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Reconsidering response threshold models — Short-term  
response patterns in thermoregulating bumblebees

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## 11 ABSTRACT

12 Social insect colonies distribute their workforce with amazing flexibility across a large array of diverse  
13 tasks under fluctuating external conditions and internal demands. Deciphering the individual rules  
14 of task selection and task performance is at the heart of understanding how colonies can achieve this  
15 collective feature. Models play an important role in this endeavor, as they allow us to investigate  
16 how the rules of individual behavior give rise to emergent patterns at the colony level. Modulation  
17 of individual behavior occurs at many different timescales and to successfully use a model we need  
18 to ensure that it applies on the timescale under observation. Here, we focus on short timescales  
19 and ask the question whether the most commonly used class of models (response threshold mod-  
20 els) adequately describes behavioral modulation on this timescale. We study the fanning behavior  
21 of bumblebees on temperature-controlled brood dummies and investigate the effect of (i) stimu-  
22 lus intensity, (ii) repeated task performance and (iii) task performance feedback. We analyze the  
23 timing patterns (rates of task engagement and task disengagement) using survival analysis. Our  
24 results show that stimulus intensity does not significantly influence individual task investment at  
25 these comparably short timescales. In contrast, repeated task performance and task performance  
26 feedback affect individual task investment. We propose an explicitly time-resolved individual-based  
27 model and simulate this model to study how patterns of individual task engagement influence task  
28 involvement at the group level, finding support for the hypothesis that regulation mechanisms at  
29 different timescales can improve performance at the group level in dynamic environments.

30  
31 **Key words:** task allocation, temporal influence, timing of behavior, task feedback, behavioral  
32 flexibility.

## 33 SIGNIFICANCE STATEMENT

34 Social insect colonies distribute their workforce flexibly across a wide range of tasks. In the absence  
35 of a central command structure it is crucial for our understanding of collective task allocation that  
36 we decipher the rules according to which individuals regulate their task engagement. Here, we  
37 explore bumblebee thermoregulation. Using temperature-controlled brood dummies we analyze how  
38 temperature, repeated task performance and performance feedback modulate the timing of individual  
39 fanning behavior. We show behavioral modulation in response to task performance. Contrary

40 to common expectation, our results show that in some cases the ability to experience success in  
41 performing a task (here cooling the brood when fanning) can result in decreased individual task  
42 engagement. Based on our analysis we construct and simulate a detailed model for individual task  
43 response to show how this individual-level behaviour can impact on group-level performance.

## 44 INTRODUCTION

45 Social insect colonies provide a dazzling example of flexible, decentralized collective organization.  
46 They cooperatively manage a complex network of simultaneous tasks ranging from scouting and for-  
47 aging to colony defense, nest building and brood care. One of the key features of colony organization  
48 is division of labor, whereby each member of the colony specializes (permanently or temporarily) in  
49 a subset of the tasks required for colony functioning. (Wilson 1971; Oster and Wilson 1978; Wilson  
50 1985; Page Jr and Mitchell 1990; Beshers and Fewell 2001; Schwander et al. 2005). Colonies demon-  
51 strate amazing flexibility in adjusting to changes in external conditions and in internal colony needs  
52 (Oster and Wilson 1978; Robinson 1992; Gordon 1996; Duarte et al. 2011). This ability to maintain  
53 a flexible but highly robust organization in complex and diverse circumstances is often cited as a  
54 key factor for the remarkable ecological success of social insects (Oster and Wilson 1978; Hölldobler  
55 and Wilson 1990; Grimaldi and Engel 2005; Hölldobler and Wilson 2009).

56 Despite a significant amount of research into division of labor and task allocation (Bakker and  
57 Traniello 2016), our understanding of the underlying proximate mechanisms is still incomplete at  
58 best.

59 Collective flexibility is based on plasticity in individual behavior. Workers in a colony are sur-  
60 rounded by a wide array of task-associated stimuli and need to continuously make decisions about  
61 if and how to respond to these stimuli. Once an individual decides to perform a task, the time and  
62 energy invested into that task can vary. Individual response decisions and task performance patterns  
63 are modulated by numerous parameters; and modulation of individual behavior can occur at many  
64 different timescales (Naug 2016). For example, age polyethism (Oster and Wilson 1978), whereby  
65 individuals' tendencies to perform a task or a subset of tasks shift with age, affects task perfor-  
66 mance over the individual lifetime. Experience and learning, e.g. when interacting with a stimulus  
67 or with nestmates can modulate individual behavior on timescales of days or hours (Jeanson and  
68 Weidenmüller 2014). Understanding the rules of individual task selection and task performance,  
69 and the parameters modulating these rules, is at the core of the study of collective behavior. Models  
70 play an important role in this endeavour, as they allow us to investigate how the rules of individual  
71 behavior give rise to emergent patterns at the colony level. However, many theoretical models in  
72 the literature have not explicitly addressed on which timescale they are applicable.

73 In this paper, we focus on the timing of task performance on short timescales. Analyzing the

74 fanning behavior of thermoregulating bumblebees, we ask whether the most commonly used class  
75 of models adequately describes individual response dynamics on short timescales. Tasks are not  
76 performed continuously but individuals often engage and disengage with a task. These temporal  
77 patterns of task performance may play an important and often overlooked functional role in task  
78 allocation. We specifically address the modulatory effect of three factors on the timing of individual  
79 behavior: stimulus intensity, repeated task performance and task performance feedback.

80 Stimulus intensity is a core ingredient in the most widely accepted models for division of labor  
81 in social insects (for reviews see Robinson 1992; Beshers and Fewell 2001; Duarte et al. 2011) – the  
82 response threshold models (Bonabeau et al. 1996; Page Jr and Mitchell 1998; Theraulaz et al. 1998).  
83 The general idea of response thresholds has been used in many different forms. It simply refers to  
84 the assumption that individuals have an internal threshold for task-related stimuli and that they  
85 will react to this task only if the stimulus exceeds the threshold or, in probabilistic versions, that  
86 the threshold of an individual regulates the probability of the individual to react (see below).

87 In this paper we are only concerned with a specific form of *probabilistic* response threshold model  
88 (Bonabeau et al. 1996; Theraulaz et al. 1998; Gautrais et al. 2002), the so-called reinforced response  
89 threshold model. Arguably, this is one of the few that have been fully mathematically formalized  
90 and the most widely used one among these.

91 In this model, the dependency of the response probability on the stimulus level is usually modeled  
92 as a sigmoid function

$$93 \quad p_{\theta}(s) = \frac{s^2}{s^2 + \theta^2} \quad (1)$$

94 where  $s$  is the stimulus intensity and  $\theta$  is the internal response threshold (Bonabeau et al. 1996).  
95 Here  $\theta$  is assumed to either be fixed (Bonabeau et al. 1996) or vary over time (Theraulaz et al. 1998).  
96 For the latter case, depending on whether the worker is engaged in the task or not,  $\theta$  can be given  
97 as:

$$98 \quad \theta(t+1) = \begin{cases} \theta(t) - \xi & \text{if the task is performed at time } t; \\ \theta(t) + \varphi & \text{otherwise} \end{cases} \quad (2)$$

99 where  $\xi$  and  $\varphi$  give the speeds of learning and forgetting respectively (Theraulaz et al. 1998; Gautrais  
100 et al. 2002).

101 Two fundamental predictions result from the core assumptions of the reinforced response thresh-  
102 old models as discussed above: (1) for fixed threshold, the probability to engage in a task increases

103 monotonically with stimulus intensity; (2) for threshold reinforcement, the probability to engage in  
104 a task gradually increases with repeated task performance. Thus frequent task performance by an  
105 individual results in a higher probability to perform the same task again. This positive feedback  
106 loop can ultimately lead to task specialization (Duarte et al. 2011; Fewell and Harrison 2016; Jeanne  
107 2016). While phrased in different terms, replacing the internal threshold with an internal stimu-  
108 lus, an early positive feedback model by Plowright and Plowright (Plowright and Plowright 1988)  
109 embodies the exact same idea.

110 In summary, while the general idea of response thresholds arose from the need to describe inter-  
111 individual differences, the reinforced threshold models add an additional layer that describes intra-  
112 individual differences over time, ie. how the behavior of an individual changes with task engagement.

113 In order to test the two predictions of the reinforced response threshold model concerning change  
114 in individual behavior, it is crucial that stimulus intensity and repeated task performance are de-  
115 coupled.

116 Most experimental studies so far have typically induced gradual changes of stimulus intensity  
117 over time, and thus implicitly over repeated task performance (O'Donnell and Foster 2001; Wei-  
118 denmüller et al. 2002; Weidenmüller 2004; Westhus et al. 2013). Using this experimental approach,  
119 it is impossible to distinguish whether any change in response probability over time is caused by  
120 the variation in stimulus intensity or simply by repeated task performance for short timescales,  
121 since stimulus intensity and task repetition both vary with time. Here we assess individual fanning  
122 response behavior in bumblebee thermoregulation under tightly-controlled experimental conditions  
123 with constant stimulus levels to separate the effects of stimulus intensity and repeated task perfor-  
124 mance and to address the question whether the timing of behavior is adequately described by the  
125 existing response threshold model.

126 Besides the two parameters addressed in the response threshold model (stimulus intensity and  
127 repeated task performance), other parameters may influence if and how an individual responds to  
128 a given task-associated stimulus on short timescales. Task performance feedback is a little studied  
129 but possibly significant factor here, as it offers an individual information about her own effectiveness  
130 in performing a task. This information may modulate future decisions concerning the task perfor-  
131 mance, thereby playing a decisive role in the process of task allocation and individual specialization.  
132 However, the extent to which collective success in social insects builds on individual specialization  
133 and on specialists measuring and optimizing their own task efficiency is unresolved (Gordon 2016).

134 In the second part of this study, we therefore analyze the effect of task performance feedback on the  
135 response and timing of behavior.

136 Our experimental system offers the possibility of experimentally manipulating stimulus inten-  
137 sity and task performance feedback and thus makes this a well-suited system to address questions  
138 about individual stimulus-response behavior. Bumblebee colonies are able to maintain a stable  
139 core temperature of 32°C in their nests (Heinrich 1979; Schultze-Motel 1991; Weidenmüller et al.  
140 2002; Goulson 2010), allowing them to raise brood and increase colony size even under unfavorable  
141 ambient temperature conditions. Workers perform thermoregulative behaviors either to decrease  
142 brood temperature by fanning their wings (thereby increasing evaporative cooling) or to increase  
143 brood temperature by directly incubating the brood (actively producing heat in their bodies and  
144 transferring it to the brood). Individual bumblebees switch in and out of the task of thermoregu-  
145 lation, performing fanning or incubating tasks at varying times and different locations within the  
146 nest. Workers in a colony differ in their thermoregulatory responses (O’Donnell and Foster 2001;  
147 Weidenmüller 2004; Gardner et al. 2007) and can be experimentally induced to perform thermoreg-  
148 ulative behavior on temperature-controlled brood dummies (Westhus et al. 2013). This allows for  
149 precise measurement and manipulation of a task-associated stimulus (brood temperature) and a  
150 fine-grained, detailed documentation of individual response behavior (fanning). Using this approach,  
151 Westhus et al. (2013) showed that individual fanning responses are modulated not just by absolute  
152 temperature, but by the rate of temperature increase, highlighting the fact that response behavior  
153 cannot be sufficiently described by a single response threshold. Individual fanning response is also  
154 modulated by experience, on longer timescales, across a period of several days (Weidenmüller 2004;  
155 Westhus et al. 2013; but see Duong and Dornhaus 2012). The precise timing patterns of thermoreg-  
156 ulative response behaviors on short timescales and how these patterns are modulated by stimulus  
157 intensity, experience and potentially other factors have not been addressed so far.

158 Here we explore the factors that influence the response patterns of thermoregulating bumblebee  
159 workers on very short timescales, from minutes to about half an hour. Specifically, we investi-  
160 gate how stimulus intensity, repeated task performance and task performance feedback influence  
161 individual-level behavioral patterns. Based on our experimental results, we develop an individual-  
162 based stochastic model of task allocation and simulate it to explore how individual behavioral rules  
163 can impact task allocation and group-level performance.

## 164 MATERIALS AND METHODS

### 165 Laboratory colonies

166 Young bumblebee colonies (*Bombus terrestris*) were obtained from a commercial breeder (Biobest,  
167 Belgium) and maintained in wooden two-chamber nest boxes ( $52 \times 40 \times 10$  cm) covered with plexiglass  
168 lids at 22°C room temperature, 50% RH and under a 12h/12h L/D cycle. At this temperature,  
169 workers often incubate to increase brood temperature and fanning is not observed. Colonies were  
170 provided with sucrose solution ad libitum in the foraging chamber of the nest boxes; defrosted, fresh  
171 honeybee-packed pollen was given every second day directly into the nest.

### 172 Experimental design

173 Workers were tested in a circular Plexiglas test arena (diameter 7.3 cm, height 4.9 cm). The wall  
174 of the test arena was equipped with 12 ventilation holes (diameter 0.4 cm, 0.5 cm above ground).  
175 The arena floor had two indentations alongside the wall where sugar water was provided during  
176 experiments and a central hole through which a brood dummy protruded into the test arena (see  
177 Fig. 1).

178 Brood dummies consisted of aluminum cones (diameter 1 cm) mimicking the size and shape  
179 of natural bumblebee brood (for details see Westhus et al. 2013). A thermocouple ran along the  
180 longitudinal axis of the dummy, ending in the tip. In this way brood dummy temperature could  
181 be precisely measured. Brood dummy temperature could be adjusted either via a connected water  
182 bath (Experimental series A) or via an internal Peltier element (Experimental series B). Dummies  
183 were covered with Parafilm and a thin layer of wax (canopy wax) that had been removed from  
184 the mother colony of the tested worker and frozen. The tip of the brood dummy was additionally  
185 covered with 0.05g wax that had been taken directly from the brood of the same colony in order to  
186 provide the necessary olfactory stimulus. The thermocouple measuring brood dummy temperature  
187 was connected to a recording device (NI cRIO-9074 and NI 9213, National Instruments, Germany)  
188 running a program (created with National Instruments LabVIEW™ 2010, Version 10.0.1, by Ste-  
189 fanie Neupert) that records time, temperature and the occurrence of fanning behavior (entered via  
190 a keyboard) at 1 Hz (Experimental series A) or at 10 Hz (Experimental series B).

191 For testing, a worker bee was carefully removed from the brood area of her nest under red light  
192 using forceps and placed in the test arena containing the brood dummy. The test arena was closed



193 with a glass plate and the bee was left undisturbed for 10 minutes. After this acclimatization phase  
194 she was continuously observed and her fanning behavior was recorded. At the end of each experiment  
195 the bee was marked and returned to her colony. The test arena and brood dummy were cleaned.  
196 Fresh Parafilm and wax were used for each tested worker. Each bee was tested only once.

### 197 **Experimental series A – stimulus intensity and repeated task performance**

198 We analyzed the fanning behavior of bumblebee workers at different, stable brood dummy tempera-  
199 tures. In order to avoid temperature ramps, individual bumblebees were moved together with their  
200 test arena between two brood dummies of different temperatures. The base of each brood dummy  
201 was attached to a water-filled aluminium plate that was heated via a connected water bath. Two  
202 aluminum plates, each heating one brood dummy, were placed next to each other and covered with  
203 one insulating Styrofoam board, through which the brood dummies protruded. One water bath (and  
204 thereby brood dummy) was set to 32°C, the second was set to either 42°C or 47°C. Both experi-  
205 mental temperatures (42°C and 47°C) were high enough to be assumed above fanning thresholds  
206 for most bees (Westhus et al. 2013).

207 At the beginning of each experiment the test arena contained the 32°C brood dummy, reflecting  
208 the optimum brood temperature (Weidenmüller et al. 2002). After a worker was placed in the test  
209 arena, and following the acclimatization phase, her fanning behavior was continuously recorded for  
210 10 minutes. The test arena containing the bee was then very carefully lifted off the brood dummy  
211 and immediately placed onto the second, adjacent brood dummy, which now protruded centrally  
212 into the test arena and had been heated to either 42°C or 47°C. The fanning behavior of the bee  
213 on this second brood dummy was recorded for another 20 minutes. 40 workers from three colonies  
214 (n=18/13/9) were tested: 20 for  $T = 42^\circ\text{C}$  and 20 for  $T = 47^\circ\text{C}$ .

### 215 **Experimental series B – task performance feedback**

216 In order to analyze if a bee’s fanning behavior is influenced by the cooling effect that she achieves  
217 while fanning we analyzed data from a study by Weidenmüller and Kleineidam (unpublished data).  
218 Here brood dummy temperature was regulated via an internal Peltier element placed in the tip of the  
219 brood dummy and controlled by a PID regulator. Bees were tested under one of two experimental  
220 conditions: (1) in the open-loop condition the heating power of the Peltier element remained constant  
221 during each experimental phase and workers could decrease brood dummy temperature via fanning,

222 comparable to the cooling effect they had in Experimental series A; (2) in the closed-loop condition  
223 the cooling effect of a fanning bee was counteracted by continuously adjusting the heating power of  
224 the Peltier element and the fanning bee had only very little impact on brood dummy temperature  
225 (no more than  $0.015^{\circ}\text{C}$ ).

226 For each experiment, a bumblebee worker was placed in the test arena containing the brood  
227 dummy at  $32^{\circ}\text{C}$ . After the acclimatization phase her fanning behavior was continuously recorded  
228 during the following experimental period. Brood dummy temperature was set to different levels, for  
229 7 minutes each, in the following sequence:  $32^{\circ}\text{C} - 39^{\circ}\text{C} - 44^{\circ}\text{C}$ . 43 workers from four colonies were  
230 tested ( $n=5/4/16/18$ ): 20 under the open-loop condition; 23 under the closed-loop condition. For  
231 this study, we analyzed only the fanning behavior shown at  $44^{\circ}\text{C}$ , as this brood dummy temperature  
232 elicited a fanning response in the majority of tested bees and was closest to the temperatures tested  
233 in Experimental series A. We compared the fanning behavior under ‘effective’ (open-loop) versus  
234 ‘ineffective’ (closed-loop) fanning conditions.

## 235 **Data analysis**

236 Fanning workers tended to frequently start and stop fanning over the experimental period (see Fig. 2).  
237 We analyzed the total fanning time and number of fanning events in Experimental series A and B  
238 using the Mann-Whitney  $U$ -test. We define a fanning event as a period of uninterrupted fanning.  
239 Besides analyzing the data in the commonly used summary form, we investigated a more finely  
240 grained picture of the behavioral patterns by studying the potential change of fanning events over  
241 time using survival analysis. This approach allows us to investigate the time sequence of stochastic  
242 events and specifically to estimate the event rate, accounting for incomplete information through  
243 censoring (Kleinbaum and Klein 2012; Liu 2012).

244 Particularly, we used the Cox regression model, a popular semi-parametric technique to determine  
245 whether a given explanatory variable (covariate) has a systematic influence on the rate of an event  
246 (Cox 1972). We recently introduced the Cox model to the analysis of social insect task allocation  
247 in this form (Meyer et al. 2015) and it has been adopted by other studies for similar purposes  
248 (Leighton et al. 2017). The central advantage of the Cox model is that to analyze the influence of  
249 explanatory variables, it is not necessary to specify the baseline rate function, which can be complex  
250 and time-dependent. The only assumption that needs to be verified is the proportional hazards (PH)  
251 assumption, which states that the influence of explanatory variables does not change over time. To

252 verify the PH assumption we measured the correlation between the Schoenfeld residuals (Schoenfeld  
253 1982) and the ranked event times.

254 We tested the influence of the potential explanatory variables (1) stimulus intensity  $T$ , (2) re-  
255 peated task performance, measured as the position  $j$  of a fanning event in the sequence of an  
256 individual worker’s fanning events in Experimental series A and (3) task performance feedback, cat-  
257 egorized by  $E$  to capture open-loop (performance feedback) and closed-loop (performance feedback  
258 suppressed) conditions in Experimental series B on (a) task engagement, quantified as the rate of  
259 starting a fanning event and (b) task disengagement, quantified as the rate of stopping a fanning  
260 event. For each individual worker  $i$ , we used the start time  $s_{i,j}$  and end time  $q_{i,j}$  of the  $j$ -th fanning  
261 event for all  $j$ . The interval between the  $j$ -th and the  $j + 1$ -th fanning events is  $\sigma_{i,j} = s_{i,j+1} - q_{i,j}$   
262 and the duration of the  $j$ -th fanning event is  $\omega_{i,j} = q_{i,j} - s_{i,j}$ . The Cox regression was used to  
263 estimate the rates of task engagement and task disengagement based on the inter-fanning intervals  
264  $\Sigma = \cup_{i,j} \sigma_{i,j}$  and the fanning durations  $\Omega = \cup_{i,j} \omega_{i,j}$  respectively.

265 In Experimental series A, 32 of the tested 40 bumblebee workers showed fanning behavior for  
266 at least one second after being positioned on the second brood dummy: 14 for  $T = 42^\circ\text{C}$ ; 18 for  
267  $T = 47^\circ\text{C}$ . A small number of workers did not fan at all (6 for  $T = 42^\circ\text{C}$ ; 2 for  $T = 47^\circ\text{C}$ ). Our  
268 analysis is implicitly conditioned on the 32 workers who fanned for at least one second. If we were  
269 concerned with the overall colony response, excluding passive workers would clearly introduce a bias.  
270 It is important to note that this is not the case here, since our analysis is only concerned with the  
271 response timing patterns of workers who engage with the task. Thus we must exclude those that  
272 do not respond at all. Among these workers, there were 1493 fanning events in total. Similarly,  
273 for Experimental series B, our analysis focused on the 36 out of 43 tested bumblebee workers who  
274 showed at least two fanning events at  $T = 44^\circ\text{C}$ : 18 for the open loop; 18 for the closed loop. Here  
275 the total number of fanning events is 1428.

## 276 Data availability

277 The data generated and analyzed during this study in Experimental series A are available in the Open  
278 Science Framework repository (<https://osf.io/kgsh9/>). The dataset analyzed in Experimental  
279 series B is available from the corresponding author on reasonable request.

## 280 RESULTS

### 281 Experimental series A – stimulus intensity and repeated task performance

282 For the two temperatures tested in our experiment, stimulus intensity did not influence the time that  
283 an individual invested into fanning. Total fanning time did not significantly differ between  $T = 42^\circ\text{C}$   
284 and  $T = 47^\circ\text{C}$  (Mann-Whitney  $U$ -test:  $P = 0.246$ ; Fig. 3A). Likewise, the number of fanning events  
285 did not significantly differ between the two tested temperatures (Mann-Whitney  $U$ -test:  $P = 0.447$ ;  
286 Fig. 3B).

287 Consistent with this summary analysis, stimulus intensity  $T$  did not have a statistically significant  
288 influence on the rate of task engagement by the Cox regression (Wald statistic  $P = 0.496$ ). The PH  
289 assumption applied to both  $T$  and  $j$ , as the residuals for both explanatory variables were uncorrelated  
290 with the ranked event times (Pearson correlation: 0.016 for  $T$ ; 0.035 for  $j$ ). The explanatory variable  
291  $j$  had a statistically significant positive effect on the rate of task engagement (Wald statistic  $P =$   
292  $4.12\text{e}-11$ ), but its influence was small (relative risk 1.005 with confidence interval  $[1.004 \dots 1.007]$ ).

293 Similarly, we applied the Cox regression to test the effect of explanatory variables  $T$  and  $j$  on  
294 the rate of task disengagement. The PH assumption applied to both  $T$  and  $j$  (Pearson correlation  
295 between Schoenfeld residuals and ranked event times: -0.039 for  $T$ ; 0.081 for  $j$ ). Consistent with the  
296 summary analysis, the results of the Cox model indicated that the rate of task disengagement was  
297 not significantly influenced by  $T$  (Wald statistic:  $P = 0.838$ ). For  $j$ , the Wald statistic ( $P = 0.019$ )  
298 suggested a statistically significant negative effect, but its influence was small (relative risk 0.998  
299 with confidence interval  $[0.997 \dots 1.000]$ ).

300 In summary, we found no significant effect of stimulus intensity on the time investment and  
301 temporal patterns of fanning behavior. Repeated task performance resulted in slightly longer fanning  
302 durations and slightly shorter inter-fanning intervals.

### 303 Experimental series B – task performance feedback

304 Neither total fanning time (Mann-Whitney  $U$ -test:  $P = 0.275$ ; Fig. 3C) nor the number of fanning  
305 events (Mann-Whitney  $U$ -test:  $P = 0.962$ ; Fig. 3D) differed significantly between the open-loop and  
306 closed-loop conditions. Thus summary analysis showed no significant effect of stimulus intensity or  
307 task performance feedback on task performance. However, our results of the Cox model showed that  
308 there was a significant effect of task performance feedback on the rates of task engagement and task

309 disengagement.

310 For task engagement, we applied the Cox regression to the inter-fanning intervals  $\Sigma$  with co-  
311 variate  $E$ . The PH assumption held for  $E$  (Pearson correlation: 0.083) and  $E$  had a statistically  
312 significant influence (Wald statistic:  $P = 0.001$ ). The Cox model suggested that the ability to reduce  
313 brood dummy temperature when fanning (open-loop condition) reduced the rate of task engagement  
314 (relative risk 0.826 with confidence interval [0.739...0.923]).

315 For task disengagement, we applied the Cox regression to the fanning durations  $\Omega$  with covariate  
316  $E$ . The PH assumption applied to  $E$  (Pearson correlation: 0.034) and  $E$  had a statistically significant  
317 influence (Wald statistic:  $P = 4.25e-7$ ). In line with the result for task engagement, the ability to  
318 reduce brood dummy temperature when fanning increased the rate of task disengagement (relative  
319 risk 1.335 with confidence interval [1.194...1.493]).

320 In summary, for both task engagement and task disengagement, task performance feedback, i.e.  
321 the ability to cool the brood dummy when fanning, influenced workers' investment into the fanning  
322 task. When lacking this ability (closed-loop condition), workers tended to show higher levels of  
323 fanning activities.

## 324 MODEL

325 Our experimental results emphasize that the timing patterns of individual task performance need  
326 to be taken into account explicitly. Here we propose a time-resolved model to describe patterns of  
327 task performance at the individual level.

328 We find that individual bumblebee workers frequently interrupt fanning (see Fig. 2), indicating  
329 that stimulus intensity can be repeatedly assessed before a decision to perform the task again is made.  
330 Fig. 4 gives a conceptual framework of task allocation in general. We assume the probability to assess  
331 the stimulus for a specific task  $i$  as  $p_i$ . A worker selects a task  $i$  according to  $p_1, p_2, \dots, p_i, \dots, p_k$  and  
332 subsequently tests whether the task-related stimulus  $s_i$  exceeds her task-related threshold  $\theta_i$ : if so,  
333 she engages in task  $i$ ; otherwise, the task-selecting process is repeated. Once engaged, task  $i$  is  
334 performed for some time before a period of task disengagement or inactivity for this task begins  
335 (in our case: fanning durations and inter-fanning intervals). Starting the period of inactivity after  
336 performing task  $i$  and ending the period of inactivity are stochastic events characterized by the rate  
337 functions  $\mu_i(t)$  and  $\lambda_i(t)$  respectively.

338 To verify the time-resolved model with the results of our experiments (in which a single task  
339 – fanning is observed), we reduced the conceptual model (illustrated in Fig. 4) to a version which  
340 only involves a single observed task  $A$  and a collection of other behaviors that a worker may engage  
341 in, represented as a task set  $B$  (see Fig. 5). We simulated this coarse-grained version of the model  
342 based on the Gillespie next reaction method (Gillespie 1976, 1977).

343 In order to compare the results of our simulations with empirical data, we analyzed the lumped  
344 distributions of inter-fanning intervals  $\Sigma$  and fanning durations  $\Omega$  at the group level. We fitted  
345 our empirical data to an exponential distribution obtained by the maximum likelihood estimation  
346 (implemented by *EstimatedDistribution* in Mathematica, Version 11.1, Wolfram Research Inc.)  
347 for both  $\Sigma$  and  $\Omega$ . An exponential distribution would be expected if the underlying process was a  
348 simple homogeneous Poisson process. Such a process would be the outcome of the standard response  
349 threshold models implemented with regular time-steps.

350 However, we found that the exponential distribution cannot be fitted well to our empirical data  
351 (Kullback-Leibler divergence: 1.858 for inter-fanning interval and 1.671 for fanning duration; Fig. 6).  
352 On the other hand, the results of our model simulation fit the empirical distributions reasonably well  
353 (Kullback-Leibler divergence: 0.110 for inter-fanning interval and 0.086 for fanning duration; Fig. 6).  
354 This shows that the simplified assumption of task engagement or disengagement as a homogeneous  
355 Poisson process is not consistent with our experimental data (Akaike 1974). The timing patterns  
356 for Task  $A$  are influenced by other behaviors (Task set  $B$ ) as described in our model.

## 357 SIMULATIONS

358 We used the proposed model to explore in simulations how individual behavioral rules can lead to  
359 group-level outcomes. We investigated how behavioral flexibility and inter-individual variability in  
360 response thresholds can modulate the patterns of task allocation and influence the colony efficiency,  
361 measured as the number of task switches.

362 Task switches, by which we here mean the number of times an individual stops the execution of  
363 a task at least temporarily, are an important aspect of task execution efficiency. We introduce the  
364 term task switching here, because under natural conditions, periods of inactivity for one task can  
365 occur in two forms: (1) as a switch to a different task; or (2) as a temporary interruption, i.e. when  
366 an individual picks up the same task again after an interruption, as we have described in this study

367 for fanning and inter-fanning intervals. In both cases, there is an impact on task efficiency. In the  
368 first case it is obvious that individuals frequently switching between tasks have no opportunity to  
369 specialize in any given task. Focusing on a single task seems even more important for an individual  
370 on very short timescales than on longer ones, as switching tasks with a high frequency is unlikely to  
371 be efficient (Charbonneau and Dornhaus 2015; Leighton et al. 2017). To understand the second case,  
372 we need to take into account that the observed number of periods of inactivity for one task (inter-  
373 fanning intervals) is not physiologically required: we know from our experiments that individuals  
374 are able of sustained task execution for much longer periods. During a inter-fanning interval, the  
375 individual will not reduce the task-related stimulus. As the stimulus remains present other workers  
376 will, with some probability, fill the role of the temporarily inactive individual and execute the task.  
377 Thus, extended interruptions in performing a task can cause additional workers to be tied up in the  
378 same task that would otherwise remain available for different tasks.

379 Energetic costs would ultimately be the relevant measure for task efficiency, but they cannot  
380 be quantified easily. However, it is clear that energetic costs in both cases would be monotonic in  
381 the number of task switches. We thus use the number of task switches as an abstract proxy to  
382 handle both possible interpretations simultaneously. Based on this measure, we show show how  
383 inter-individual variability can be a key factor in combining efficient workforce use with short-term  
384 collective flexibility.

385 A group-level simulation is required to adequately represent the indirect interactions between  
386 workers via the task-associated stimulus. We integrated a statistically faithful simulation of our  
387 model with a simple collective cooling process (see supplementary material). Standard Newtonian  
388 heat conduction processes were used to approximate the effects of ambient temperature and internal  
389 (brood) heat on the nest. Here we simply assume that all bees have identical fixed cooling capacity  
390 per time unit.

391 We started our exploration with the oversimplified assumption that, in the static environment,  
392 workers' task-selecting probabilities do not change over time and their thresholds are identical at the  
393 ideal level for all individuals. The colony remained closely regulated near the optimal temperature  
394 (see Fig. 7), but there was a large number of task switches (646 task switches for 100 workers in 500  
395 time periods). The reason behind this is simple: since every worker will interrupt its task execution  
396 after some time to re-sample the stimulus, some other workers will immediately step in and perform  
397 the task if there is demand. Thus the task is rotated between a large number of individuals.

398 We investigated how the following two factors may reduce such frequent task rotation: (1) the  
399 possibility that individuals switch into a task-specific behavioral context and (2) inter-individual  
400 variability in thresholds. In our model, switching into a task-specific context corresponds to increas-  
401 ing the probability  $p_A$  as soon as Task  $A$  is entered and conversely by significantly decreasing  $p_A$   
402 once Task  $B$  is started. Thus, in the context of Task  $A$ , a worker is less receptive to the stimulus  
403 of Task  $B$ . As one expects, we found that such a context switching reduced the number of workers  
404 involved (see Fig. 7A) and consequently the number of task switches (by more than an order of  
405 magnitude to 35).

406 Next, we used our model to explore the ramifications of inter-individual variability in thresholds.  
407 As a starting point we assumed a uniform distribution of thresholds  $\Theta \sim U(31, 47)$ . For such a  
408 threshold distribution, there was a further reduction in the numbers of workers and task switches  
409 (6), while the colony temperature remains effectively regulated with minimal fluctuations (see Fig. 7).  
410 This is not surprising as a threshold distribution can pre-select a subgroup of individuals that have  
411 the opportunity to engage.

412 We then investigated whether the same mechanism would still work in a variable environment  
413 where different workers are above their thresholds at different times. On short timescales it is  
414 reasonable to assume a single rapid change of environmental conditions rather than multiple frequent  
415 changes. Clearly, the threshold distribution determines in which range the nest temperature can be  
416 maintained. If  $n$  individuals are required to keep the nest temperature below some level  $T$  but less  
417 than  $n$  individuals have thresholds below  $T$ , the nest temperature will obviously rise to  $T$  and above  
418 (see Fig. 8B).

419 To demonstrate the effect of the threshold-distribution shape we repeated the simulation with  
420 a distribution that is biased towards lower values (thresholds assumed to be beta-distributed and  
421 rescaled into the interval  $[31, 47]$ :  $\Theta \sim 31 + (47 - 31) \cdot \beta(2, 20)$ ). Such a distribution can thus ensure  
422 that a sufficient number of workers can rapidly be deployed before a desirable upper temperature  
423 level (here around  $34^\circ\text{C}$ ) is exceeded (see Fig. 8B). Yet, at the same time it ensures that only an  
424 appropriate number of workers are active when not much work is required for temperature regulation  
425 (see Fig. 8A). It is conceivable that a threshold distribution is adapted to a typical environment to  
426 balance efficiency gains with provisions for extraordinary circumstances by a different mechanism  
427 that acts on a much longer timescale (colony lifetime or evolutionary).



## DISCUSSION

Understanding how social insect colonies achieve their highly flexible yet stable organization remains a challenge even after decades of focused research. Underlying the coordinated collective patterns and behaviors are individual behavioral rules shaped by numerous intrinsic and extrinsic factors. To decipher these rules, we need detailed empirical data on individual behavior, from which we can build models that allow us to move from description to prediction. We can then explore behaviors by simulating these models in hypothetical conditions that have not been investigated empirically and that may be difficult to approach in biological experiments.

We argue that it is necessary to explicitly specify on what timescales theoretical models apply, since behavioral rules and the factors modulating these rules will often differ across different timescales. In this study we follow a bottom-up approach, starting with a thorough exploration of short timescales. On these timescales, temporal response patterns can play an important role in the overall function of a colony (Johnson 2009). For example, the interplay between active and inactive phases of task performance strongly influences the opportunity for workers in a group to sample task-associated stimuli and switch between tasks. It is thus important to explicitly describe and model the temporal patterns of behaviors. This is the approach we have pursued in this study. Our study provides fine-grained experimental data on individual responses with well-controlled stimulus levels, which makes it possible to explicitly analyze the temporal response patterns at comparably short timescales.

In our first series of experiments we analyzed the modulatory effect of the two factors that are explicitly part of the assumptions of the response threshold models: (1) stimulus intensity and (2) repeated task performance. We found important discrepancies between our experimental data and the predictions of these models. We reemphasize that our analysis is only concerned with the way that the reinforced threshold models as given in the introduction describe task engagement behavior. The discrepancies found do not invalidate the general idea of an internal threshold for a task-associated stimulus.

Our results show that one fundamental prediction of the response threshold models is not confirmed in the response patterns observed at our experimental timescales of up to 20 minutes; namely that stimulus intensity and the probability of task engagement are positively correlated (Bonabeau et al. 1996; Theraulaz et al. 1998). In our experiments, for those bees that showed fanning behavior,

458 stimulus intensity did not significantly influence the total fanning time, the number of fanning events  
459 or the rates of task engagement and task disengagement.

460 Note that this is not due to a saturation effect in our experiments, even though the temperature  
461 levels we used seem high. Previous studies have demonstrated that workers measure and respond  
462 to an increase of brood temperature itself, even when the surrounding air and their own body  
463 temperature remains low. However, when only brood temperature increases, bees tend to respond at  
464 higher temperatures; and usually show no fanning response before brood wax temperatures of around  
465 39°C, with a substantial proportion of bees not fanning before wax temperatures of at least 42°C  
466 have been reached (Westhus et al. 2013; Garrison et al. 2018). Fanning workers in our experiments  
467 were not investing a maximum of their energy; some individuals regularly paused for up to a few  
468 minutes between fanning events, whereas others showed several minutes of uninterrupted fanning (as  
469 can be seen in Fig. 2). The bees were also not in danger of overheating, as in our experimental setup  
470 only brood-dummy temperature increased, and had ad libitum sugar water supplies available. We  
471 conclude that workers were not at their physiological limit and could have modulated their response  
472 even at high temperatures, as shown by our results for the modulatory effect of task performance  
473 feedback (see below). The fact that there were slightly more non-responders at 42°C than 47°C in  
474 our experiments (see Fig. 2) could indicate that the decision whether or not to engage in a task at  
475 all and the task response patterns may be independent processes.

476 The second prediction of the response threshold models is that repeated task performance leads  
477 to an increased probability of task engagement. We demonstrated that survival analysis provides  
478 the analytical methods to quantify and analyze repeated task performance by taking the temporal  
479 influence into account. Our results revealed a significant albeit small impact of previous task perfor-  
480 mance on workers' fanning behavior in both task engagement and disengagement, underlining the  
481 modulatory effect of experience on task performance. Importantly, in the response threshold models,  
482 the increase of the observed activity level can only be achieved via a decrease of the threshold with  
483 repeated task performance when stimulus intensity keeps constant. However, this only influences  
484 the process of task engagement, whereas our data shows that the process of task disengagement is  
485 subject to the same dynamics. This aspect is not captured in standard response threshold models.

486 Our results lend support to the view that response probability, threshold and duration are dif-  
487 ferent independent parameters, a point that has been put forward in previous empirical studies  
488 (Weidenmüller 2004; Mattila and Seeley 2010; Duong and Dornhaus 2012; Westhus et al. 2013).

489 These parameters need to be integrated into a temporal framework, in order to gain a view of the  
490 detailed response patterns, specifically the rates of task engagement and disengagement. We cap-  
491 tured this integration in an individual-based model and demonstrated the potential of this model  
492 by implementing it in simulations for understanding the impact of the observed activity dynamics  
493 on group-level task allocation.

494 In the model simulations we considered group-level outcomes in a homeostatic scenario where  
495 nest temperature needs to be regulated within a small interval. The number of workers required to  
496 keep the temperature within this interval depends on external factors such as ambient temperature  
497 and exposure to sunlight. In a homeostatic scenario and from the perspective of an individual  
498 worker, the temperature stimulus does not provide the key to this requirement, as it is kept stable.  
499 Workers can only be recruited to regulation if nest temperature exceeds their thresholds. Thus, a  
500 sufficient number of workers must have their threshold within the regulation range. If we consider  
501 the workers whose thresholds are within the regulation range as the “candidate” workforce, we must  
502 assume that the number of candidate workers is much higher than the number of workers required  
503 under normal conditions in order to accommodate for short-term demand fluctuations. A central  
504 question then is whether, on short timescales, any mechanism exists to divide the group of candidate  
505 workers effectively into “active” and “inactive” subgroups according to short-term requirements.

506 The simulation outcomes appear to be insensitive to parameter changes on the scale derived from  
507 the Cox model, which suggests that repeated task performance does not result in any meaningful  
508 differentiation of workers’ behavior during the time window under investigation. It would be inter-  
509 esting to use the framework of timing to explore whether the effect of repeated task performance  
510 on individual task decision-making would significantly increase on a longer timescale, such as over  
511 a few days.

512 As our simulations and others’ (Myerscough and Oldroyd 2004) bear out, group-level task alloca-  
513 tion in fluctuating environments can be facilitated by inter-individual variation in response thresh-  
514 olds. For this variation to be effective, the group-level threshold distribution has to be adapted  
515 to typical environmental conditions. We make no assumption as to what may shape this distri-  
516 bution. Possibilities include intrinsic factors, such as genetics and morphology, as well as other  
517 mechanisms acting on longer timescales than the one empirically addressed in our study (Jeanson  
518 and Weidenmüller 2014).

519 The response threshold model for task allocation in social insects considers only stimulus intensity

520 and repeated task performance as modulatory parameters of individual response behavior. In the  
521 second series of experiments, we explored the impact of task performance feedback, which is not  
522 captured in the response threshold models. Task performance feedback may play an important role  
523 in the specialization of individuals. Our results show that bumblebees are able to perceive and  
524 respond to the output of their own fanning behavior. Bees that experienced no cooling effect when  
525 fanning showed a higher rate of task engagement over time and a lower rate of task disengagement,  
526 when compared to those that were able to reduce brood dummy temperature by fanning. This  
527 modulatory effect remains hidden in the summary analysis and is revealed only by survival analysis,  
528 emphasizing the importance of considering the temporal influence in details.

529 Why do unsuccessful workers fan more than successful ones in our experiments? It is generally  
530 expected that workers are more likely to perform the task in which their performance is effective  
531 (Oster and Wilson 1978; Plowright and Plowright 1988), with support of empirical evidence in  
532 foraging ants (Tripet and Nonacs 2004; Ravary et al. 2007) and wasps (O'Donnell and Jeanne 1992).  
533 However, the extent to which collective success in social insects depends on individual specialization  
534 and task efficiency remains unclear (Gordon 2016). Honeybees with more foraging experience tend  
535 to bring in larger loads than unexperienced foragers (Dukas and Visscher 1994), and bees that are  
536 active in the task of undertaking remove corpses faster than less active ones (Trumbo and Robinson  
537 1997); but in *Temnothorax* ants individual specialization is not correlated with efficiency (Dornhaus  
538 2008).

539 Our study suggests that timescale may be an important factor when considering the influence of  
540 task performance feedback. All workers tested in our experiments were presumably naïve to the task  
541 of fanning; as colonies were kept at 22°C room temperature and no fanning occurred in the colonies  
542 before individual bees were tested. The increased effort of workers that did not succeed in cooling the  
543 brood when fanning may suggest that workers have an internal expectation concerning the output  
544 of their action and adjust their behavior in an effort to achieve this goal. As a consequence, on  
545 short timescales, an increase in workers' effort may occur, while the effect may be inverted on longer  
546 timescales, ultimately leading to reduced effort or even to completely dropping out of a task when  
547 no success in task performance is experienced (Ravary et al. 2007). Future studies will investigate  
548 this possible time-dependent effect of task performance feedback.

549 Task type may also lead to different effects of task performance feedback. Workers in a colony  
550 tend to reduce the stimulus to low levels for a maximizing task such as foraging, while for a home-

551 ostatic task like fanning, it is adequate to maintain the stimulus level within a narrow range. It  
552 remains to be seen in future studies how our results translate in settings with an additional con-  
553 trolled task such as foraging. These studies could be used to verify whether the difference between  
554 the effect of task performance feedback on fanning behavior and on foraging behavior discussed  
555 above is caused by the type of task and/or the timescale on which it occurs.

556 Future studies will also shed light on how individual response dynamics are modulated within  
557 the social environment. A recent study demonstrates that individual fanning response behavior,  
558 namely whether a bumblebee responds to an increase in brood temperature or not, and at what  
559 stimulus levels she starts showing fanning behavior, is modulated in the social context (Garrison  
560 et al. 2018). Modulation of response to temperature by social environment has also been described  
561 for thermoregulating honey bees (Cook and Breed 2013). If and how the dynamics of response  
562 behavior are also modulated by the social environment remains to be investigated. A detailed  
563 understanding of the individual stimulus-response relationship is a prerequisite for understanding  
564 how these individual rules are then modified by the social context and how individual behavior is  
565 integrated into a functioning unit in order to result in appropriate group-level responses.

566 In this study, we explored in detail the temporal patterns in the fanning responses of isolated  
567 individual bumblebees on short timescales. Future research will provide more detail on the pa-  
568 rameters modulating the timing of individual behavior and integrating individual responses into  
569 a collective. Building models that explicitly deal with individual response dynamics based on a  
570 hierarchy of timescales layer by layer from the bottom up provides us the tools to tackle these im-  
571 portant questions and to deepen our understanding of the complex, decentralized organization of  
572 insect societies.

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## 679 FIGURE LEGENDS

### Fig. 1

680 The set-up: the test arena contains one temperature-controlled brood dummy (b) with an internal thermocouple; brood dummy temperature could be adjusted either via a connected heating plate (h), which is isolated by an insulation layer (i) from the test arena (Experimental series A) or via an internal Peltier element (Experimental series B) (setup modified from Westhus et al. 2013).

### Fig. 2

681 Fanning behavior of bumblebee workers at constant brood dummy temperatures (**A**:  $T = 42^\circ\text{C}$ ,  $n = 20$ ; **B**:  $T = 47^\circ\text{C}$ ,  $n = 20$ ) over 20 minutes. Workers are sorted in ascending order from top to bottom by total fanning time. Each row represents a single worker and each column represents an interval of one second. White space represents inactivity or any activity other than fanning.

### Fig. 3

682 The total fanning time (**A** and **C**) and number of fanning events (**B** and **D**) of bumblebee workers in Experimental series A (**A** and **B**) and Experimental series B (**C** and **D**). Here each box-and-whisker plot gives the median, quantiles and fences. The figure shows that on the aggregate level statistically significant influence can neither be shown for temperature levels nor for open/closed loop conditions. Note, however, that the fine-grained survival analysis reveals a difference between open and closed loop conditions that is not visible in this summary analysis (see main text).

### Fig. 4

683 The time-resolved model of task allocation for a single worker and multiple tasks.

### Fig. 5

684 The simplified time-resolved model of task allocation for a single worker and for a single observable task. Task  $A$  refers to the fanning task observed in experiments. Task  $B = \{B_1, \dots, B_{k-1}\}$  is a set of all other possible behaviors.

### Fig. 6

685 Distributions of inter-fanning intervals (**A**) and fanning durations (**B**) of workers in a log-log scale. The empirical data is from Experimental series A. The simulation results are based on our time-resolved model with  $s_A = 42$ ,  $\theta_A = 32$ ,  $\lambda_A = 0.575$ ,  $\mu_A \sim U(0, 1.25)$ ,  $\lambda_B \sim U(0, 1)$  and  $p_A \sim U(0, 1)$ . The rates of fitted exponential distributions are  $\lambda = 0.061$  for inter-fanning intervals and  $\lambda = 0.172$  for fanning durations. Both fitted distributions are obtained by the maximum likelihood estimation (implemented by *EstimatedDistribution* in Mathematica, Version 11.2, Wolfram Research Inc.). Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .

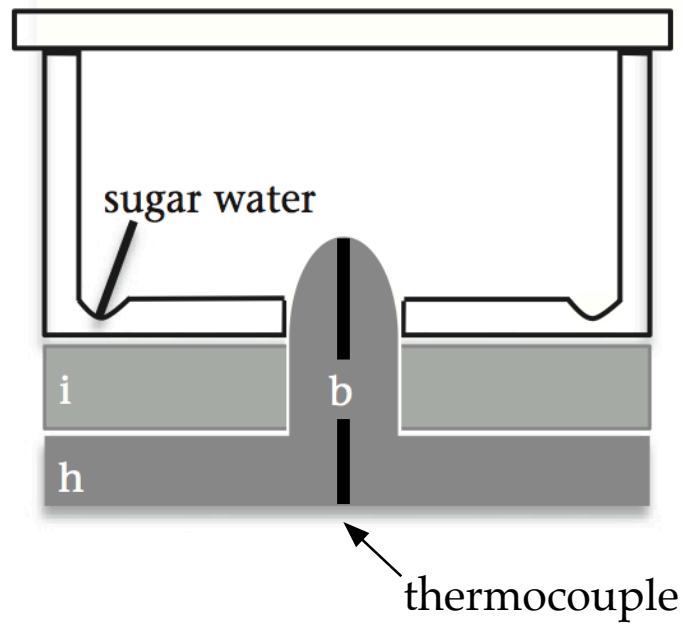
**Fig. 7**

Number of fanning events (**A**) and nest temperatures (**B**) for a group of bumblebee workers in the simulated static environment. The simulation results are drawn from 30 replicates and based on our time-resolved model with  $n = 100$ ,  $\theta_A = 32$ ,  $\lambda_A = 0.75$ ,  $\mu_A = 1$ ,  $\lambda_B \sim U(0, 1)$ ,  $p_A \sim U(0, 1)$ ,  $\alpha = 0.1$ ,  $\beta = 0.05$ ,  $K = 1$  and  $r = 1/60$ . In **A**, workers are sorted from left to right in descending order based on their number of fanning events. Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .

**Fig. 8**

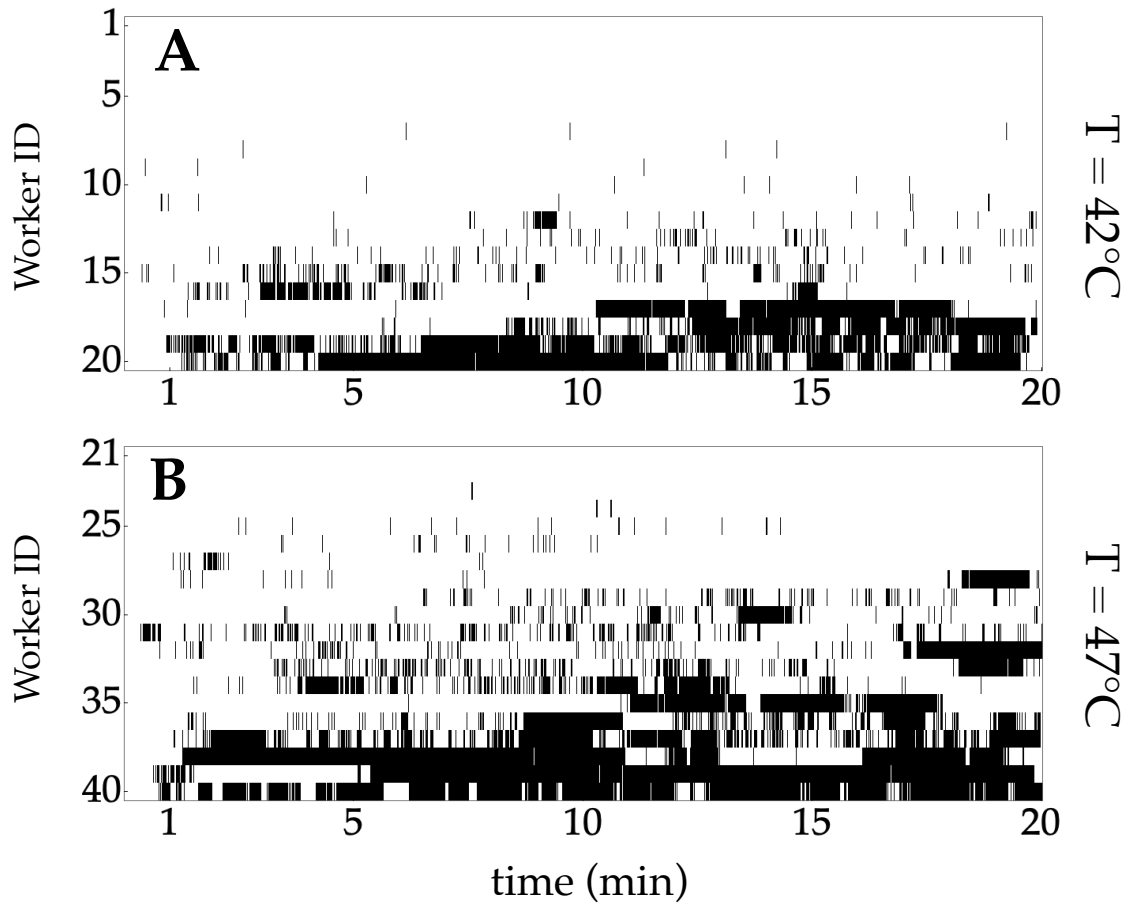
Number of fanning events (**A**) and nest temperatures (**B**) for a group of bumblebee workers in the simulated dynamic environment. The simulation results are drawn from 30 replicates and based on our time-resolved model with  $n = 100$ ,  $\lambda_A = 0.75$ ,  $\mu_A = 1$ ,  $\lambda_B \sim U(0, 1)$ ,  $p_A \sim U(0, 1)$ ,  $\alpha = 0.1$ ,  $\beta = 0.05$ ,  $K = 1$  and  $r = 1/60$ .  $s_A = 28$  before the time passed 100 and  $s_A = 32$  after the time 100. In **A**, workers are sorted from left to right in descending order based on their number of fanning events. In **B**, the probability density function of beta-distributed thresholds is given on the left. Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .

688 **FIGURES**

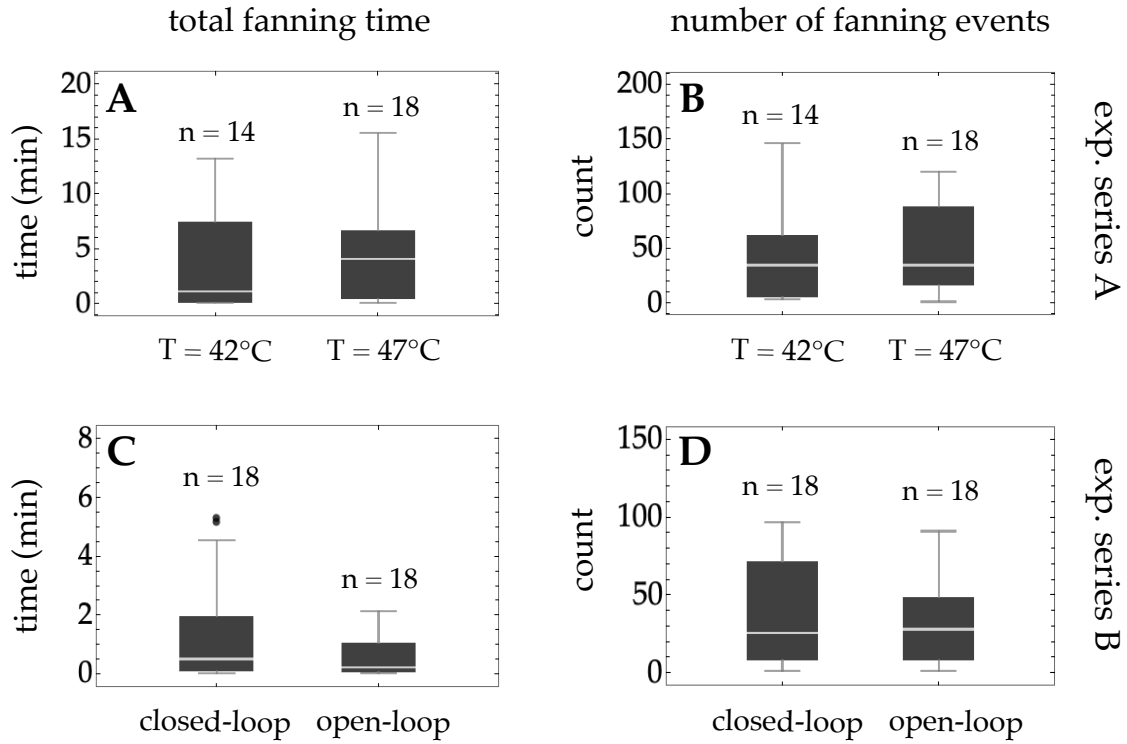


**Fig. 1**

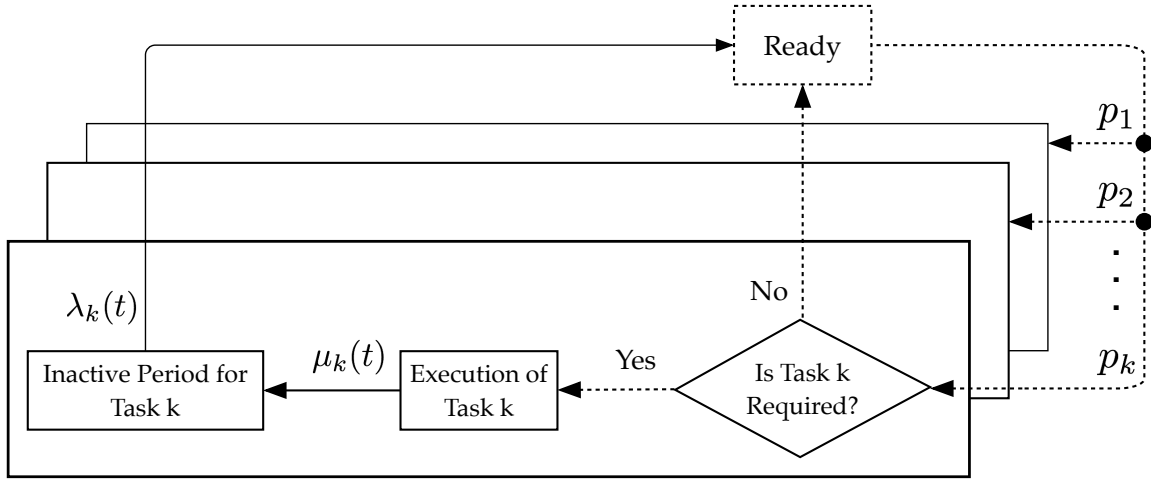
The set-up: the test arena contains one temperature-controlled brood dummy (b) with an internal thermocouple; brood dummy temperature could be adjusted either via a connected heating plate (h), which is isolated by an insulation layer (i) from the test arena (Experimental series A) or via an internal Peltier element (Experimental series B) (setup modified from Westhus et al. 2013).



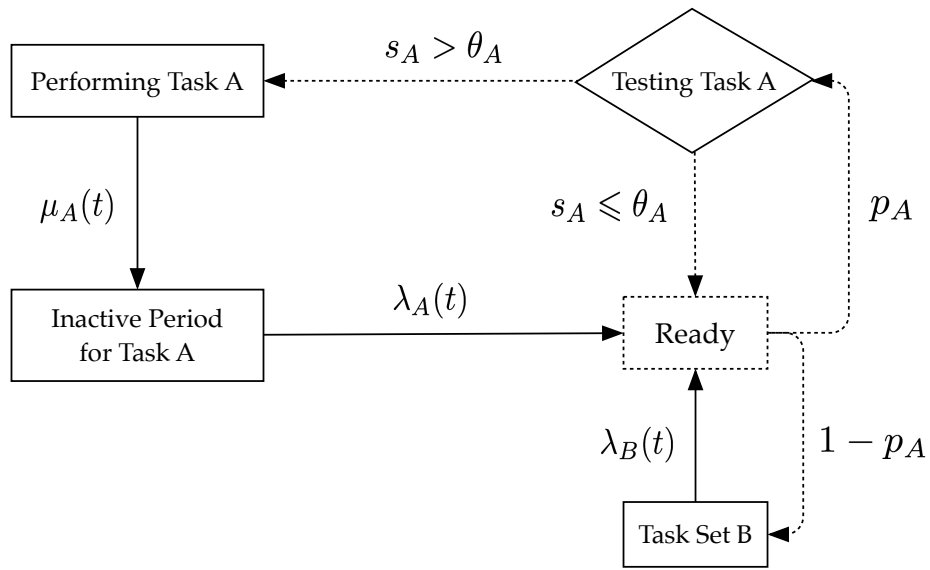
**Fig. 2**  
 Fanning behavior of bumblebee workers at constant brood dummy temperatures (**A**:  $T = 42^\circ\text{C}$ ,  $n = 20$ ; **B**:  $T = 47^\circ\text{C}$ ,  $n = 20$ ) over 20 minutes. Workers are sorted in ascending order from top to bottom by total fanning time. Each row represents a single worker and each column represents an interval of one second. White space represents inactivity or any activity other than fanning.



**Fig. 3** The total fanning time (**A** and **C**) and number of fanning events (**B** and **D**) of bumblebee workers in Experimental series A (**A** and **B**) and Experimental series B (**C** and **D**). Here each box-and-whisker plot gives the median, quantiles and fences. The figure shows that on the aggregate level statistically significant influence can neither be shown for temperature levels nor for open/closed loop conditions. Note, however, that the fine-grained survival analysis reveals a difference between open and closed loop conditions that is not visible in this summary analysis (see main text).

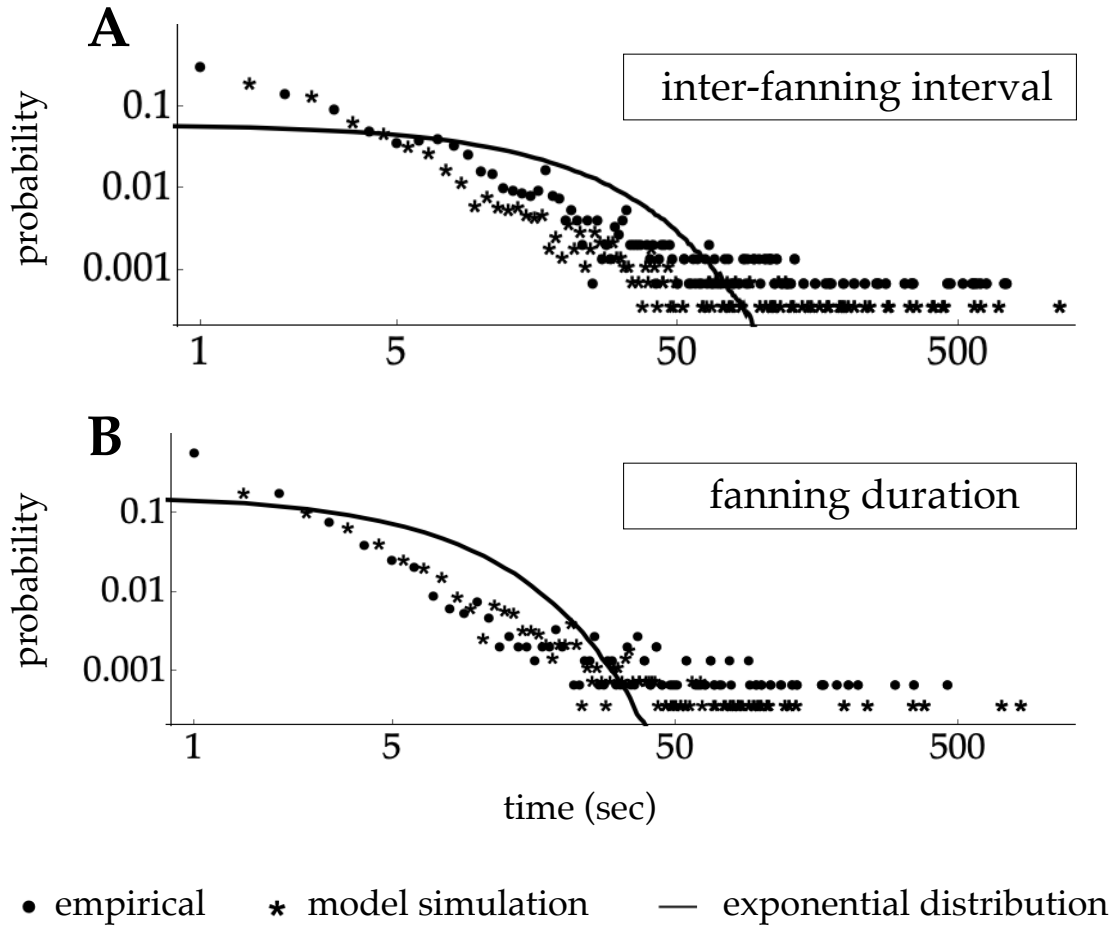


**Fig. 4**  
The time-resolved model of task allocation for a single worker and multiple tasks.

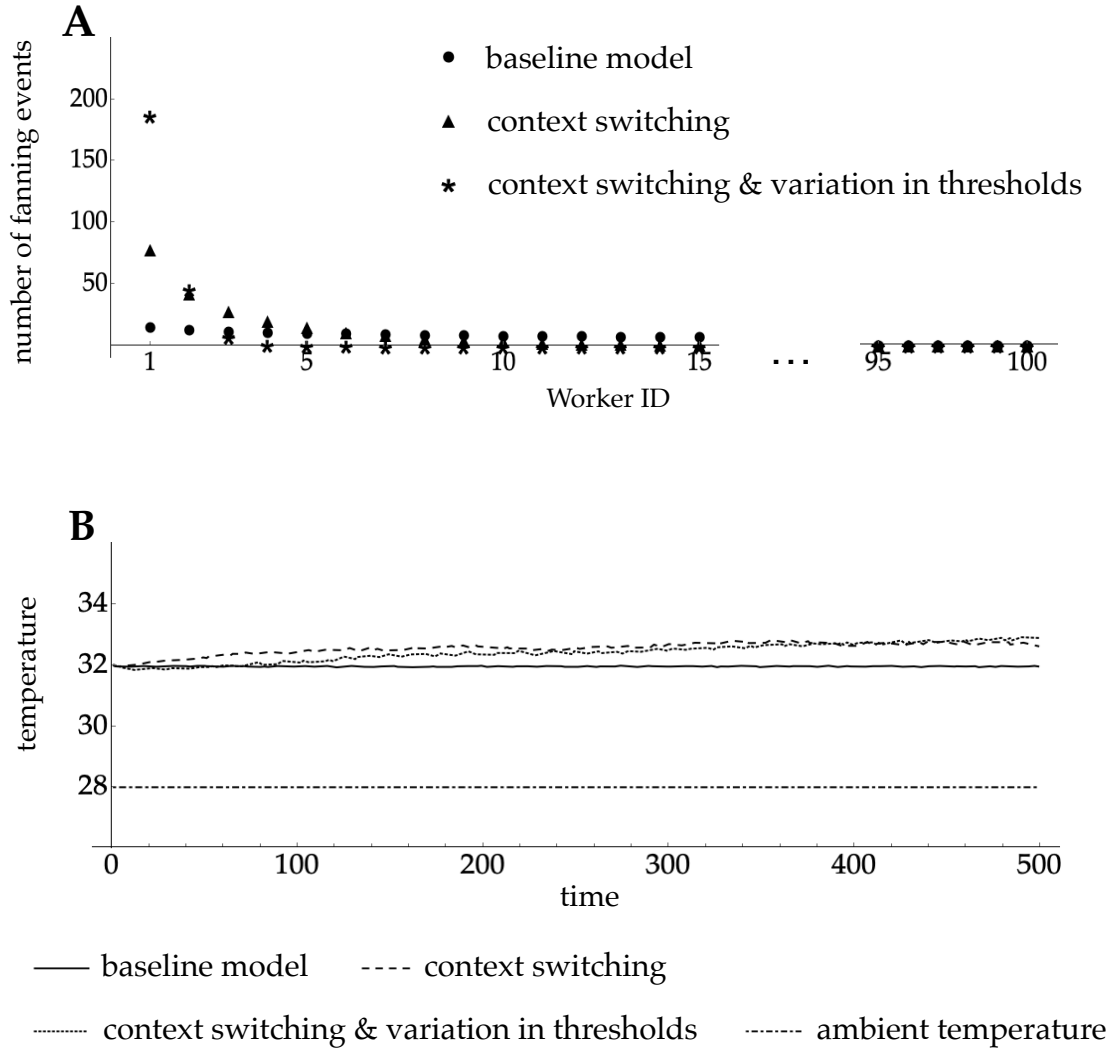


**Fig. 5**  
The simplified time-resolved model of task allocation for a single worker and for a single observable task. Task  $A$  refers to the fanning task observed in experiments. Task  $B = \{B_1, \dots, B_{k-1}\}$  is a set of all other possible behaviors.

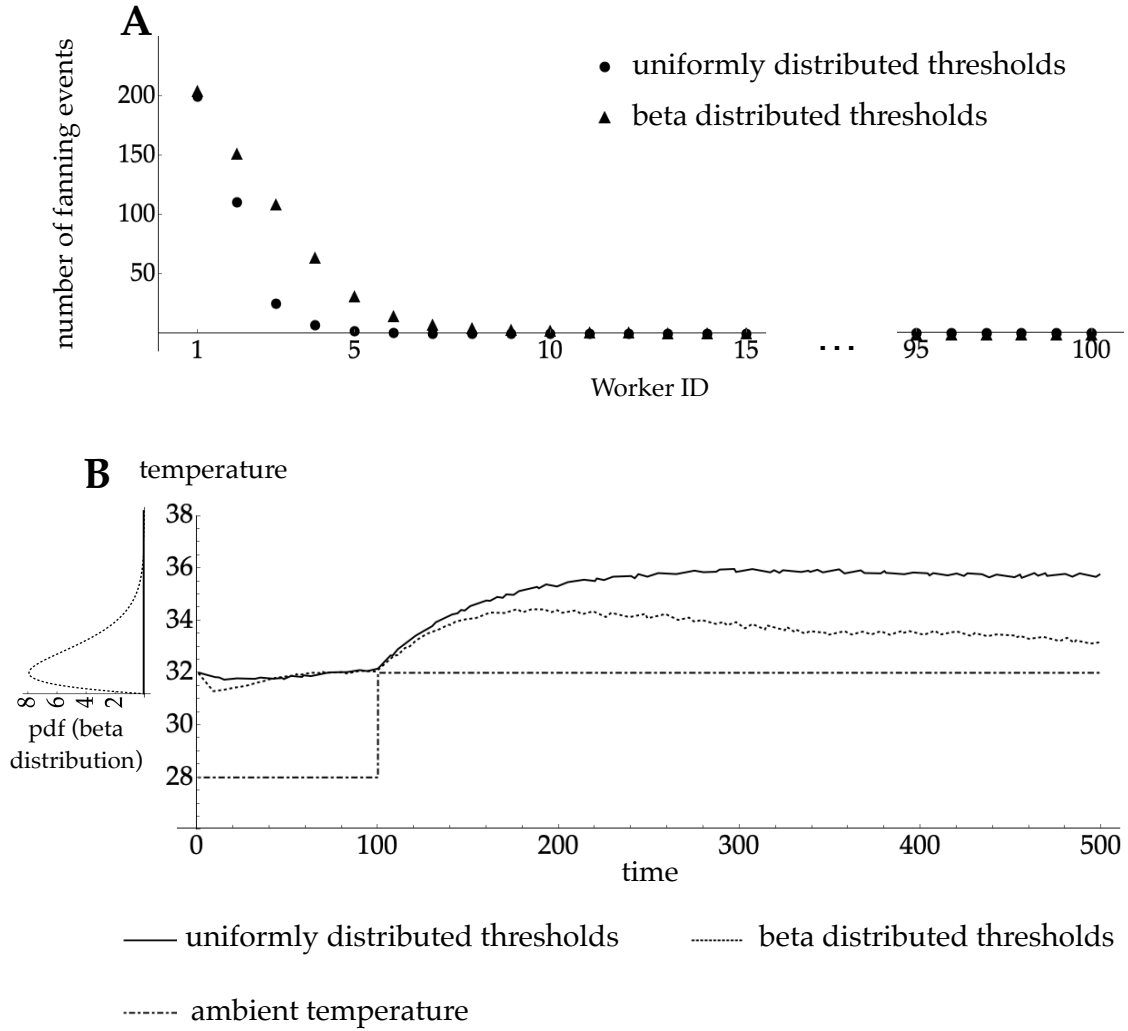




**Fig. 6** Distributions of inter-fanning intervals (**A**) and fanning durations (**B**) of workers in a log-log scale. The empirical data is from Experimental series A. The simulation results are based on our time-resolved model with  $s_A = 42$ ,  $\theta_A = 32$ ,  $\lambda_A = 0.575$ ,  $\mu_A \sim U(0, 1.25)$ ,  $\lambda_B \sim U(0, 1)$  and  $p_A \sim U(0, 1)$ . The rates of fitted exponential distributions are  $\lambda = 0.061$  for inter-fanning intervals and  $\lambda = 0.172$  for fanning durations. Both fitted distributions are obtained by the maximum likelihood estimation (implemented by *EstimatedDistribution* in Mathematica, Version 11.2, Wolfram Research Inc.). Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .



**Fig. 7** Number of fanning events (**A**) and nest temperatures (**B**) for a group of bumblebee workers in the simulated static environment. The simulation results are drawn from 30 replicates and based on our time-resolved model with  $n = 100$ ,  $\theta_A = 32$ ,  $\lambda_A = 0.75$ ,  $\mu_A = 1$ ,  $\lambda_B \sim U(0, 1)$ ,  $p_A \sim U(0, 1)$ ,  $\alpha = 0.1$ ,  $\beta = 0.05$ ,  $K = 1$  and  $r = 1/60$ . In **A**, workers are sorted from left to right in descending order based on their number of fanning events. Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .



**Fig. 8** Number of fanning events (**A**) and nest temperatures (**B**) for a group of bumblebee workers in the simulated dynamic environment. The simulation results are drawn from 30 replicates and based on our time-resolved model with  $n = 100$ ,  $\lambda_A = 0.75$ ,  $\mu_A = 1$ ,  $\lambda_B \sim U(0, 1)$ ,  $p_A \sim U(0, 1)$ ,  $\alpha = 0.1$ ,  $\beta = 0.05$ ,  $K = 1$  and  $r = 1/60$ .  $s_A = 28$  before the time passed 100 and  $s_A = 32$  after the time 100. In **A**, workers are sorted from left to right in descending order based on their number of fanning events. In **B**, the probability density function of beta-distributed thresholds is given on the left. Here  $U(a, b)$  represents a continuous uniform distribution on the interval  $[a, b]$ .