Barascou et al. 2022; Prado et al. 2020, 2019; Requier et al. 2020). Then, the number of flights and the total flight duration (in hours) for each bee were measured following the method of Requier et al. (2020), assuming that a flight is a temporal sequence starting by a passage outwards from the hive and followed by a passage towards the hive.

2.3. Cohort profiles

We separated the bees into seven cohort profiles, based on their emerging date and longevity. Bees emerging from May to August were classified as short-lived bees. Given that the October cohort comprised both short-lived and long-lived honey bees (see supplementary material, Fig. S1), we classified bees who died before January 5th 2022 (first favorable flying window of the year) as short-lived bees and those still alive as long-lived winter bees (resulting in a lifespan threshold of 75 days from October to January the 5th, Fig. S2). This arbitrary threshold distinguishes the two cohorts of October bees by the longest period without bee mortality (Fig. S2). Thus, we distinguished seven cohort profiles as follows: two spring cohorts of short-lived bees (May short-lived bees and June short-lived bees); three summer cohorts of short-lived bees (July-A short-lived bees, July-B short-lived bees, and August short-lived bees); one autumn cohort of short-lived bees (October short-lived bees); and one cohort of long-lived bees (October long-lived bees, also referred to as long-lived winter bees).

2.4. Statistical analysis

All statistical analyses were performed using the R software version 4.3.3 (R Core Team 2024). Survival probabilities were estimated from lifespan using the *Surv* function from the 'survival' R-package (Therneau 2024). Pairwise

log-rank tests with *Bonferroni* adjustment (*pairwise_survdiff* function from the 'survival' R-package) were performed to test whether survival probabilities (response variable) were affected by cohort profiles (fixed factor).

A Generalized Linear Model (GLM) with *quasi-Poisson* distribution (*glm* function from the 'stats' R-package) was used to test whether the number of flights (response variable) was affected by cohort profiles (fixed factor). A Linear Model (LM, *lm* function from the 'stats' R-package) was used to test whether the total flight duration (\log_{10} -transformed response variable) was affected by cohort profiles (fixed factor). Pairwise Tukey comparisons were used as post hoc tests for all models, in order to compare cohort profile categories using the *glht* function from the 'multcomp' R-package (Hothorn et al. 2008).

To study the division of flight activity among long-lived winter honey bees, we first calculated the proportions of bees performing flight activity. We used January 5th 2022 (first favorable flying window of the year) as the limit to distinguish between bees that were active (i) only before winter, (ii) before and after winter, or (iii) only after winter. Wilcoxon tests were used to compare the number of flights and the total flight duration between these three activity profiles. Finally, we compared the division of flight activity among foragers between long-lived winter bees and short-lived bees following the method of Tenczar et al. (2014). For that, we ranked foragers by their flight activity contribution to the total activity for each cohort profile by using Lorenz curves (Dalton 1920; Gastwirth 1972), and we calculated the Gini coefficient to measure distribution inequality, ranging from 0 (equality) to 1 (inequality) (Dalton 1920).

3. RESULTS

3.1. Survival probabilities of winter bees compared to spring and summer bees

Two-thirds (65.2%) of the October cohort bees died before January 5th 2022 and were considered short-lived autumn bees, while the

one-third (34.8%) survived and were considered as long-lived winter bees (Fig. S2). We found that the survival probabilities of honey bees were significantly different between cohort profiles (Table S1). Overall, we can see that the probability of survival decreases from May to August, with the lowest probability of survival in August, which then increases in autumn (Fig. S1). We found that October long-lived bees (mean \pm sd: lifespan 143.5 ± 23.5 days) lived longer than short-lived spring bees from May (lifespan 39.6 ± 13.8 days) and June (lifespan 28.5 ± 10.5 days). They also lived longer than the short-lived summer bees from July-A (lifespan July 2nd; 18.1 ± 9.9 days), July-B (lifespan July 23rd; 25.1 ± 11.7 days), and August (lifespan 19.3 ± 3.7 days), as well as longer than the short-lived autumn bees from October (lifespan 27.0 ± 21.5 days) (Fig. 1.A). Among the short-lived bees, we found that short-lived bees from May lived longer than all other cohort profiles except short-lived bees of October (Table S1). Finally, we found that short-lived bees from June, July-B, and October lived longer than short-lived bees from July-A and August (Table S1). Survival probabilities for all other combinations of cohort profiles were not significantly different, notably between July-A and August (Table S1).

3.2. Flight activity performance

The number of flights was also significantly different between cohort profiles (GLM, $p < 0.001$, Fig. 1.B). The Tukey pairwise comparison test revealed that short-lived bees from May (62.8 ± 57.5 flights) and June (55.0 ± 75.8 flights) performed more flights than short-lived bees from July-A (25.7 ± 33.1 flights), July-B (20.4 ± 18.8 flights), August (3.6 ± 7.9 flights), and October short-lived bees (1.6 ± 2.9 flights) (Table S2). Short-lived bees from July-A and B performed more flights than short-lived bees from August and short-lived bees from October (Table S2). Moreover, we found that long-lived bees from October (37.5 ± 44.2 flights) performed more flights than bees from August and short-lived bees from

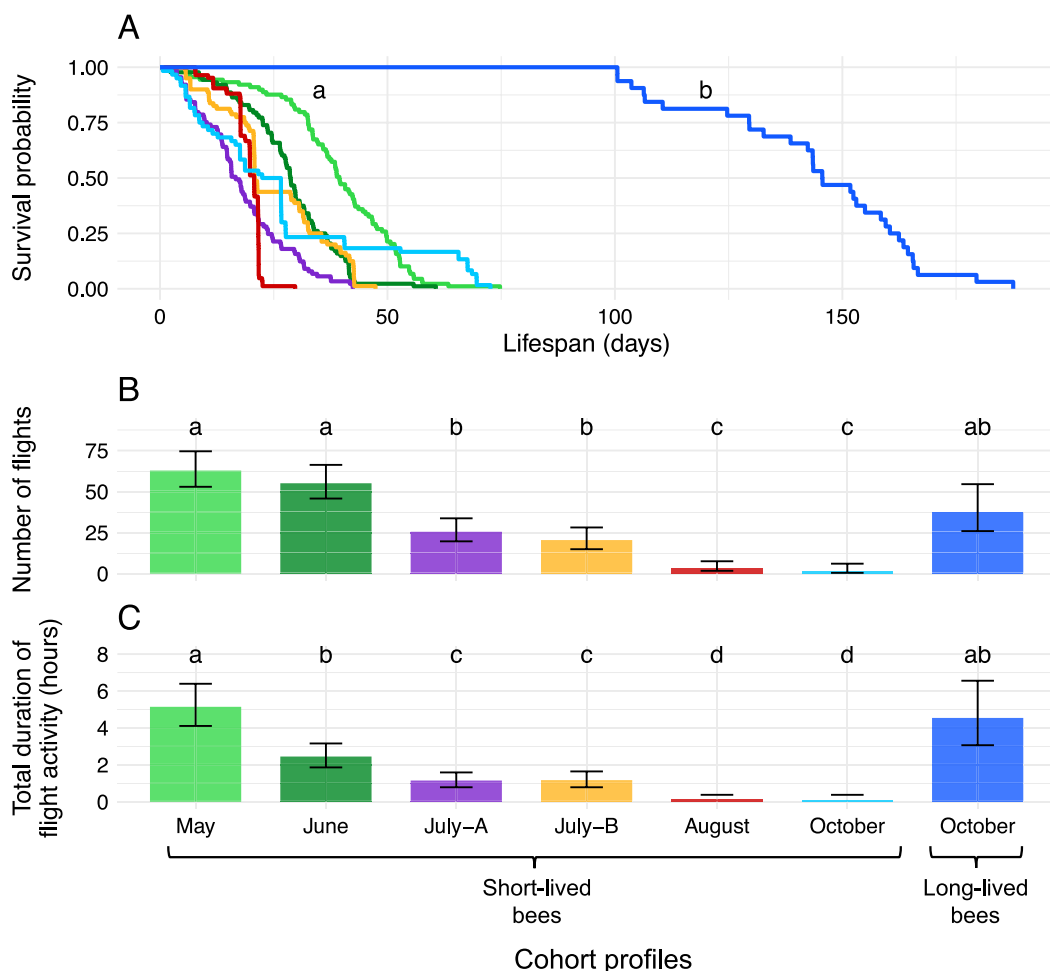


Figure 1. Survival probabilities and flight performance of bee cohorts tracked by RFID and profiled between short-lived bees (lifespan < 73 days) and long-lived winter bees (lifespan > 73 days). **A** Survival probability represented by Kaplan–Meier survival curves, **B** predicted number of flights, and **C** predicted total flight duration (hours) of honey bees over the course of a year, including short-lived summer bees and long-lived winter bees. The predictions are obtained from generalized linear models. Colors correspond to cohort and longevity profile combinations. Letters indicate significant differences between groups ($p < 0.05$) with **(A)** Log rank post hoc test on survival probabilities, **B, C** Tukey post hoc test of generalized linear models.

October (Table S2). Conversely, we found no significant differences when comparing the number of flights of long-lived bees from October with the number of flights of bees from spring (May and June) and summer (July-A and B) (Table S2).

We also found a significant effect of cohort profiles on the total flight duration (LM, $p < 0.001$, Fig. 1.C). Overall, we found that the flight activity performance of short-lived bees decreased

progressively from spring to autumn for both the number of flights and the total flight duration. We found that short-lived bees from May (9.4 ± 9.7 h) had higher total flight duration than short-lived bees from June (5.0 ± 6.1 h), July-A (2.2 ± 3.4 h), July-B (2.2 ± 3.6 h), August (0.3 ± 1.1 h), and October short-lived bees (0.1 ± 0.3 h) (Table S3). We found that the total flight duration of short-lived bees from June was higher than the total

flight duration of short-lived bees from July-A, July-B, August and October (Table S3). We also found that short-lived bees from July-A and July-B had higher total flight duration than short-lived bees from August and October (Table S3). Moreover, we found that the long-lived bees from October (12.7 ± 15.5 h) had higher total flight duration than short-lived bees from July-A, July-B, August and October (Table S3). However, we found no significant differences in the total flight duration of long-lived bees from October and short-lived bees from spring (May and June cohorts) (Table S3). No significant differences were found in flight activity between long-lived and short-lived October cohorts between the two colonies (Fig. S3).

3.3. Individual contributions to the total flight activity

A total of 96.8% long-lived winter bees performed flight activity, for which 53.1% of them were active before the winter and 90.6% after the winter. Overall, 46.9% of long-lived winter bees performed flights before and after winter. The Wilcoxon tests revealed no statistically significant differences in the number of flights ($p = 0.24$) or total flight duration ($p = 0.50$) between bees performing flights both before and after winter and bees performing flights only after winter.

We found inequalities in the division of flight activity (number of flights and total flights duration) between foragers for all cohort profiles including the long-lived winter bees (Fig. 2, supplementary material, Table S4). Weighted average inequality is higher for the number of flights (Gini coefficient = 0.52 ± 0.06) than for total flight duration (Gini coefficient = 0.66 ± 0.10).

4. DISCUSSION

In this study, we measured flight activity performances of long-lived winter honey bees and compared them with the performances of short-lived spring, summer, and autumn honey bees. We showed that lifespan decreases reaching a

minimum in autumn and then increasing into winter. We showed that long-lived winter bees have among the highest flight activity performance. Their number of flights was as high as spring and summer honey bees and higher than autumn bees. Their total flight duration was similar to spring bees and higher than summer and autumn bees.

We investigated the longevity profiles of bees from spring to autumn. Short-lived and long-lived October bees were distinguished by their ability to survive up until the arbitrary date of January 5th, 2022 (age 75 days). Based on this criteria, we confirm that only a part of the bees that emerge before winter (i.e. October) shows the typical long-lived profile of winter bees, and that the wintering period (centered on the date of January 5th, 2022) is a period of reduced mortality for bees (Mattila et al. 2001). At the arrival of the winter season, the reduction in pollen intake, foraging activities, and brood surface transforms the hormonal environment inside the hive (for a review see Döke et al. 2015), leading to the gradual emergence of long-lived bees (Mattila et al. 2001). The physiological qualities of these winter bees (Amdam et al. 2012; Fluri et al. 1982; Shehata et al. 1981) grant them an extended lifespan, enabling survival through winter. In contrast, the non-winter bees emerging in autumn do not show these qualities and present a short lifespan, similar to bees from other seasons, and will die during winter. In our study, the proportion of long-lived bees for the autumn cohort (34.8%) is lower than in the literature (about 60%; Mattila et al. 2001). This difference could be linked to a methodological bias in this previous study, where they used visual inspection method during the winter. Indeed, opening the hives during cold periods is not possible, limiting the time windows of mortality counting. This could have affected the accuracy of their monitoring compared to our automatic monitoring. On the other hand, the lifespans of spring, summer and autumn short-lived bees are in the same range as data from the literature (Fukuda and Sekiguchi 1966; Mattila et al. 2001; Sakagami and Fukuda 1968; Seeley and Visscher 1985).

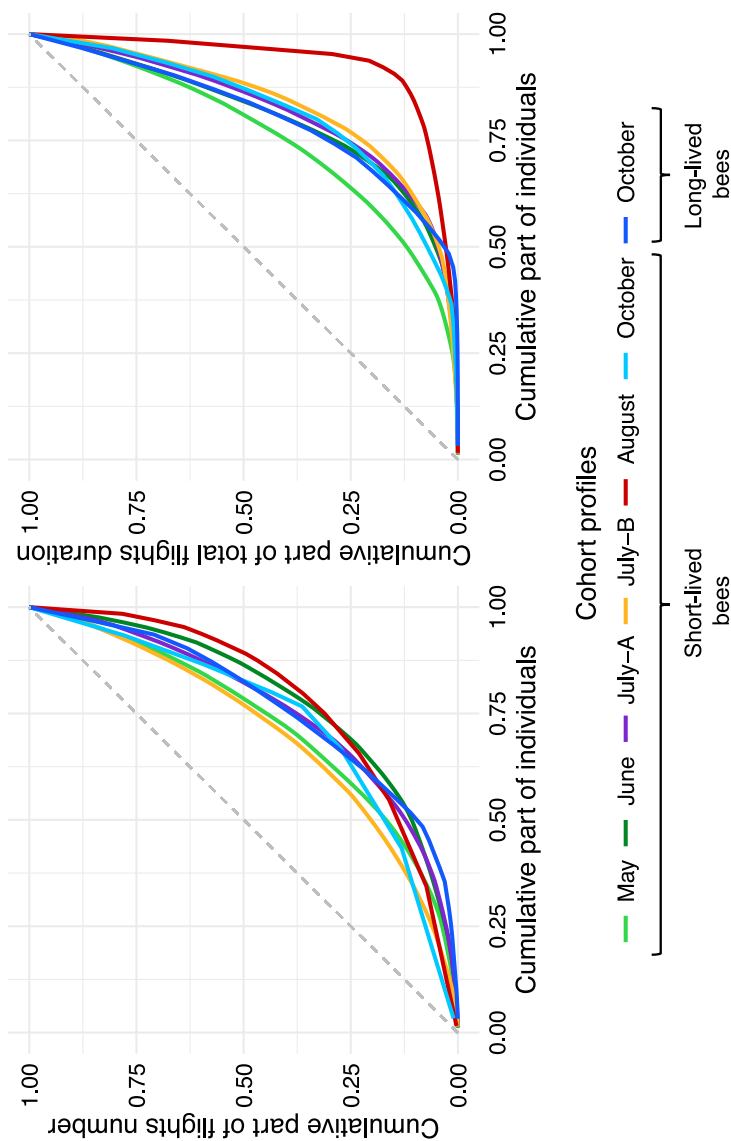


Figure 2. Lorenz curves of relative individual contributions to the (A) total number of flights, and (B) total flight duration, for cohorts and longevity profile combinations. Colors correspond to cohorts and longevity profile combinations. The fraction of the individual contribution to the total flight activity performance was cumulatively plotted in the Y axis. Gray dotted lines represent the distribution predicted by an evenly distributed contribution of each bee. Conversely, a Lorenz curve that deviates significantly from the identity line suggests a more unequal task distribution between individuals, highlighting the presence of individuals who contribute significantly more than others.

We found that long-lived winter bees had similar flight performance to spring bees, and performed more flights than autumn bees and longer total flight durations than summer bees and autumn short-lived bees. The number of flights performed by long-lived winter bees (average of 37.5 flights) was similar to the average number of flights for summer bees in the literature (about 30 flights; Requier et al. 2020; Barascou et al. 2022; Colin et al. 2022). The total flight duration performed by long-lived winter bees (average of 12.7 h of flight) was substantially higher than the average total flight duration for summer bees in the literature (about 5.5 h of flight; Requier et al. 2020; Barascou et al. 2022; Colin et al. 2022). The unexpectedly high levels of flight activity performance of long-lived winter honey bees could be related with their physiology. Indeed, the overall flight capabilities of foragers may be related to the size of individual energy reserves (including glycogen reserves stored in their flight muscles) that are depleted at the end of the flight period (Neukirch 1982). Thus, the high levels of fat, protein, and glycoproteins (including vitellogenin) of long-lived winter bees (Amdam et al. 2012; Fluri et al. 1982; Smedal et al. 2009) could represent a larger reserve than that available to summer honey bees, and thus may support higher flight activity performance.

Furthermore, we showed that almost all long-lived winter bees take part in activities outside the hive in spring. At this period floral resources are abundant, which has already been shown to be correlated with high flight activity (Rodet and Henry 2014) and could thus explain their higher performance compared to summer or autumn bees. This result suggests that they play an active role in the rebound of the colony in spring. We also observed that almost half of long-lived winter bees have pre- and post-winter flight activity. However, their total flight activity performance was no higher than that of the bees which only fly after winter, which corroborates with the hypothesis of flight capabilities related with the size of individual energy reserves (Neukirch 1982).

Finally, we found that both the number of flights and the total flight duration decreased over the course of a year. This may be linked to

differences in colony demands, with high demand in spring for rapid rebound of the colony (Seeley and Visscher 1985), followed by lower demand later in the season in preparation for overwintering. This annual variation could also be linked to variations in colony population size and pathogen load. Indeed, if colony demand remains stable and more foragers are present, each individual will present lower flight activity due to division of the work between foragers. However, the unequal distribution of flights among bees does not support this hypothesis (Klein et al. 2019; Tenczar et al. 2014). Indeed, we found an unequal distribution of flight activity performance among the foragers independently of the season, with a small proportion of bees performing the majority of flight activities for both the number of flights and the total flight duration. The inequality distribution (Gini coefficient) of flight activity performance for summer bees confirms data from the literature (Klein et al. 2019; Tenczar et al. 2014). The higher inequality in flight duration we found for summer short-lived bees (August cohort) may be related with the presence of a small proportion of scouts searching for new food sources. Indeed, the proportion of scouts in forager bees varies between 5 and 35% depending on the forage availability (Seeley 1983). Although the climatic conditions between August and October are favourable to bee flight activities in France (Requier et al. 2020), a potential limitation exists in the availability of floral resources (Requier et al. 2015), with a potential effect on the time for scouting or collecting food. Notably, it could be longer between periods of mass flowering periods, when flower resources are more dispersed in the landscape (Requier et al. 2015).

5. CONCLUDING REMARKS

While previous studies on winter honey bees have predominantly concentrated on their physiology and longevity, our research expands the focus by comparing their flight activity performance of spring, summer, and autumn bees. We confirm that only a fraction of the bees emerging before winter are long-lived winter bees. We showed that long-lived winter

bees performed more flight activities than short-lived summer bees. Long-lived winter bees were active in the spring during the critical period of colony rebound. Overall, we found that long-lived winter bees can live longer while maintaining high levels of flight activity performance, which seems to be critical for colony rebound in the spring.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-024-01144-x>.

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AUTHOR CONTRIBUTIONS

Conceptualization, Fabrice Requier; Methodology, Etienne Minaud, François Rebaudo, and Fabrice Requier; Formal analysis, Etienne Minaud and Fabrice Requier; Investigation, Fabrice Requier; Writing – Original Draft, Etienne Minaud and Fabrice Requier; Writing – Review & Editing, Etienne Minaud, François Rebaudo, and Fabrice Requier; Supervision, Fabrice Requier; Project Administration, Fabrice Requier; Funding Acquisition, Fabrice Requier.

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DATA AVAILABILITY

The data presented in this manuscript are available through the figshare repository <https://doi.org/10.6084/m9.figshare.27629688.v1>.

DECLARATIONS

Disclosure The authors have no relevant financial or non-financial interests to disclose.

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