Original article

The effect of forager loss on honeybee workers temporal polyethism and social network structure

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Abstract – The western honeybee *Apis mellifera* is perhaps the best-known example of an advanced eusocial species displaying temporal polyethism, a process in which workers perform different tasks in the colony as they age. Previous studies demonstrated that this temporal division of labour is not only regulated by the age of the bees but also by the proportion of workers performing the required tasks in the colony. As we progress through the Anthropocene, the Intergovernmental Panel on Climate Change predicted that a significant increase in both the frequency and intensity of severe weather events can be expected in the coming decades. Here, we performed a controlled interrupted time series experiment with the objective of quantifying the possible effects that these weather events might have in the honeybee colony dynamics. By simulating a significant loss of foragers in the colony, we observed that honeybee workers quickly replaced the missing foragers by accelerating their transition to a subsequent task and, in some cases, completely skipped several of the natural task transitions with respect to their age. In addition, we analysed how the colony social network structure is affected by the sudden loss of foragers. Indeed, our data show that honeybee colonies increased their network cohesion with workers having a higher number of interactions as well as becoming more closely connected to one another soon after the disturbance. Overall, our data shows that even when faced with a substantial perturbation, honeybees can respond swiftly in order to maintain colony homeostasis and likely increase their resilience against future perturbations.

Apis mellifera / **age polyethism / task allocation / social network / climate change**

1. INTRODUCTION

Social behaviour is ubiquitous in nature, with varying degrees of social organization being observed across the animal kingdom and beyond (Székely et al. 2010). The most advanced level of social organization, namely eusociality, was first described in the Hymenoptera but later also found to occur in several other taxa (Gadagkar 1987; Grimaldi and Engel 2005). Eusocial, or "truly" social, species are characterized by having cooperative broodcare, overlapping adult generations and the presence of reproductive and non-reproductive castes (Wilson 1971). The last trait is also used to distinguish between primitive and advanced eusociality with respect to whether there are noticeable morphological differences between the female castes or not (Michener 2007). The best known example of an advanced eusocial species is perhaps the western honeybee *Apis mellifera*, which presents clear behavioural and morphological differences between the queen that monopolizes reproduction and the workers that specialize in colony maintenance tasks such as feeding the young and defending the colony (Michener 1969; Peso et al. 2016).

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This division of labour is a hallmark of eusociality and is not only characterized by the reproductive division of labour between queen and workers but also among workers themselves. Indeed, rather than specializing in fixed morphological castes, honeybee workers perform different tasks as they age in a temporal division of labour pattern called age polyethism (Robinson 1992). Almost immediately after emerging from the brood rearing cells, they begin cleaning the cells previously occupied by brood, transitioning to caring for the young, storing food resources, defending the nest and, finally, to foraging (Johnson 2008; Seeley and Kolmes 1991). Nevertheless, age polyethism is not fixed and workers may in fact shift tasks according to the colony needs (Bernadou et al. 2015; Naug and Gadagkar 1998; Woyciechowski and Moroń 2009). That is, not all bees perform all tasks for the same amount of time. For example, some workers in poor health will make a faster transition to the riskier foraging task (Lecocq et al. 2016; Natsopoulou et al. 2016; Tofilski 2009). The overall colony condition might also influence the temporal division of labour with some honeybee colonies being observed to adapt their social organization according to nutritional resources requirements or to specific environmental changes (Schmickl and Crailsheim 2002, 2004). This flexibility in the age polyethism enables the workers, and ultimately the entire colony, to adjust their social organization in order to optimally exploit resources as well as to deal with both biotic and abiotic adversities (Robinson 1992; Seeley 1995).

The number of wild populations of honeybees in both Europe and the USA has been decreasing rapidly in the last decades, up to a point where almost no feral honeybees are left (Jaffé et al. 2010; Panziera et al. 2022). Among the most important drivers for this ongoing pollinator crisis are changes in land use, habitat fragmentation, the use of pesticides, pollution, invasive species, pathogens and climate change (Cox-Foster et al. 2007; Hendrickx et al. 2007; Kevan et al. 1997; Potts et al. 2010; Stout and Morales 2009; Winfree et al. 2009). According to the Intergovernmental Panel on Climate Change (IPCC), severe precipitation events are likely to have increased in their occurrence and intensity and will continue to do so in the future (IPCC 2014). Extreme rainfall and storm conditions can be detrimental for honeybees, particularly when workers are out foraging. Rainfall can decrease their body temperature leading to a chill comatose status where the honeybee metabolic activity ceases to a minimum (De Joy 1998). In addition, rainfall can have a significant detrimental impact on broodcare behaviour (Schmickl et al. 2003; Schmickl and Crailsheim 2002). Strong winds may also hinder foragers from returning to the hive, increasing the probability that they do not survive these events (Neov et al. 2019).

Aiming to quantify the possible effects that these weather events might have on the honeybee colony dynamics, we performed an interrupted time series experiment where we simulated the effect of an extreme weather event on the colony and tested how bees may adapt their task allocation in response to a significant loss of foragers. Whether colonies are resilient and able to swiftly adapt to adverse conditions leading to a significant impact on colony homeostasis might have direct implications on the maintenance of stable populations in future climate scenarios. More specifically, we tested whether the time taken for young workers to transition to a subsequent task is dependent on the proportion of foragers present in the colony, accounting for the effects on colony social stability. In addition, we mapped the social interactions of a subset of workers from all age cohorts during an entire generation and compared several social network properties before and after the experimental manipulation.

2. MATERIAL AND METHODS

2.1. Experimental setup

The experiments were conducted in the apiary of the Laboratory of Socioecology and Social Evolution at KU Leuven (50°52′27.6″ N, 4°41′44.3″ E) in three one-sided experimental observation hives (hives A, B and C) of *A. mellifera carnica* honeybees consisting of a single

standard frame covered by a transparent sheet of plexiglass. Two weeks prior to the beginning of the experiments, empty bee frames were added to eight beehives in the laboratory apiary which served as stock colonies for the observation hives. Observation hives were provisioned with water and sugar paste ad libitum during the first days and presented a regular colony development until the experiments were performed. Once foraging activity was established, we ceased feeding the experimental hives. We then selected three of these colonies and collected the frames together with the queen and a subset of about 200 workers and placed them onto the observation hives. In addition, we collected frames containing capped brood cells from the same stock colonies and kept them in an incubator at constant temperature (36 °C) and humidity (50%). For the next 3 weeks, bees emerging in the incubator were individually marked with numbered opalite bee tags at every 2 days. During each session, we marked 20 bees with a different colour and introduced them into their corresponding observation hive in order to replace the majority of bees in the hives by individuals of known age (total of 10 sessions and 200 bees added per observation hive).

Once all observation hives contained marked bees of most age groups, we recorded the hives at every 2 days with a Panasonic camcorder (HC-VX870) in 4K resolution for 15 min for 3 weeks. The recording started 2 weeks after we began introducing tagged newly emerged bees and persisted for 2 weeks. Hence, newly emerged tagged bees were still introduced 1 week after the beginning of the recording sessions. The experimental removal of foragers was performed 1 week after the start of the recordings in order to have a baseline "control period" before the manipulation with four recording sessions and an "experimental period" with a recording on the day of the manipulation plus four subsequent sessions. Therefore, we performed nine behavioural data observations (i.e. four before treatment, on the day of the treatment, and four after the experimental manipulation). The interrupted time series experiment was designed to simulate an abrupt and significant loss of foragers due to an extreme weather event such as a sudden heavy rainfall or storm. During the manipulation, 50% of the foragers were removed (from a total of 15 in hive A, 16 in hive B and 23 in hive C) by adding a sampling box at the entrance of the hives during the evening and collecting, counting and removing the foragers in the morning of the next day. The remaining 50% of the foragers that were not removed were reintroduced to their respective observation hives.

2.2. Behavioural observations

The recordings were analysed with VLC media player (VideoLAN Organization), whereby five tagged bees were randomly selected from all age cohorts that were present at each recording day. The individual bees were closely followed for 3 min after which its specific task in the hive was determined. The specific tasks consisted of the exact behaviour the bees were performing during the observation. This behaviour included (1) nest maintenance work, (2) performing broodcare, (3) working in food storage, (4) guarding behaviour and (5) foraging. Workers were considered as foragers when they were observed leaving and entering the hive entrance during observation sessions. Workers that did not fit any of the previous categories but still interact with nestmates were labelled as "idle" for the social network analysis. Aside from the tasks of the focal bees, we also noted the individual ids of the bees in which the focal bee interacted with as well as the type of interaction (i.e. antennation, trophallaxis or interactions with the queen). The behavioural observations were not performed blindly to colony identity. Nevertheless, they followed a precise behavioural catalogue in order to clearly identify the tasks performed by workers. To determine the tasks of the bees from the same age group which were not directly observed, we analysed the task that was most common among the bees that were directly observed within the same age cohort. When no specific task was single outed as the most common, we then assigned a task from the equally possible tasks in that age group randomly. This particular dataset of inferred tasks was utilized

exclusively for the purpose of completing the social network analysis. In addition, the entrance of each observation hive was observed for 6 min to account for the bees performing extranidal activities such as guarding and foraging, to confirm whether the bees were indeed performing extranidal tasks or were just at the hive entrance by chance.

2.3. Statistical analyses

All statistical analyses were carried out using the R software version 4.0.2 (R Core Team 2020). In order to test the effects of the experimental manipulation in the age polyethism dynamics, particularly on the onset of foraging behaviour, we ran a multinomial model using the function *multinom* from the package *nnet* version 7.3–14. The different tasks recorded in the dataset were first grouped by similar behaviours into five general task groups i.e. nest maintenance, broodcare, food storage, guard or forager. The task groups were then coded as the response variable and an interaction term containing the timing of treatment (before or after manipulation) and the age of the bees was coded as a fixed co-factor. Hive id was also added as a second fixed factor. This was followed by an analysis of variance (ANOVA) to test the overall effects of hive, treatment and age on the proportion of task allocation. Tukey post-hoc pairwise tests were performed to check pairwise treatment effects within each specific task groups (package *emmeans* version 1.5.1). In addition, we tested if the experimental manipulation affected the time taken for bees to switch to a subsequent task. To this end, we first calculated the average age of the bees performing each task and then subtracted from the following possible task progression and age cohort according to the literature and our own data (Johnson 2008; Seeley 1995; Seeley and Kolmes 1991). Chronological transitions from one task to the next were then assessed for all individual workers before and after treatment. A multinomial model was then carried out with the transitions (i.e. possible progressions patterns from a previous to

a subsequent task) as dependent variable with an interaction term between the timing of treatment (before or after) and the number of days between transitions. Finally, Tukey post-hoc tests were performed to check for differences among all possible pairwise transitions.

2.4. Social network analyses

We performed a social network analysis with the program UCINET version 6.738 (Borgatti et al. 2002) to study the effects of treatment on the social network structures of the colonies. For each observation hive, we created two datasets and subsequent social networks with one containing the tasks and one containing the interactions of the observed bees 4 days before and 4 days after the treatment (see "Behavioural observations" section for details). The interaction dataset contained both actors of each interaction and the type of interaction for each day in each hive. This dataset was loaded in UCINET before constructing the network. After the creation of the network, the task dataset was added to the network. This task dataset contained the specific task of each observed bee per day of each hive and functioned as the attribute table corresponding to all the interacting bees in the network. We then calculated network metrics such as the diameter, density, global clustering coefficient, average interaction rate, K-core index and Wiener index for all observation days within each hive. The averages of the individual metrics were calculated per hive before and after treatment. These measures are indicators of the structure and connectedness and give a good indication of the overall cohesion present in a given network (Grandjean and Jacomy 2019; Tabassum et al. 2018). Next, a primary component analysis (PCA) was performed with the metrics of each social network before and after treatment, and the primary components extracted to deal with possible multicollinearity effects as network cohesion parameters are often correlated to each other. We selected the two first principal components for the subsequent analysis since they explained 72.8% of the observed variance.

The normality of the residuals was checked with Shapiro–Wilk tests. Subsequently, we ran linear models (package *stats* version 4.0.2) with the two primary components coded as response variables, time of treatment (before or after manipulation) and hive id as fixed co-factors to test for the impact of treatment on the social network structure of the colonies. ANOVA's were used to test for overall differences of network metrics primary components among hives and treatments (package *car* version 3.0-13).

3. RESULTS

3.1. Effect of forager loss on task allocation distribution

Before the experimental manipulation, the percentage distribution of worker bees aged between zero and 30 days that were performing specific tasks in the hive was the following based on the total number of behavioural observations: nest maintenance 42% ($n = 515$), broodcare 21% ($n = 253$), food storage 28% ($n = 343$), guarding the nest 9% ($n = 116$) and only 0.2% ($n = 3$) of

foragers. After the removal of 50% of the foragers (that were older than 30 days), it is possible to observe a shift in the proportion of bees performing all tasks, except for the broodcare which was unaffected with 21% ($n = 383$) of the workers still performing this task. For the remaining tasks, we observed a decrease in the proportion bees performing nest maintenance (34%, $n = 616$) and guarding the nest (4%, $n = 73$), while there was an increase in the proportion of food storers (39%, $n = 725$) and foragers (2%, $n = 41$). There is, therefore, a clear pattern of workers adapting their task allocation with respect to the different age groups as a response to the sudden loss of foragers in the hive (multinomial model, $F_{4,20} = 15.572$, $p < 0.001$) (Figure 1). The specific tasks that were significantly affected by our treatment was guarding behaviour (Tukey post-hoc test, $t = -7.376$, $p < 0.001$, df $= 20$) and food storage (Tukey post-hoc test, $t = 2.417$, $p < 0.025$, df $= 20$).

An additional aspect of our study was to analyse if the time taken for bees to transition from one task to the next would be affected by the experimental removal of foragers. Indeed, there is a strong overall effect on the proportion and average time that workers took to transition
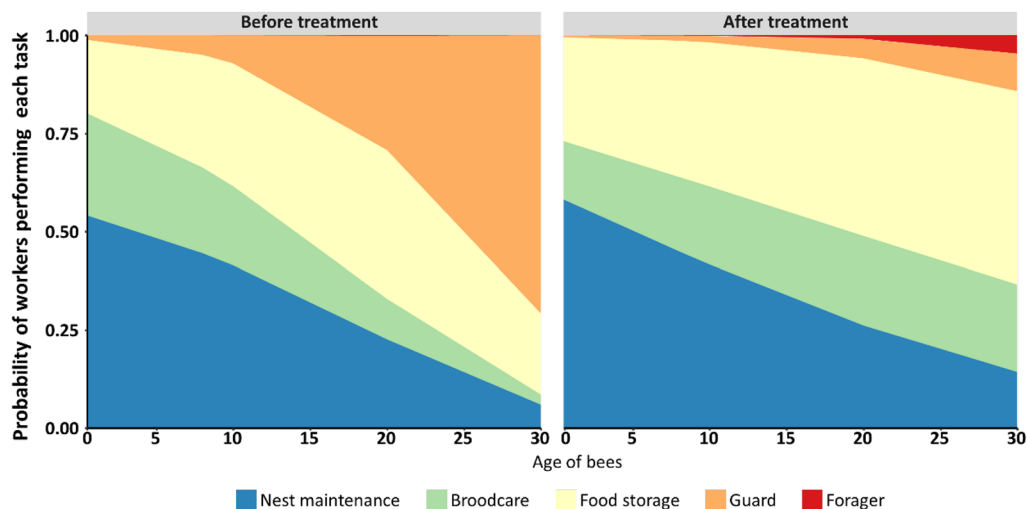

Figure 1. The proportion of task allocation groups according to age before and after the experimental manipulation (removal of foragers) based on a multinomial model fitted to the observed frequency of tasks over time in *A. mellifera*. The data shows that worker bees adapt their distribution as a response to an abrupt loss of foragers.

among the different tasks before and after the experimental manipulation (multinomial model, $F_{8,32} = 1291.79$, $p < 0.001$). More specifically, there were significant differences on the transition from broodcare to food storage (Tukey post-hoc test, $t = -2.837$, $p = 0.008$, df = 32) and from nest maintenance to guard (Tukey post-hoc test, $t = 2.097$, $p = 0.044$, df = 32). It is worth mentioning two not significant task transitions that did not occur before the treatment that were from nest maintenance directly to foraging behaviour, completely skipping several tasks under regular circumstances (Tukey post-hoc test, $t = -1.753$, $p = 0.089$, df = 32) and from food storage to forager (Tukey post-hoc test, $t = -0.805$, $p = 0.427$, df = 32) (Figure 2). In addition to completely skipping some tasks, workers also performed quicker transitions. The workers shifting from broodcare to food storage decreased in proportion but transitioned 2 days earlier and food storers advanced their transitioning time to guards by 1.6 days after treatment. Some broodcare workers skipped the task of food storage and made the transition to guards also half a day quicker after the removal of foragers.

3.2. Effect of treatment on social network dynamics

We performed nine social network analyses for each of the treatment hives (4 days before, the day of the treatment, and 4 days after treatment). Overall, networks become more closely clustered after treatment and they also present higher k-core scores, particularly for hives B and C (Figure 3). The latter hive also shows high number of nodes in the inner and outer k-cores without many bees in the middle k-core. Overall, the hives showed an average interaction rate of 2.55 and had a k-core index of 2.5 before the experimental manipulation, whereas after treatment the values increased to 3.74 and 3.6, respectively. Visual inspection of the specific task groups in the networks before and after manipulation shows that different tasks are well represented at both the periphery and centre of the networks, indicating that workers with high and low levels of interaction are equally represented within each type of task in the colony. The Wiener index followed the same trend as the average interaction rate and K-core index, increasing after treatment from 7137 to 32055.
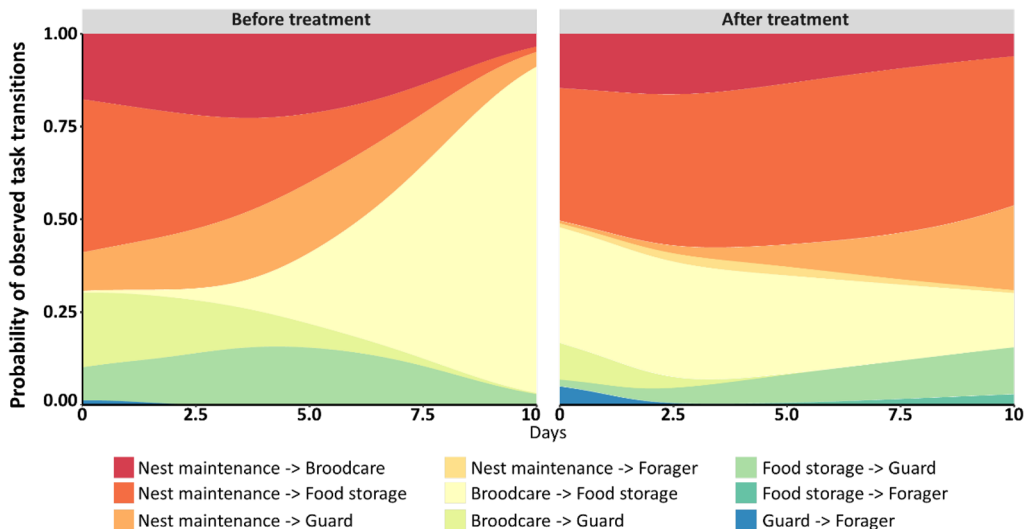

Figure 2. Workers adjust both the proportion and time taken to transition to a new task when faced with a substantial loss of foragers as seen by the outcome of a multinomial model fitted to the relative frequency of task progression in function of the time before and after the treatment in *A. mellifera*.
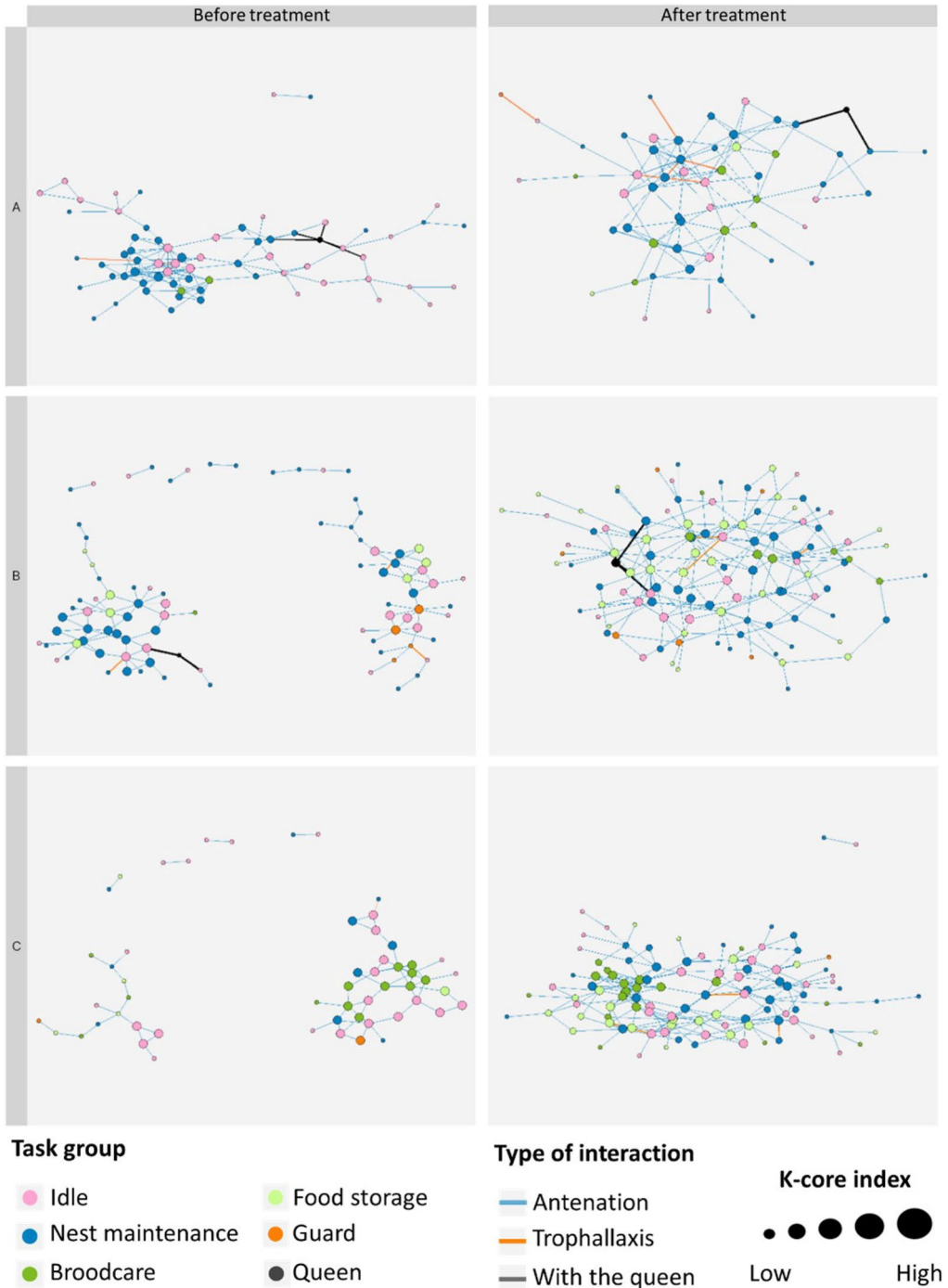
Figure 3. Social network structures of the three experimental hives **A**, **B** and **C** before and after the removal of foragers. The colours of the nodes correspond to task workers were performing and tie colours represent the type of interaction. The larger the k-core, the larger is the node. Foragers are not present because the observations are primarily focused on tasks within the nest.

The total variance on the social network metrics explained by the two first principal components was of 72.8% (PC1 38.8% and PC2 34%, Figure 4a). Nevertheless, only the second component differed significantly between the period before and after the treatment (ANOVA, $F_{1,23} = 23.476$, $p < 0.001$, Figure 4b), which was mostly determined by the average interaction rate, K-core index, and Wiener index. The first component was mostly influenced by the diameter, density, average interaction rate and K-core index though not significantly (ANOVA, $F_{1,23} = 1.533$, p = 0.228).

4. DISCUSSION

4.1. Effect of treatment on task allocation

Our results show that the task allocation in the honeybee *A. mellifera* was impacted not only by age but also by the proportion of individuals performing each specific task in the hive. Despite some bees becoming specialized in certain task groups, we observed most workers following a pattern of temporal division of labour (Seeley 1995; Seeley and Kolmes 1991; Wilson 1971). Both before and after the treatment, the temporal pattern of task allocation was in agreement with previous finding in the literature whereby newly emerged bees engage mostly in nest maintenance tasks and broodcare, shifting to storing food, guarding the nest and ultimately becoming foragers (Johnson 2008; Seeley 1995; Seeley and Kolmes 1991). Guarding and foraging behaviour is mostly seen in older bees because these are the riskiest tasks. Hence, by having the older bees performing these tasks, colonies are able to maintain a good overall fitness as these workers are at the end of their lifespan and a loss of young bees could otherwise severely impair colony functioning (Tofilski 2002).

Interestingly, the proportions of workers performing food storage and guarding tasks were most affected by our treatment, resulting in an increase of food storers but a decrease in guards after treatment. There was also a trend, though not significant, of an increase in the abundance of foragers after the experimental manipulation.
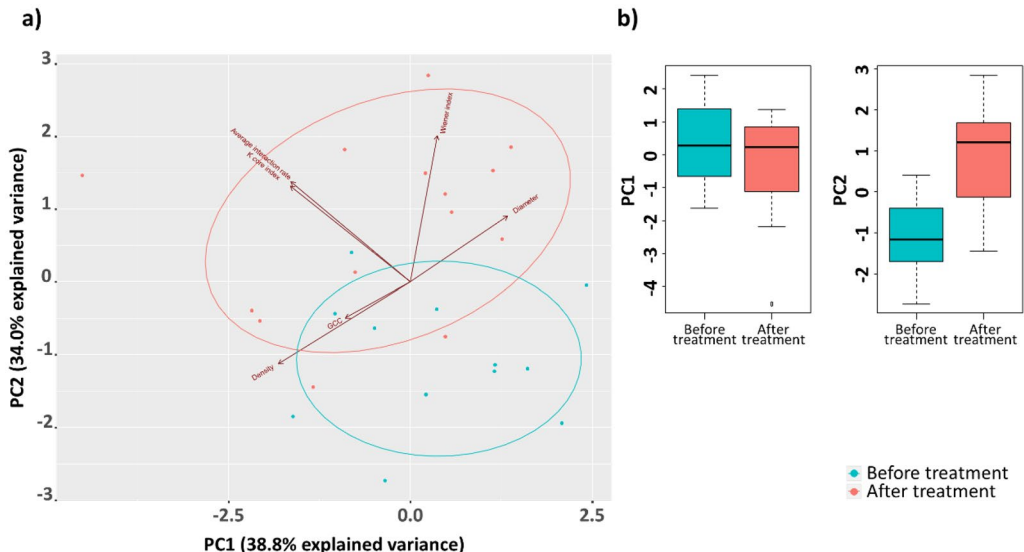

Figure 4. Principal component analysis of the social network metrics. **a** Primary component analysis shows that some network measures are more affected than others when colonies are faced with a significant loss of foragers. Different colours represent social network analyses carried out before (cyan) and after (red) the experimental manipulation. **b** Boxplots demonstrating the significant effect observed in PC2 (p < 0.001) in function of the treatment, mostly caused by variations on the network average interaction rate, K-core index and Wiener index.

The decrease in the proportion of guards might be linked with the fact that workers skipped the guarding task completely, transitioning immediately to a foraging role to supply the sudden demand for new foragers. There was no immediate significant effect of treatment on workers performing nest maintenance or broodcare tasks. This is logical from a resource allocation perspective (Schmickl and Crailsheim 2007), since the removal of foragers does not immediately impact the brood condition of the hive i.e. the demand of cleaning the rearing cells and feeding the brood remains and the survival of the colony partly relies on the survival of the progeny (Lee and Winston 1987). Nevertheless, the manipulation does impact the food storing which is directly linked with the foraging task partitioning as well as guarding which precedes the foraging role (Anderson and Ratnieks 1999; Ratnieks and Anderson 1999; Seeley 1995).

Workers making the transition from broodcare to food storage decreased substantially in their proportion through treatment, and a significant increase was seen in the proportion of workers moving from nest maintenance to guarding. This observation supports our previous observation, showing that, workers will react by skipping tasks like broodcare and food storage and immediately transition to more external tasks such as guarding and foraging in response to the removal of foragers. Our data shows that before the experimental manipulation workers performing broodcare gradually proceed to food storage. However, a similar proportion transition from nest maintenance to guarding after treatment, despite the greater age difference observed between these tasks under regular age polyethism (Seeley 1995; Seeley and Kolmes 1991; Wilson 1971). In addition to completely skipping some tasks, workers also performed quicker transition between tasks, ranging from half a day to 2 days earlier when compared to before manipulation.

4.2. Social network dynamics

Our social network analyses indicated that some network cohesion metrics are significantly affected by the experimental treatment. The principal component analysis showed that treatment caused a significant change in its second dimension which was mostly determined by the increase of the average interaction rate, the K-core and the Wiener indices. Both the average interaction rate and K-core index undergo similar changes through the treatment. This pattern can be explained by the strong positive correlation present between nodal coreness and interaction rate (Shin et al. 2018). An increased average interaction rate corresponds to an increased number of interactions by every actor in the network. The removal of foragers increased the average interaction rate of the social networks meaning that, on average, workers interacted with more nestmates when compared to before the manipulation. A higher connectedness inside the network leads to a faster flow of information among all actors in the network (Mersch 2016). A colony may quickly adapt to changing external and internal conditions, and our results suggest that colonies might increase their information flow to swiftly communicate the sudden loss of foragers to all nestmates as fast as possible (Biesmeijer and Slaa 2004; Franks et al. 2002; Seeley 1986). Social insects are well-known for their plasticity in interaction networks. Notably in the context of famine relief in which starved ant colonies showed an increased in the overall number of interactions i.e. average interaction rate and decrease in spatial fidelity or workers (Sendova-Franks et al. 2010). In addition, social insect colonies are able to adapt the topology of their interaction network to reduce disease transmission by increasing the modularity and clustering of the network (Stroeymeyt et al. 2018), or by favouring interactions between specific age or task cohorts (Naug and Smith 2007; Naug 2008; Quevillon et al. 2015).

In addition, the manipulation caused the social networks to increase their number of cores as a consequence of individuals that were more closely connected to others after the treatment. The K-Core index gives an indication of the stability of a network against possible decay (Pusceddu et al. 2021). It has been shown that the distribution of the k-core network has an

influence in the network resilience and that networks with a high number of individuals in the most centralized and peripheral k-cores are better protected against network deviations (Burleson-Lesser et al. 2020). The removal of foragers could have prompted the colonies to adapt to this disturbance and strengthen themselves as a response to possible future losses. Our data is consistent with previous findings where the resilience of the communication network was maintained after experimental removal of foragers (Gernat et al. 2018). Another explanation could be linked with the fact that the colonies were just in a phase of colony expansion and that the higher K-cores are a result of the increased growth of the colony. This could also explain the increase in the Wiener index, which is somewhat contradictory. An increased Wiener index after treatment might be related to more openly clustered structures (Scardoni and Laudanna 2011) or, alternatively, be an artifact of the increase in the number of nodes (Tian and Choi 2013). Nevertheless, when analysing specific task groups in the networks before and after removal, we can observe that each task is well represented in both the periphery and centre of the networks, indicating that workers with high and low degrees of interactions are equally represented within each type of task in the colony. Indeed, the sparse sampling methodology employed in this study through direct behavioural observations may pose quantitative limitations in capturing the multitude of social interactions within the honeybee colony. Consequently, exploring more comprehensive sampling approaches, such as utilizing advanced techniques like automated tracking, presents an interesting avenue for future research.

Overall, our results support the assumption that removal of foragers causes some workers to deviate from the normal sequence of age polyethism and transition quicker or even completely skip tasks in order to compensate for a sudden loss of foragers. This behaviour is an adaptation to the precarious situation in which a colony is in when it has lost a substantial part of its foragers (Huang and Robinson 1996; Robinson et al. 1994). Foragers are fundamental for the collection of food resources and the overall homeostasis and survival of the colony (Prado et al. 2020). Without a strong foraging force, a colony would likely be weakened and ultimately collapse. It is therefore paramount that the workers, as showed by our results, act quickly in restoring a well-established foraging role in the colony. Indeed, social network parameters also changed after the experimental treatment with the removal of foragers causing the colony to develop a more connected interaction network suggesting an increased resilience. Even when faced with a substantial perturbation such as losing half of their foragers, hives can react and swiftly adapt to these situations maintaining homeostasis and survival of the colony, which might suggest that they may be resilient to the likely uncertain climatic scenarios of the future.

AUTHOR CONTRIBUTION

RCO and TW conceived the original idea. EB and RCO performed the experiments and data analyses. EB wrote the first draft of the manuscript. All authors edited and approved the final version of the manuscript.

FUNDING

CODE AND DATA AVAILABILITY

The data and codes generated during the current study are available in the Mendeley Data (Beck et al. 2022).

DECLARATIONS

Ethics approval   According to Belgian law, research with insects is exempt from ethics committee approval.

Consent to participate   Not applicable.

Consent for publication   Not applicable.

Competing interests   The authors declare no competing interests.

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