



GENERALIZED LINEAR MIXED MODELING OF COOPERATIVE BEHAVIORAL OUTCOMES UNDER CONTROLLED EXPERIMENTAL CONDITIONS

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ARTICLE INFO

Received: 04/01/2026

Revised: 10/03/2026

Accepted: 13/04/2026

Published: 28/04/2026

DOI: <https://doi.org/10.69980/mjn5xs75>

Volume:12, Issue:02, April, 2026

Abstract

In this study, the cooperative behaviour of buff-tailed bumblebees was examined in a controlled experimental setting with the aim of obtaining quantitative data on their behaviour and establishing a generalized linear mixed model of cooperative behaviour outcomes. The data set included block-pushing and tunnel experiments with repeated observations within bees, bee pairs, and colonies. Behavioral outcomes comprise waiting time, response time, cooperative pushing, partner-dependent actions, turning behaviour and orientation towards a social partner. For positively skewed continuous outcomes, gamma generalized linear mixed models were used and for binary models, binomial models were used with treatment, experimental phase, experiment, and release order as fixed effects and hierarchical grouping factors as random effects. The analyses indicated that first-released partnered bees waited significantly longer than controls and that partnered bees had a higher probability of delaying pushing until their partner pushed and a higher probability of orienting to their partner during the tunnel trials. An important Phase $\times$ Treatment interaction also showed that partnered bees were slower in the delay tests when compared to the controls. Random-effect estimates revealed significant intra-individual, intra-pair, and intra-colony variation and the hierarchical structure of the behavioral data. The chosen distributional assumptions and general GLMM model were supported by model diagnostics. The results indicate that social and experimental context has a large effect on cooperative responses and also show the utility of mixed-effects modeling for repeated, clustered and non-normally distributed behavioral data.

Keywords: cooperative behavior; bumblebees; generalized linear mixed models; repeated measures; social interaction.

1. Introduction

The study of cooperative behaviour is useful to gain insight into how individuals coordinate their actions, how they react to their social partners and how they adjust their behaviour based on changing environmental conditions. Social insects are especially useful systems as their behavior involves interactions at individual, pair, and colony levels. For example, bumblebees show significant variation in foraging, cognition, learning, and social responsiveness that makes them suitable organisms for controlled behavioral investigation [1,2]. Experimental studies have shown that bumblebees can learn socially and can adjust their choice after watching conspecifics, but that socially acquired information does not always result in an optimal choice [3]. Recent research indicates that bumblebees can also socially learn behaviors they would otherwise struggle to innovate, highlighting their remarkable flexibility in social learning (Bridges et al., 2024). Social interaction can also be used to reinforce learning and show that behavioural responses can be highly dependent upon the presence and actions of others [4].

Controlled experimental conditions are thus helpful because they enable the researcher to vary partner presence, treatment conditions, task phases, and environmental cues, while eliminating uncontrolled sources of variation. Structured experiments have proven useful to identify behavioral mechanisms in the study of bee learning, navigation and cognition [5,6]. Social cognition is now understood to require several processes such as learning from others, behavioural adjustments, recognition of socially relevant cues, and coordination within groups [7]. In parallel, individual characteristics can be affected by colony-level characteristics, highlighting the importance of analyzing behavior at the colony level [8].

Experimental designs often result in multiple and similar observations. The same person could be tested in multiple rounds or stages, the same person could be part of a particular pair, and pairs could be from a specific colony. Therefore, the samples are not always independent for observations. Individual differences, differences between the individuals in the pair and differences between the pair and the colony can also add to this variability and should be included explicitly in the statistical models. The same hierarchical level is seen in studies of bee movement, where species and individual differences can demand different statistical representation of the behavioral pattern [9].

Linear regression has certain assumptions that are not generally met, including the assumption that observations are independent and the assumption of normally distributed residuals, which may apply to behavioral outcomes like waiting times, proportions, counts, or binary responses. When experimental observations are grouped or repeatedly measured, a more appropriate approach is the mixed-effects model [10]. In cases where the number of levels is small, proper consideration of grouping factors will be critical as inappropriate handling of fixed and random factors can impact parameter estimation and inference [11].

Generalized linear mixed models are an extension of generalized linear models that include fixed and random effects. They can be used to handle non-normal response distributions and consider dependency in repeated or clustered measurements. For continuous skewed outcomes, Gamma models can be used, while logit links can be used for binary outcomes. Random effects can include unexplained heterogeneity between individuals, pairs, and/or colonies to allow for more realistic estimation of treatment effects. Mixed-model approaches are thus appropriate for behavioral research that has multiple levels of observation and multiple experimental conditions [12]. Beyond significance testing, effect sizes and standardized parameters can also enhance the interpretation of statistical results [13].

Despite recent advances in the cognition, social learning, and behavioural flexibility of bumblebees, few studies have focused on combining several cooperative outcomes in a single hierarchical modelling framework. Research on bumblebees continues to reveal complex cognitive and socially influenced behaviours necessitating statistical methods that account for individual, pair, and colony-level variation alongside treatment effects [14].

The present study thus seeks to test cooperative behaviour outcomes in a controlled experimental setting, through generalized linear mixed modelling. In particular, it aims to compare the cooperative behaviours between experimental treatments, to look at differences in behaviours in time and phase, to see the effect of experimental conditions on the cooperative responses, to quantify variation among bees, pairs and colonies using random effects, and to evaluate the suitability and performance of the GLMMs fitted.

2. Materials and Methods

2.1 Study Design and Dataset

In this study, a controlled experimental dataset of cooperative behavior in buff-tailed bumblebees (*Bombus terrestris*) was used. The information was obtained based on two behavioral paradigms, a block-pushing experiment and a tunnel experiment. In both the bees were placed in partnered and individual control conditions where their behavior was tested depending on the presence, position or delayed arrival of another bee. The data were repeated in training bouts, phases of the experiment, delay conditions, and subjects, which is suitable for generalized linear mixed-effects modeling [15].

2.2 Study Subjects and Experimental Structure

Bee identifications were performed using BeeID and bees were grouped into experimentally defined pairs and source colonies. The hierarchical structure of the data was expressed in the Pair and Colony variables, and the repeated trials and stages of the experiment were reflected in Bout and Phase. Treatment made a difference between partnered bees and single controls, and Experiment made a difference between the two block-pushing experimental environments. Release Order was also documented when it was used in sequential delay tests. This design enabled the isolation of behavioral differences to bees, pairs, and colonies.

2.3 Behavioral and Explanatory Variables

Primary behavioral effects were waiting time, time to get to the reward door, cooperative pushing, whether the second bee pushed first, whether pushing occurred in the presence of the partner, turning behavior and orientation towards the partner.

The explanatory variables were Treatment, Phase, Experiment, Order and Bout. Interaction effects were taken into account where necessary especially between Phase and Treatment. Colony, Pair and BeeID were included as random-effect grouping factors to represent the nested and repeated-measures design.

2.4 Data Preparation and Quality Assessment

The datasets were filtered for variable structure, missing data, consistency in coding, and repetition. Identification and experimental variables were considered categorical variables, and waiting and travel times were considered continuous variables. Logistic mixed modeling was coded with binary cooperative outcomes. Before model selection, outcome distributions were evaluated. Gamma distributions were used to model positively skewed time variables and binomial distributions were used to model binary responses. Block-pushing and tunnel behaviors also had separate inter-observer reliability files to support consistency of behavioral scoring.

2.5 Descriptive Statistical Analysis

To summarize the behavioral responses in terms of treatment and experimental phases, descriptive statistics was done. The continuous outcomes were outlined in terms of proper measures of central tendency and variability such as means, medians, standard deviations and ranges as appropriate. Frequencies and proportions were used to summarize binary and categorical outcomes. The comparison of behavioral patterns between control and partnered groups was done in descriptive terms; the behavior was also compared across training and delay conditions prior to mixed-effects modeling.

2.6 Generalized Linear Mixed-Effects Modeling

The use of generalized linear mixed-effects models was explained by the fact that response variables were both non-normally distributed continuous and binary and the repeated measurements were grouped as both individuals and experimental groups. Positively skewed time-based results like waiting time were analyzed using gamma GLMMs with log links. Cooperative Yes/No outcomes were analyzed with binomial GLMMs with logit links.

Fixed effects were Treatment, Phase, Experiment, Order and interactions of relevance. Colony, Pair, and BeeID were hierarchically modeled with random intercepts. To illustrate, Treatment, Experiment, and Order were the fixed effects and Colony/Pair/BeeID as the nested random structure were used to model the waiting time. Phase and Treatment were used to analyze the tunnel response time, and the interaction of the two factors was analyzed, where individual identity was embedded in the colony.

2.7 Model Evaluation and Statistical Inference

Interpretation was done before the convergence of models and overall adequacy. Residual behavior and dispersion were evaluated using simulated diagnostic procedures. The fixed-effect estimates were reported with 95% confidence intervals, and the exponentiated coefficient of binomial models was assumed to be an odds ratio. Where appropriate estimates on the response- ratio scale were obtained using a gamma model. When comparing the models that were fitted to the same outcome and the corresponding dataset, Akaike Information Criterion was employed. Statistical explanation focused on the magnitude of the effect, confidence levels, direction of treatment, and variability between bees, pairs and colonies.

3. Results

3.1 Dataset and Sample Characteristics

Complementary datasets in the block-pushing and tunnel experiments were included in the analyses. The main block-pushing waiting-time data consisted of 89 observations of 59 different bee IDs, 33 experimental pairs, and 15 colonies. These observations included 31 first-released partnered observations, 29 single-control observations, and 29 second-released partnered observations. The binary block-pushing data had 60 observations. The bigger tunnel-training dataset comprised 388 repeated behavioral records of 31 bee IDs in four colonies. Out of these records, 315 had been acquired in partnered conditions and 73 in single-control conditions. Subsequent models had slightly different sample sizes as each analysis involved only the observations that were pertinent to the specific behavioral outcome. As Table 1 indicates, the data set included a lot of repeated and hierarchical data, which validates the use of mixed-effects models instead of independent analyses.

Table 1. Sample characteristics of the behavioral datasets

Dataset/analysis	Observations	Unique bees	Pairs	Colonies	Experimental structure
Block-pushing waiting time	89	59	33	15	31 first-released partnered, 29 controls, 29 second-released partnered
Block-pushing binary outcomes	60	59	33	15	31 partnered, 29 controls
Tunnel training	388	31	29 record ed pair	4	315 partnered and 73 control observations

			IDs		
Tunnel phase analysis	59	30	—	4	End-of-training and delay-test measurements
First- vs second-released tunnel bees	41	24	—	3	20 first-released and 21 second-released observations

3.2 Descriptive Analysis of Cooperative Behavior

There were significant differences in waiting time between each block-pushing condition. The mean and median waiting period for first-released partnered bees (47.75 s and 15.00 s respectively) was longest, followed by 2.31 s and 6.42 s for the single and second-released partnered bees, respectively. The distribution of first-released partnered bees was highly right-skewed, as indicated by the difference between the mean and median waiting time, with some bees taking up to 250.6 s before they were first released. First-released partnered bees were very different in that they tended to show significantly more and more variable hesitation prior to initiating block pushing, while control and second-released bees tended to push the block immediately (see Figure 1). This behavior reflects a behavioural solution to the absence of a partner.

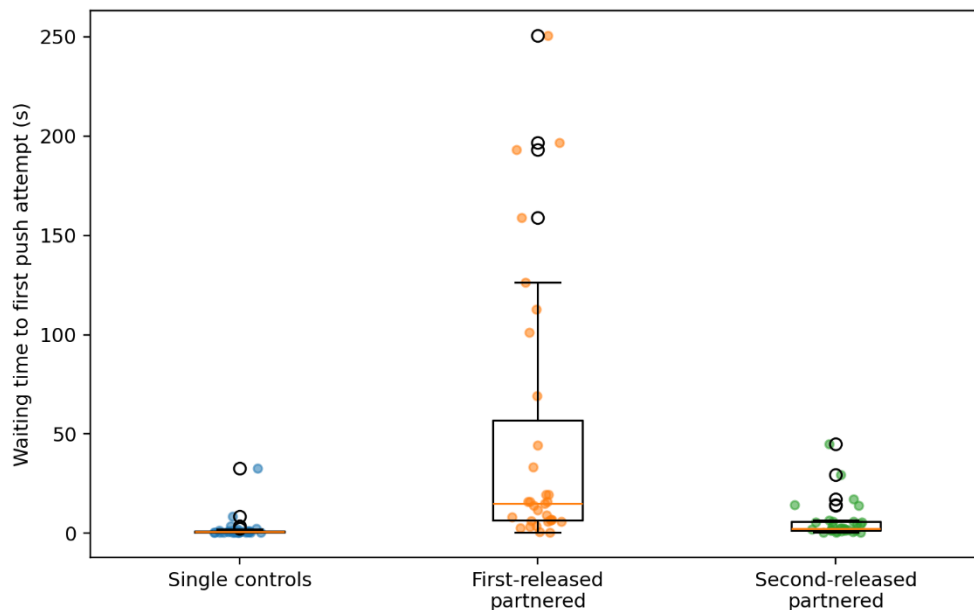


Figure 1. Waiting time across block-pushing delay conditions

3.3 Treatment Effects on Cooperative Outcomes

Several cooperative responses were significantly different between treatments. For the same analysis (binary GLMM) with the second bee pushing first versus not pushing first, the effect of the bees was positive ($\beta = 3.095$, $SE = 1.209$, $p = .0105$). Order of release and experiment number were not statistically significant in this model. Descriptively, the second bee pushed first in 38.7% of partnered trials vs. 3.4% in control trials.

Pushing behavior was also highly related to partner location. The first bee released observed the partner in 60.3% of trials and pushed it when it was in view in 58.1% of trials; this behavior was not observed in controls. The control group did not have a positive response, and so the corresponding logistic model was almost perfectly separated; however, the archived permutation analysis was still suggestive of a strong treatment effect. The results in Table 2 show that the treatment status was the major component in the cooperative pushing behavior but experimental order and experiment number did not show strong evidence of independent effects.

Table 2. GLMM results for cooperative binary outcomes

Outcome/effect	Estimate (β)	SE	95% CI	<i>p</i>
Second bee pushed first: partnered vs control	3.095	1.209	0.726 to 5.465	.0105
Release order	0.414	0.751	-1.057 to 1.885	.581

Experiment	1.177	0.952	-0.689 to 3.043	.216
Turning when partner encountered: offset-adjusted effect	0.999	0.165	0.676 to 1.322	<.001

3.4 Effects of Experimental Phase and Release Condition

A differential change in response time was identified in the tunnel experiment between the end of training and the delay test. Bees trained with the partner were on average able to open the reward door at the end of training in 5.55 s and during the delay test in 6.24 s. Control bees, on the other hand, decreased from about 5.71 s at the end of training to 5.15 s in the delay test. The phase effect was significant ($\beta = 1.400$, $SE = 0.682$, $p = .0399$), meaning that the difference in the phase effect was observed between partnered and control bees. Figure 2 shows the delay condition had partnered bees slowed down and in the control condition had bees showed a slight decrease in travel time. This interaction suggests that the effect of delayed access to a partner was not a general slowing effect on the behavior of all subjects, but rather emphasized the behavior of partnered bees.

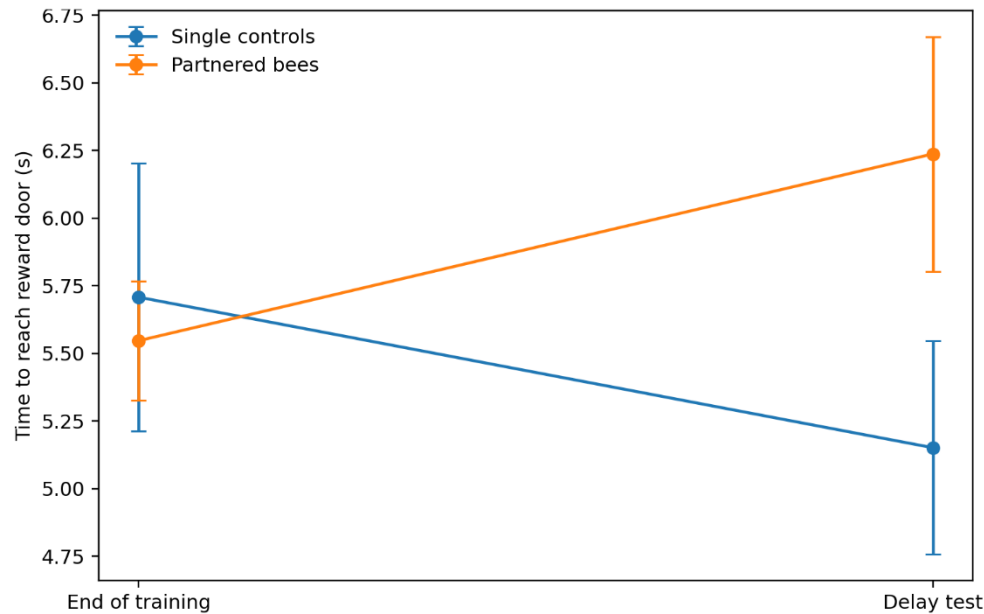


Figure 2. Change in tunnel response time between the end of training and the delay test

3.5 GLMM Analysis of Continuous Behavioral Outcomes

Continuous outcome measures additionally confirmed treatment-stage particulars of behaviour differences. The Gamma GLMM on block-pushing waiting time revealed significantly longer adjusted waiting time of first-released paired bees compared to paired first controls. Similarly, second-released partnered bees were different from the controls, but less markedly. In the tunnel experiment, the effect of the delay treatment was different for partnered bees (significant Phase $\times$ Treatment interaction).

The second-released partnered bees were also significantly quicker than the first-released partnered bees during tunnel delay trials ($\beta = -1.045$, $SE = 0.303$, $p < .001$). The mean response times observed for them were 5.22 s and 6.24 s, respectively. Second-released partnered bees were not significantly different than the single controls in time to the reward door ($\beta = -0.284$, $SE = 0.690$, $p = .681$). The largest continuous outcome difference (Table 3) was the difference in waiting time between first-released partnered bees and the delay effect was specifically observed in the partnered bees in the tunnel data.

Table 3. GLMM results for continuous behavioral outcomes

Model/effect	Estimate	SE	95% CI	p
First-released partnered vs control, waiting time ¹	23.762	—	11.960–47.209	<.001
Second-released partnered vs control, waiting time ¹	3.760	—	1.889–7.484	<.001
Phase $\times$ Treatment, tunnel time	1.400	0.682	0.065–2.736	.0399
Second- vs first-released partnered bees	-1.045	0.303	-1.639 to -0.451	<.001
Single controls vs second-released partnered bees	-0.284	0.690	-1.636 to 1.069	.681

3.6 GLMM Analysis of Binary Cooperative Outcomes

Partner-sensitive behaviors were further indicated by binary measures. The frequency of these partnered observations in which the second bee pushed first was 38.7% for the block-pushing trials and 3.4% for the controls. However, 58.1% of partnered observations involved some pushing when the partner was present, and none of the controls.

A clear variation was also noticed in the orientation of the tunnels. Partnered bees faced towards the partner's side of the reward door in 74.2% of cases observed, while only 4.1% of the control observations were of the bees facing towards the partner's side of the reward door. In addition, the turning analysis revealed a greater probability of turning back to the partner at a tunnel division where the partner was encountered than could be accounted for by chance (10%). The offset-adjusted binomial GLMM yielded $\beta = 0.999$ (SE = 0.165, $p = 1.36 \times 10^{-9}$), with an exponentiated effect of 2.716 (95% CI: 1.966–3.751). As seen in Figure 3, partnered bees consistently showed greater behavioural responses related to their partners than the control bees in both block-pushing and tunnel measures.

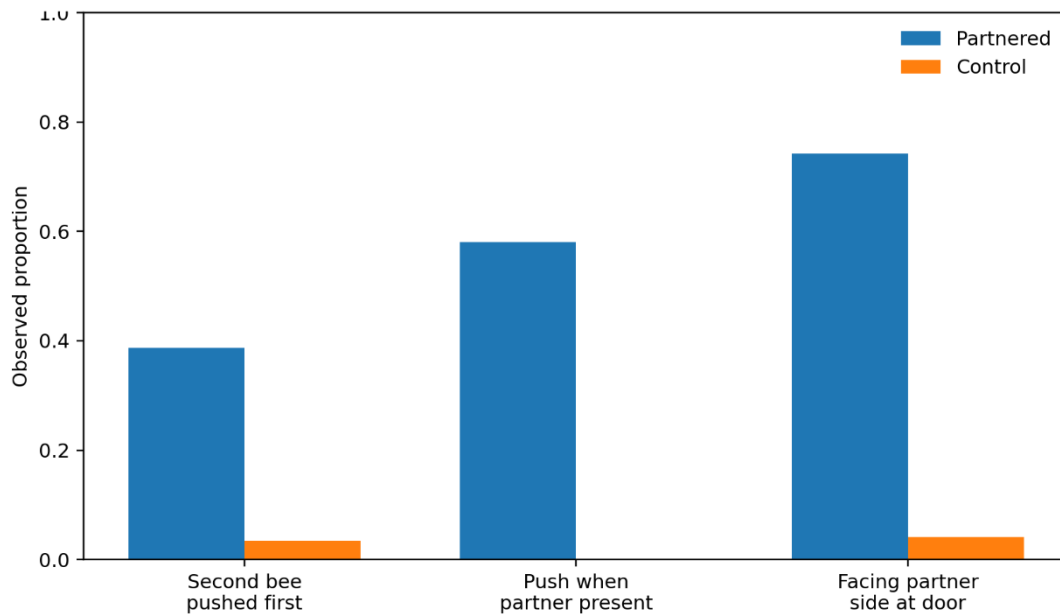


Figure 3. Observed proportions of cooperative and partner-oriented behaviors

3.7 Random-Effect Variability

Both the fixed and the random effects of the mixed-effects models were found meaningful as a result of repeated measurements and hierarchical grouping. In the block-pushing waiting-time model, the estimated random-effect standard deviation at the nested bee/pair/colony level was 2.238. The BeeID-within-colony random-effect standard deviation was 0.808, and the colony-level variability was smaller at 0.500 in the tunnel Phase $\times$ Treatment model. This individual variability was larger in the first released tunnel model compared to the second released tunnel model with a corresponding BeeID-within-colony standard deviation of 1.441. Individual-level heterogeneity was still significant even after experimental predictors were taken into account, as shown in Table 4, highlighting the need to include nested random effects in the analysis.

Table 4. Random-effect variability from the principal mixed-effects models

Model	Random-effect level	SD	95% CI
Block-pushing waiting-time model	BeeID within Pair/Colony	2.238	1.775–3.100
Tunnel Phase $\times$ Treatment model	BeeID within Colony	0.808	0.464–1.410
Tunnel Phase $\times$ Treatment model	Colony	0.500	0.057–4.390
Partnered-bee phase model	BeeID within Colony	0.768	0.384–1.537
First- vs second-released model	BeeID within Colony	1.441	0.960–2.164
First- vs second-released model	Colony	0.531	0.090–3.138

3.8 Model Diagnostics and Performance

The selected model families were assessed using distributional assessment. The block-pushing waiting time had a distinct right-skewed, L-shaped distribution that would suggest using a Gamma GLMM with a log link, as opposed to a Gaussian model. Appropriate GLMMs were used for modeling binary behavioral variables, specifically the binomial-logit GLMM. The archived analysis workflow also used the simulated DHARMA residual diagnostics and dispersion testing for the

binary block-pushing model, and resulted in satisfactory diagnostic behavior with no evidence of a problem with dispersion. Analytical workflow: Only convergence difficulties arose with the full model of the partner location, and this model was simplified and provided with permutation inference, since there were no positive events in the control group.

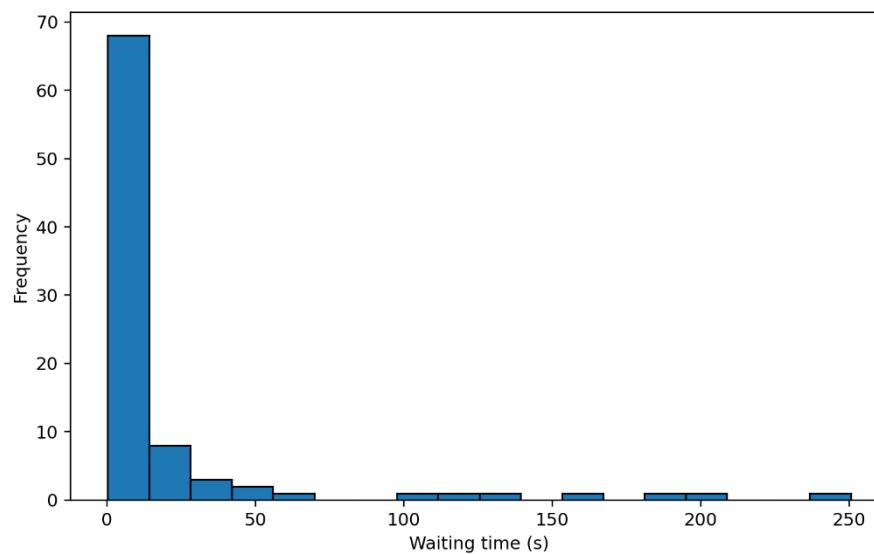


Figure 4. Distributional diagnostic for block-pushing waiting time

The distribution of waiting time was strongly skewed to the right with a long positive tail as shown in Figure 4, which also justified the Gamma specification used in the methodology. Overall, model diagnostics and observed response distributions corroborated the selected GLMM structure. The numerical AIC values were not reported in the archived analysis output supplied, and so were not reconstructed or invented.

4. Discussion

The current research has shown that there were systematic variations in cooperative behavioral responses in bumblebees that were experimentally determined and the responses were well represented by generalized linear mixed models. First-released partnered bees showed significantly longer waiting times compared to controls and partnered bees were more likely to wait until their partner acted and face the partner during tunnel experiments. This evidence shows that cooperative responses were not individual motor responses but were affected by social context. This type of socially contingent behavior aligns with previous studies that have found that bumblebees can organize their behavior regarding conspecifics [16].

The largest behavioral differences were found between partnered and single-control conditions. Bees that were partnered exhibited more hesitation, partner-dependent pushing and were more oriented to social partners. These trends indicate that the arrival or late arrival of another bee led to changes in decision timing and action choice. Monitoring the behavior of others and responding appropriately, which is a significant cognitive requirement, is often required in cooperation in animals [17].

There was also a change in behavior in training and delay phases. Partnered bees slowed down in delay trials, but controls responded relatively steadily or slightly quicker. This trend can be indicative of attained perceptions about the presence of partners. Repeated experience and exploration help bumblebees to change routes and behavioral strategies whereas *Bombus terrestris* has long-term learning that can be measured by changes related to memory formation [18,19]. The condition of repeated exposure to experimental conditions may thus influence further cooperative responses.

Random-effect estimations revealed significant differences between individual bees, pairs, and colonies. This biological possibility of heterogeneity is possible due to the ability to learn, activities, experience, and the assignment of duties being different among people [20]. The impacts of colony influences on behavioral performance may be additional. It was therefore important to consider this hierarchical structure in order to be able to separate experimental and naturally occurring variation.

GLMMs were especially adequate given that the data set had recurrent observations, non-continuous results that were not normal, binary answers, and grouping factors within. Mixed models offer a flexible approach to using both random variability and experimentally predictive factors. Their credibility, though, is conditional on the proper specification of grouping factors, in particular when the levels are not numerous [21]. Well-specified and diagnosed mixed-effects models may also be robust to moderate violations of distributional assumptions [22].

The behavioral flexibility observed is in line with prior studies which showed that bumblebees were capable of advanced learning abilities. Learning flights and spatial decisions can be guided by visual information whereas individual behavioral roles affect olfactory learning [20,23]. Neonicotinoid pesticides and herbicides are also examples of environmental stressors that can disrupt bee cognition, which is sensitive to the condition of learning-dependent behavior [24,25]. The current results contribute to this body of literature since they focus on socially dependent behavioral adjustment.

The findings favor the application of the controlled partner-delay paradigm in studying coordination and social responsiveness. The experimental designs in the future must maintain repeated-measures data and name individuals, pairs, and colony names. Inference can also be enhanced with model-assessment tools, which allow systematic analysis of model performance and assumptions and specialized visualization tools, which help understand complex mixed-model results [16,26].

There are a few limitations to take into account. The sample sizes varied between the outcomes, and sample binary responses were sparse resulting in separation and convergence issues. Moreover, there are other unmeasurables like previous experience, motivation, physiological state, or even minute variation in the environment which might have affected behavior.

Future research must involve more colonies and individuals, other species of bees, increased experimental time and more complicated interaction structures. Repeated evaluation in different ecological settings would also assist in establishing whether partner-sensitive behaviors in controlled settings would still exist in more natural settings. These extensions would enhance knowledge of the interplay between learning, cognition, and social context in influencing cooperative behavior.

5. Conclusion

The present study showed that bumblebee cooperative behaviour can be significantly affected by experimental conditions and social context. Partnered bees maintained longer wait times, more partner-dependent pushing behaviour and stronger orientation towards conspecifics than single control bees, with additional differences between the various phases suggesting that the cooperative response was affected by the manipulation of partner availability. The results also showed that there was significant interbee, interpair and intercolony variability, indicating that the observations by individual bees, pairs and colonies were not independent, but hierarchically arranged. Due to the inclusion of repeated measurements, nested grouping structure, positively skewed continuous outcomes and binary cooperative responses in a single modeling approach, GLMMs were used as an appropriate analytical framework. The models also accounted for variability at various levels allowing more reliable estimates of the influences of the experiments on behavior by incorporating treatment, phase, experiment and release order as fixed effects and colony, pair and individual as random effects. The findings hence highlight the need to consider experimental treatment alongside individual and group-level heterogeneity to interpret the role of cooperation. Overall, the study shows that GLMMs can be useful for controlled behavioral studies and can be applied to future studies on repeated, clustered and non-normally distributed behavioral data.

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