Models of Task Allocation in Social Insects

by

Rui Chen, BCompSc

Thesis

To *Bombus*

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Abstract

Social insects such as ants and bees live in colonies of up to millions of individuals. In order to satisfy the colony needs, individual workers have to perform a variety of tasks only relying on their limited local knowledge. The proper allocation of workers to tasks in different environments is fundamental to the organisation of insect colonies and crucial to their ecological success. This research explores how mechanisms of task allocation in social insects are influenced by environmental conditions from different novel perspectives. We apply mathematical and computational models to explain and simulate the mechanistic processes of task allocation.

We consider the temporal influence, which tends to be overlooked by most models in the literature, as an important factor, and in particular, focus on task allocation on short timescales. We perform survival analysis for the data from biological experiments in order to take the factor of time into account. Particularly in these experiments, the environmental condition can be measured and controlled at a precise level. The results of our analysis suggest that surprisingly, neither stimulus intensity nor individual experience has a strong effect on workers' task engagement. However, we find that individual workers tend to be less active when receiving rewards, in contradiction to a general expectation that workers' perception of rewards for performing a task should encourage them to engage in the task more strongly. We also find that the processes of task allocation appear not to be homogeneous Poisson but close to power laws, demonstrating that the timing-patterns of workers' activities cannot be omitted at short timescales.

We study the effect of social interaction on colony-level task allocation by applying game theory as an alternative framework to traditional approaches. Our game-theoretical models indicate that specialisation can emerge based on the interaction dynamics between workers and their environments without intrinsic inter-individual variation, which is typically assumed to cause specialisation. We evaluate and discuss the efficiency that can

be achieved by colonies based on our models as well as their performance in dynamic environments. Particularly, we find that not only the current environmental condition but also the history of previous environmental conditions can influence the behavioural patterns and efficiency achievements of colonies in dynamic environments. This provides new insights into our understanding of how task allocation in social insects can adapt to environmental fluctuations, as in general, it is only assumed that task allocation responds to the current environmental conditions.

The outcomes of this research contribute to the knowledge of how task allocation at the colony level emerges from individual task choice in social insects. Our approaches exemplify a methodology for exploring this interdisciplinary field of study. Our models can be used to explain and predict colony behaviours in social insects and to guide further biological experiments. Our results may ultimately benefit the bio-inspired applications of task allocation, such as swarm robotic systems and factory multi-task scheduling.

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.
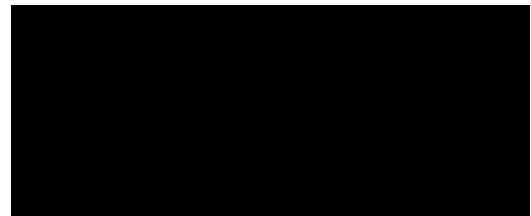
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<div align="right">Rui Chen</div>

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Chapter 1

Introduction

1.1 Task Allocation in Social Insects

Social insects such as ants, bees, wasps and termites live in groups, typically called colonies, of up to millions of individuals. A colony includes one or few queens, and sometimes males, both of which are responsible for reproduction. The majority of individuals in a colony are workers, taking charge of the maintenance and expansion of the colony. Social insect colonies are regarded as one of the most successful organisations in nature (Hölldobler and Wilson, 1990, 2009; Charbonneau et al., 2013; Oster and Wilson, 1978; Grimaldi and Engel, 2005). They dominate most terrestrial habitats around the world (Charbonneau et al., 2013; Charbonneau and Dornhaus, 2015a; Hölldobler and Wilson, 2009) and some species may have evolved for millions of years (Grimaldi and Engel, 2005).

The collective behaviours of social insect colonies, adapted to a variety of environmental and social conditions, are complex and diverse (Dornhaus et al., 2012; Charbonneau and Dornhaus, 2015a) and thus provide a rich field to investigate. Within such a colony, individual members appear to act in a decentralised way and make simple decisions according to their limited local knowledge (Bonabeau, Theraulaz, Deneubourg, Aron and Camazine, 1997; Camazine et al., 2001; Duarte et al., 2011; Couzin, 2009). This makes social insect colonies experimentally more tractable than many other collective organisations and as a result, they are widely used as model systems for the study of collective behaviour (Beshers and Fewell, 2001; Charbonneau and Dornhaus, 2015a). The principles of collective behaviour are potentially transferable from social insect colonies to other social systems or even multicellular organisms (Beshers and Fewell, 2001; Duarte et al., 2011; Wilson, 1985).

Workers within a colony can cooperate in sophisticated ways for various tasks such as brood care, nest construction, foraging and defence in order to satisfy the colony needs that cannot be managed by a single individual (Charbonneau et al., 2013; Charbonneau and Dornhaus, 2015a; Duarte et al., 2011; Mersch, 2016). Without any central control,

workers can be appropriately allocated to each task in response to numerous environmental contexts such as variation of food resources, predation pressures and climatic conditions (Duarte et al., 2011; Gordon, 1996; Oster and Wilson, 1978; Robinson, 1992). This process is called *task allocation* (Gordon, 1996, 2002, 2016). It is fundamental to the organisation of insect colonies and crucial to their survival and ecological success (Beshers and Fewell, 2001; Jeanson and Weidenmüller, 2014; Oster and Wilson, 1978; Schwander et al., 2005; Wilson, 1971, 1985; Page Jr. and Mitchell, 1990). Task allocation is one of the core questions in the study of social insects and connected with a wide range of areas including behavioural syndromes (Jandt et al., 2014), scaling laws (Fewell and Harrison, 2016) and network dynamics (Charbonneau et al., 2013; Mersch, 2016).

Task allocation is a fast and highly dynamic process that describes how distributions of colony workforce across different tasks interact with environments (Oster and Wilson, 1978; Gordon, 2016; Fewell and Harrison, 2016; Mersch, 2016; Kang and Theraulaz, 2016). Over a certain time period, workers can behave with statistically consistent preferences towards particular tasks, which is called *task specialisation* (Duarte et al., 2011; Fewell and Harrison, 2016; Jeanne, 2016). To satisfy various demands within a colony, workers can specialise in different subsets of tasks, called *division of labour* (Michener, 1974; Oster and Wilson, 1978; Robinson, 1992; Fewell and Harrison, 2016; Jeanne, 2016). Here a stable, long-term division of labour is out of scope of this thesis. This research mainly focuses on the dynamics of task allocation on short worker-life timescales.

Particularly, specialisation can be used to describe the behavioural patterns of task allocation. For example, there are 100 workers who need to tackle two tasks (A and B) in a colony. In order to satisfy the associated demands, Task A requires 30 workers' engagement and Task B needs 70. At the colony level, one pattern of task allocation is that all workers are engaged in both tasks with 30% of chance for Task A and 70% for Task B, which does not involve specialisation at all; Another pattern is that 30 workers are allocated to Task A, 70 to Task B and all workers make 100% effort at their target tasks, which represents a complete colony-level specialisation; There can be other patterns of task allocation in between the above two.

Although there is little evidence that workers permanently specialise into tasks (Gordon, 2016), the colony-level specialisation can statistically occur on certain timescales (Duarte et al., 2011; Jeanne, 2016). In the study of task allocation, there are some major questions such as what are the sources that can generate specialisation (Gordon, 2016) and how specialisation is related to behavioural efficiency and flexibility (Charbonneau and Dornhaus, 2015a). At the colony level, it is assumed that tasks can be performed more efficiently by specialised workers (Oster and Wilson, 1978; Charbonneau and Dornhaus, 2015a; Leighton et al., 2017). We will explore and discuss these questions in the following chapters of this thesis.

1.2 Research Questions

To study any animal behaviour, the most fundamental and significant approach is to ask *Tinbergen's four questions* (Tinbergen, 1963; Bateson and Laland, 2013): causation (How does it work?), ontogeny (How did it develop?), adaptive value (What is it for?) and evolution (How did it evolve?). These questions provide complimentary insights and lead to a comprehensive understanding of the focal behaviour (Bateson and Laland, 2013). Among these questions, we focus on the underlying mechanisms of task allocation in social insects on short worker-life timescales, which are connected with causation and ontogeny, as well as the associated efficiency achievement, which is related to the adaptive value of task allocation. Here the evolutionary dynamics of task allocation are out of scope of this thesis. We propose the following questions for this research:

1) What are the underlying factors that can influence task allocation in social insects? (causation)

2) What mechanisms potentially determine the dynamics of workers' strategies for task allocation over time in social insects? (ontogeny)

3) How can environmental conditions affect task allocation in social insects? (causation)

4) How well can social insect colonies perform in terms of task allocation? (adaptive value)

5) How and how well can task allocation in social insects adapt to dynamically changing environments? (ontogeny & adaptive value)

1.3 Methodology

Task allocation in social insects exhibits a *self-organised* process which emerges from interactions of workers who follow simple behavioural rules in response to environmental conditions (Bonabeau, Theraulaz, Deneubourg, Aron and Camazine, 1997; Robinson, 1992; Duarte et al., 2011; Page Jr. and Mitchell, 1998; Gordon, 2016; Kang and Theraulaz, 2016). We divide the behavioural rules that potentially determine workers' task allocation into individual and social: Individual behavioural rules represent the factors within a worker; Social behavioural rules refer to the interactions between workers. For individual behavioural rules, we perform survival analysis on the data from experiments in bumblebees (see Chapter 3). Based on this analysis, we explore the influence of potential factors on workers' task selection and propose a novel model which is then verified with the empirical data. To explore the effect of social interaction, we use game theory as a basic framework (see Chapter 4). We integrate a task-allocation game with different mechanisms of how workers' strategies for task allocation can develop over time. Then we build computer simulations based on these integrated models with a range of environmental conditions. Our models for both individual and social behavioural rules are simulated for the analysis of efficiency and flexibility in dynamic environments (see Chapter 5).

1.4   Key Contributions

1.4.1   Knowledge

The outcomes of this research make the following contributions to the knowledge of task allocation in social insects:

- Neither stimulus intensity nor individual experience has a significant effect on the moment-to-moment task allocation in bumblebee thermoregulation under certain environmental conditions;

- Bumblebee workers tend to be less active after receiving rewards from a homeostatic task on the moment-to-moment timescale;

- The timing-patterns of workers' activities in bumblebees are close to power laws rather than homogeneous Poisson on the moment-to-moment timescale;

- Specialisation can emerge from the interaction dynamics between workers alone under certain environmental conditions;

- Variation of environmental conditions and mechanisms that determine the dynamics of workers' strategies over time can lead to different behavioural patterns and efficiency achievements of task allocation;

- The history of previous environmental conditions can influence how social insect colonies adapt to dynamic environments.

1.4.2   Methodology

The results of this study make the following contributions to the methodology of task allocation in social insects:

- Exploring task allocation of social insect colonies in a bottom-up approach based on timescales;

- Conducting survival analysis for the influence of within-worker factors on task allocation in social insects;

- Using game theory as a basic framework to study the effect of social interaction on task allocation in social insects.

1.5   Thesis Outline

In Chapter 2, we review current theoretical models of task allocation as well as empirical studies in the literature. Based on this, we identify the limitations of these models and accordingly make suggestions for future research directions. In Chapter 3, we explore the influence of potential factors within an individual worker based on the results of survival analysis for experimental data in the thermoregulation of bumblebees. Accordingly, we

construct an agent-based model which explicitly takes the temporal effect into account. In Chapter 4, we apply game theory as a basic framework to study the impact of social interaction between workers on task allocation. We build computer simulations based on different mechanisms of how workers' strategies for task allocation can develop over time with a range of environmental contexts. In Chapter 5, we analyse the efficiency of task allocation based on our models introduced in the previous chapters and discuss the flexibility in dynamic environments with illustration by computer simulations.

Chapter 2

Literature Review

2.1 Introduction

There are numerous studies that have explored potential mechanisms underlying the processes of task allocation in social insects. Empirical work suggests that patterns of task allocation can be determined by workers' internal properties, such as body size and age, as well as external interactions with other workers and their environments (Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Robinson, 1992; Gordon, 1996). However, this may not be sufficient as the mechanistic processes linking individual decisions to colony-level task allocation are generally too hard to analyse only by conceptual reasoning or verbal argument (Beshers and Fewell, 2001; Couzin, 2009; Charbonneau and Dornhaus, 2015a). Consequently, computational and mathematical modelling techniques become increasingly popular in explaining how different factors may affect task allocation in social insects. These models are adopted to simulate the interplay between individual workers and their environments as well as the process of how colony-level patterns of task allocation can emerge from simple individual behavioural rules (Beshers and Fewell, 2001; Duarte et al., 2011). Moreover, such models facilitate our communication and can be used to generate testable hypotheses for guiding further empirical studies (Beshers and Fewell, 2001).

In this chapter, we first describe the factors empirically found to influence behavioural patterns of task allocation. Then we review the models used to explain the mechanisms of task allocation. Finally, we identify the limitations of models in the literature and accordingly make suggestions for future research.

2.2 Empirical Background

Empirical studies have identified a number of factors that can determine individual task preference and be used to gain some insights into behavioural patterns of task allocation at the colony level (Robinson, 1992). These empirical factors can be categorised into internal and external (Beshers and Fewell, 2001): Internal factors represent the state or property

of an individual worker, including genes, morphology, developmental variation and individual experience (Jeanson and Weidenmüller, 2014; Duarte et al., 2011); External factors correspond to the contexts in which a worker lives, such as social interactions, environmental conditions and spatial distribution (Jeanson and Weidenmüller, 2014; Beshers and Fewell, 2001; Duarte et al., 2011).

Internal and external factors are not mutually exclusive and can interact with each other in an insect colony (Beshers and Fewell, 2001; Charbonneau and Dornhaus, 2015a). The processes of task allocation based on internal factors are comparatively stable and can gain from the potential benefits of specialisation (Jeanson et al., 2005; Charbonneau and Dornhaus, 2015a). In contrast, the mechanisms based on external factors are highly dynamic and can adapt to transient fluctuations in task demands (Jeanson and Weidenmüller, 2014; Charbonneau and Dornhaus, 2015a). Internal factors can be used to predict the tasks a worker is likely to perform, but workers often respond to variation in social and environmental contexts by switching their tasks (Gordon, 2016).

2.2.1   Internal Factors

Genetic Diversity

To satisfy the demands of different tasks in a colony, workers tend to have different preferences in task choice. Genetic variation can provide a long-term basis for inter-individual differentiation in workers' task preference (Jeanson and Weidenmüller, 2014). Most studies on behavioural variability of workers within a colony have focused on genetic factors simply because of easy manipulation in experiments (Jeanson and Weidenmüller, 2014). In social insects, there are three potential sources that give rise to genetic diversity: polyandry (multiple patrilines), polygyny (multiple matrilines) and genetic recombination (Oldroyd and Fewell, 2007; Jeanson and Weidenmüller, 2014). Empirical evidence shows that workers' task choice is determined by their patrilines in honeybees (Kryger et al., 2000; Jones et al., 2004; Robinson and Page Jr., 1989; Scheiner and Arnold, 2010) and ants (Waddington et al., 2010; Eyer et al., 2013). Similarly, workers from different matrilines tend to perform different tasks in natural and experimentally constructed ant colonies (Julian and Fewell, 2004; Blatrix et al., 2000; Snyder, 1992; Stuart and Page Jr., 1991). Besides polyandry and polygyny, high combination rates (Wilfert et al., 2007) may also be a potential factor that influences workers' task preference (Oldroyd and Thompson, 2007; Oldroyd and Fewell, 2007; Smith et al., 2008).

Morphological Differentiation

In some species of social insects, workers can be distinguished by their morphological castes (Oster and Wilson, 1978; Charbonneau and Dornhaus, 2015a). These castes are permanent features for adult workers as their body size or shape does not generally change. In a colony workers from different castes are often associated with different types of tasks (Hölldobler and Wilson, 1990; Oster and Wilson, 1978; Charbonneau and Dornhaus,

2015a). For example, in the ant genus *Pheidole*, majors of large size generally specialise in colony defence or food storage (Wilson, 2003) and rarely engage in brood care, which is typically performed by minors of small size (Mertl and Traniello, 2009). Another example is found in the bumblebee *Bombus terrestris* where large workers are more likely to perform the tasks stimulated by odour than small workers (Spaethe et al., 2007).

Developmental Variation

Variation of the preimaginal environments is likely to have an important influence on workers' behaviour and task choice at their adult stage (Duarte et al., 2011; Jandt et al., 2014; Jeanson and Weidenmüller, 2014). For example, the temperature experienced during larval development may affect task choice carried out by adult workers in honeybees (Tautz et al., 2003). In the ant *Camponotus rufipes*, pupal temperature is shown to modulate the response behaviour of adult workers in brood-tending tasks (Weidenmüller et al., 2009). Apart from temperature, other environmental factors, such as humidity and light experienced, during the larval period may also affect task preferences of adult workers (Duarte et al., 2011; Jeanson and Weidenmüller, 2014).

Young workers tend to be engaged in tasks within their nest, and later in their lives, switch to tasks outside the nest, such as foraging. This pattern of task allocation associated with age, called *temporal polyethism* or *age polyethism* (Oster and Wilson, 1978; Charbonneau and Dornhaus, 2015a; Jeanson and Weidenmüller, 2014; Jandt et al., 2014), is observed in wasps (Naug and Gadagkar, 1998), honeybees (Robinson, 1987b; Seeley, 1995; Waddington and Hughes, 2010), termites (Hinze and Leuthold, 1999) and ants (Hölldobler and Wilson, 1990; Julian and Fewell, 2004). The benefit of the age-related task allocation can be that risky tasks are allocated to older workers, who are less valuable as the amount of work they can perform in the future is smaller than younger workers (Charbonneau and Dornhaus, 2015a). The age-dependent task transition of honeybee workers tends to be correlated with juvenile hormone (Robinson, 1987b; Huang et al., 1994), which also interacts with the nutritional state, another physiological factor that can determine workers' task decisions (Duarte et al., 2011; Jeanson and Weidenmüller, 2014; Robinson et al., 2012; Toth and Robinson, 2005; Ament et al., 2010).

Individual Experience

Workers in an insect colony may select tasks based on their own experience (Jeanson and Weidenmüller, 2014; Charbonneau and Dornhaus, 2015a). Empirical evidence suggests that workers are more likely to choose tasks that they have performed before (Franklin et al., 2012; Ravary et al., 2007; Robinson et al., 2012). However, current knowledge of how individual experience affects the decisions made by workers on task engagement is still limited, as the processes of workers' response to task demands are difficult to precisely measure and control (Jeanson and Weidenmüller, 2014). For example, conflicting evidence on the relationship between individual experience and task responsiveness appears in studying the thermoregulation of two closely related bumblebee species (Duong and Dornhaus,

2012; Weidenmüller, 2004; Westhus et al., 2013). Consequently, the studies on individual experience have mainly focused on theoretical approaches (Jeanson and Weidenmüller, 2014) and proposed the concept of self-reinforcement (Beshers and Fewell, 2001), which gives a positive feedback loop (Charbonneau and Dornhaus, 2015a) and promotes short-term specialisation that can be adjusted to environmental fluctuations (Ravary et al., 2007; Jeanson and Weidenmüller, 2014; Robinson et al., 2012).

2.2.2   External Factors

Social Context

Interactions between workers are likely to have a significant effect on behavioural patterns of task allocation and colony-level response to environmental fluctuations (Duarte et al., 2011; Charbonneau and Dornhaus, 2015a). For instance, being involved in a social context is shown to make workers more likely to undertake the fanning task in the honeybee *Apis mellifera* (Cook and Breed, 2013). In the harvest ant *Pogonomyrmex barbatus*, the decision made by a worker to undertake a particular task, can depend on how frequently the worker has interacted with those who engaged in the same task or other related tasks (Gordon and Mehdiabadi, 1999; Greene and Gordon, 2007). Workers can interact with each other in a direct way by tactile contacts or chemical signals (Duarte et al., 2011; Billen, 2006; Richard and Hunt, 2013). Interaction rates, which may contain the information about the numbers of workers already allocated in like or unlike tasks, can influence workers' decisions on task engagement (Gordon, 1996). Interactions between workers are considered to facilitate efficient information transfer within a colony and regulate task allocation in a flexible and dynamic way to environmental changes (Duarte et al., 2011; Charbonneau and Dornhaus, 2015a). In addition, social interactions can reveal and amplify even minor intrinsic differences among individual workers, thus reinforcing behavioural asymmetry in a colony (Camazine et al., 2001).

Task allocation of workers may change with colony size (Fewell and Harrison, 2016; Dornhaus et al., 2012; Jeanson and Weidenmüller, 2014; Duarte et al., 2011) partially because colony size can affect social structure and organisation (Anderson and McShea, 2001) including worker-worker interaction rates (Gordon, 1996; Thomas and Elgar, 2003) and task demands (Holbrook, Eriksson, Overson, Gadau and Fewell, 2013). Empirical and theoretical studies suggest that group size can positively influence the degree of task specialisation (Jeanson et al., 2007; Karsai and Wenzel, 1998; Holbrook et al., 2011; Holbrook, Kukuk and Fewell, 2013; Thomas and Elgar, 2003). For example, workers in a small-size wasp colony tend to be generalists for a variety of tasks while colonies of large size consist of more task specialists (Karsai and Wenzel, 1998). In the ant *Rhytidoponera metallica*, temporal polyethism is observed only in the colonies of large size rather than in those of small size (Thomas and Elgar, 2003). Although variation of colony sizes is usually correlated with transitions in the colony life cycle (Duarte et al., 2011), colony size is shown to promote task specialisation independently of the stage of colony development (Holbrook et al., 2011).

Environmental Stimuli

Social insect colonies tend to react to variation of task demands by adjusting the ratios of workers allocated to the corresponding tasks (Duarte et al., 2011). In the harvest ant *Pogonomyrmex rugosus*, for example, workers can change their engagement in tasks such as guarding, attacking and foraging in response to predation of spiders (MacKay, 1982). The number of bee workers undertaking the fanning task for control of nest climate is found to vary with changes of environmental conditions such as temperature and humidity (Egley and Breed, 2012; Weidenmüller, 2004; Westhus et al., 2013). In the bumblebee *Bombus terrestris*, the response of a worker to foraging can depend on the nectar store in honeypots, which in turn provides information about nectar foraging of other nest workers (Dornhaus and Chittka, 2005). Typically, modulating the magnitude of shared environmental stimuli by task execution without direction communication can constitute an indirect way for workers to interact with each other in a colony (Jeanson and Weidenmüller, 2014).

Spatial Distribution

Individuals in a colony naturally spread throughout the space of the nest and peripheral areas (Charbonneau and Dornhaus, 2015a). Which task a worker encounters can depend on her location (Jeanson et al., 2005). The spatial organisation of workers in some species is non-random, consistent over their lifetime and may be correlated to the colony-level task allocation (Charbonneau and Dornhaus, 2015a; Jandt and Dornhaus, 2009; Sendova-Franks and Franks, 1994, 1995; Tschinkel, 2004; Holbrook et al., 2009). Workers close to the centre of the nest tend to take care of the brood while those at the periphery are more likely to forage (Jandt and Dornhaus, 2009). Remaining non-random and limited areas in the nest may minimise the moving distance of workers and thus improve the colony-level efficiency (Wilson, 1976; Seeley, 1982).

The extent to which the factors reviewed above contribute to task allocation in a colony may depend on the situation and remains to be further investigated. Whether a factor applies or not in a specific scenario can depend on the species or type of tasks involved (Charbonneau and Dornhaus, 2015a). The processes of task allocation do not appear to be influenced by any single factor all the time. Differentiation in workers' task selection in a colony is found to occur independently of a particular factor such as age or body size (Beshers and Traniello, 1996; Egley and Breed, 2012; Gordon, 1989; Kolmes, 1986; Robinson et al., 2009; Duarte et al., 2011; Jandt et al., 2014). There is a need for more rigorous comparative studies to explore behavioural patterns of task allocation potentially influenced by multiple confounding factors (Jeanson and Weidenmüller, 2014; Dornhaus et al., 2012).

2.3   Models

To advance our understanding of proximate causation of task allocation in social insects, mathematical and computational models are applied to explain and simulate the mechanistic processes influenced by different factors. Most models focus on the response-threshold concept (Jeanson and Weidenmüller, 2014; Jeanne, 2016), which identifies the interplay between workers' internal properties and their environments as a primary driving force (Beshers and Fewell, 2001). The response-threshold assumption is typically regarded as a fundamental framework that can be integrated with other factors such as social interaction and spatial distribution (Fewell and Bertram, 1999; Richardson et al., 2011). Moreover, recent studies concentrate on the idea that task allocation can be regarded as a set of distributed processes driven by interactions between individuals and their environments (Gordon, 2016). In addition, spatial distribution provides another modelling perspective which links spatial arrangements of workers and tasks to behavioural patterns of task allocation. Here we review these models categorised by the main concept involved.

2.3.1   Response Threshold

The *response-threshold* assumption is widely accepted as the main modelling concept for task allocation in social insects (Bonabeau et al., 1996; Jeanson and Weidenmüller, 2014; Jeanne, 2016). For a single worker, it is assumed that the decision made to respond to a task-associated stimulus is determined by whether the perceived stimulus intensity exceeds the internal task-related threshold (Page Jr. and Mitchell, 1998; Jeanson et al., 2007; Gove et al., 2009; Graham et al., 2006; Duarte, Pen, Keller and Weissing, 2012). For example, bumblebee workers can start the cooling task by fanning their wings if the within-nest temperature outstrips a certain level (Weidenmüller, 2004).

As performing a task reduces the corresponding stimulus intensity, workers with lower thresholds tend to maintain the stimulus intensity under the level at which workers with higher thresholds start to respond. Even small variation of individual thresholds for different tasks thus can lead to consistent task specialisation. When workers with lower thresholds fail to keep the stimulus intensity at a lower level, workers with higher thresholds subsequently perform the task. Therefore, followed by this mechanism, task allocation in a colony can be flexible to environmental fluctuations (Jeanson and Weidenmüller, 2014; Beshers and Fewell, 2001; Camazine et al., 2001; Duarte et al., 2011; Charbonneau and Dornhaus, 2015a).

For any task in a colony, workers' response thresholds tend to be intrinsically different. The distributions of thresholds across tasks and workers can determine the behavioural patterns of task allocation at the colony level (Charbonneau and Dornhaus, 2015a). For instance, immensely active or inactive workers with no task specialisation can be generated by correlated response thresholds over different tasks; Alternatively, task specialisation can

emerge from the situation when there is at least one large threshold for each worker (Pinter-Wollman et al., 2012). The response-threshold models can further be generalised into a function that gives the stimulus-response dynamics between workers' internal properties and environmental contexts (Castillo-Cagigal et al., 2014). Here we briefly review different types of models that are used to elucidate the stimulus-response dynamics.

The Fixed-Threshold Model

The *fixed-threshold* model assumes that the thresholds for a set of tasks that a worker performs remain constant on a short timescale (Bonabeau et al., 1996). Empirical evidence suggests that workers do not always perform a task even when the level of stimulus intensity is sufficiently high (Weidenmüller, 2004; Westhus et al., 2013; Duong and Dornhaus, 2012). In general, individual-level task selection is not deterministic as there are potentially numerous factors involved. Therefore, it is more reasonable to explicitly assume that response probability, the likelihood of a worker to engage in a task, is determined by the relative difference between the task-associated stimulus and her internal threshold.

The mathematical framework for the fixed-threshold model is built based on this probabilistic assumption (Bonabeau et al., 1996, 1998). It is simply assumed that in a colony, there are N workers who need to perform one task. Worker i has a threshold θ_i associated with stimulus s for $i = 1, 2, ..., N$. The probability of worker i to be allocated to the task, denoted by p_i, is defined as

$$p_i = \frac{s^2}{s^2 + \theta_i^2}$$

where θ_i is assumed to be invariable.

There is a negative feedback loop that performing the task reduces the level of s. In addition, s is assumed to increase naturally by a constant demand δ at each time-step. Then stimulus s at time-step t is given as

$$s(t) = s(t-1) + \delta - \frac{\alpha}{N} n(t-1)$$

where α is a scale factor that measures the efficiency of individual task performance and $n(t)$ is the number of workers allocated to the task at t.

The Threshold-Reinforcement Model

The *threshold-reinforcement* model integrates the experience-based variation into the fixed-threshold model (Theraulaz et al., 1998; Gautrais et al., 2002; Castillo-Cagigal et al., 2014). Performing a task by a worker is assumed to decrease her threshold for this task, while not performing the task increases the threshold. The mathematical framework for this model describes the response threshold θ_i as a function of time-step t:

$$\theta_i(t+1) = \theta_i(t) - \xi$$

if worker i performs the task at t;

$$\theta_i(t+1) = \theta_i(t) + \varphi$$

if worker i does not perform the task at t. Here ξ and φ are the rates of learning and forgetting respectively. Based on this mechanism, specialisation can emerge even from a colony of initially identical workers (Theraulaz et al., 1998).

Artificial Neural Network

The process that describes how individual workers respond to task-related stimuli can be generalised into more complex functions, which involve more internal parameters than the response thresholds in individual task selection. In some models, the stimulus-response dynamics are regarded as artificial neural networks (Lichocki et al., 2012; Duarte, Scholtens and Weissing, 2012), with an example illustrated in Figure 2.1. Lichocki et al. (2012) used partially-connected artificial neural networks with no hidden layer to represent response-threshold models (see Figure 2.2). The feed-forward neural network (see Figure 2.3(a)) and recurrent neural network (see Figure 2.3(b)) with fully connected weights were also implemented as the mechanisms that workers follow in their task selection (Duarte, Scholtens and Weissing, 2012). Although artificial neural networks have more open features to explore (Duarte et al., 2011; Duarte, Scholtens and Weissing, 2012), the interpretation of these models is difficult and may need more support from empirical studies in neurobiology (Duarte et al., 2011).

Empirical evidence for the response-threshold models comes from studies on physiology (Robinson, 1987a,b) and genotypes (Fewell and Page Jr., 2000; Page Jr. et al., 1998; Pankiw and Page Jr., 1999; Robinson and Page Jr., 1995) in honeybees, castes and larval development in ants (Wilson, 1984; Detrain and Pasteels, 1991, 1992; Weidenmüller et al., 2009) and thermoregulation in bumblebees (O'Donnell and Foster, 2001). The assumption that response thresholds are modified by individual experience is supported with evidence in food exploration of the ant *Cerapachys biroi* (Ravary et al., 2007) and thermoregulation of the bumblebee *Bombus terrestris* (Weidenmüller, 2004; Westhus et al., 2013), among others.

2.3.2   Social Interaction

Task allocation can be modulated by social interactions which facilitate efficient information transfer at the colony level (Beshers and Fewell, 2001). In an insect colony, tasks are performed by interdependent groups of workers and the number of workers engaged in one group can be influenced by the number of workers involved in others (Gordon, 1996, 2002, 2010). Most models based on social interaction assume that there is no intrinsic difference among workers in a colony (Gordon, 1996; Beshers and Fewell, 2001). These models provide an alternative view to those based on intrinsic inter-individual variation in task preference such as the response-threshold models and can be used to figure out what
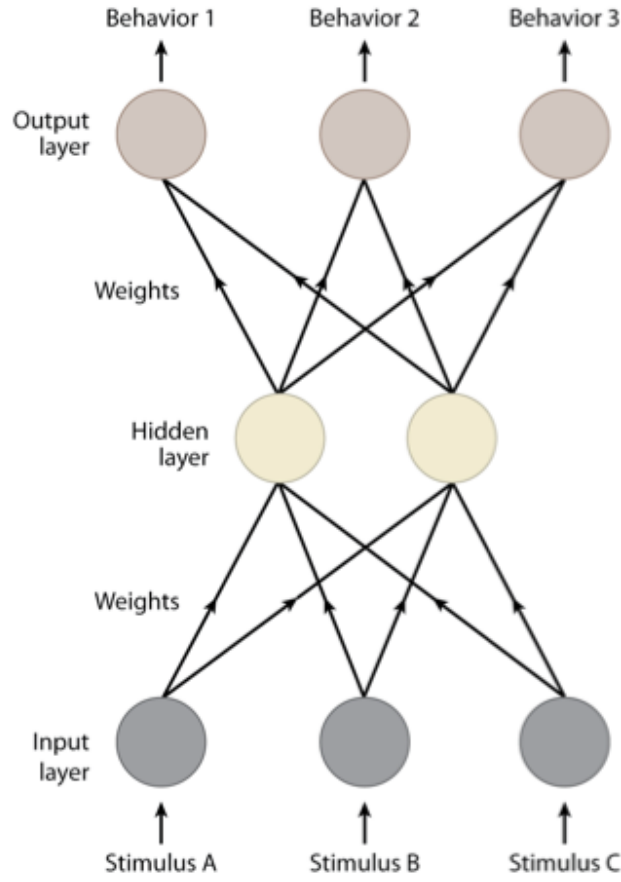
Figure 2.1: An example of the feed-forward artificial neural network (Duarte et al., 2011)

(a) Deterministic response threshold

(b) Extended response threshold
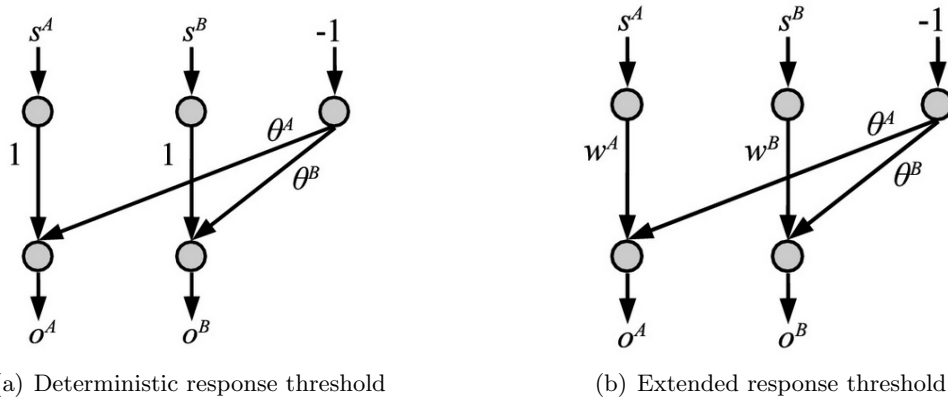
Figure 2.2: Neural network representation of two versions of the response-threshold model (Lichocki et al., 2012). Here in a colony, two tasks need to be performed: A and B. s^A, s^B represent the stimuli for Tasks A, B respectively; -1 is the bias node; θ^A, θ^B stand for the response thresholds of A, B; w^A, w^B are the weights of stimuli for A, B. Output $o^i = w^i s^i - \theta^i$ for Task $i = A, B$. For the deterministic response-threshold model (a), $w^A = w^B = 1$.

(a) Feed-forward neural network   (b) Recurrent neural network
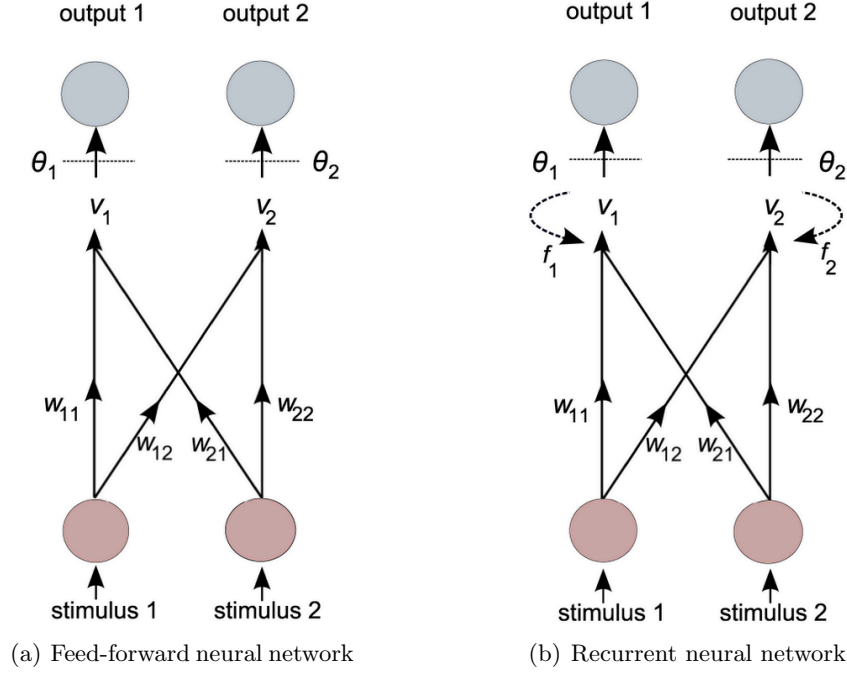
Figure 2.3: Fully-connected neural network models of task allocation (Duarte, Scholtens and Weissing, 2012). An output neuron is excited when the activation energy v, resulting from the stimuli and weights, is larger than the threshold θ. For a recurrent neural network (b), current activation energy also depends on the self-feedback f at previous time-steps.

behavioural patterns of task allocation can arise only from interactions between workers and their environments (Gordon, 1996, 2016).

Some models based on social interaction use the representations by network structures. For example, Gordon et al. (1992) built a network model in which workers are regarded as nodes. Task selection of a worker is determined by the weighted sum of her interactions with others and a threshold value. The results show that in an ant colony, even through simple worker-worker interactions, variation in the number of workers in one task group causes changes in the number of workers in another group, and eventually, the colony tends to reach an equilibrium of allocation of workers across tasks. There are other network models used to reveal the dynamics of switches between tasks (Fewell, 2003; Charbonneau et al., 2013) or to predict the speed of information transfer (Pinter-Wollman et al., 2011), which may in turn determine patterns of task allocation.

Apart from the network representation, other models explore numbers of workers that switch between tasks based on social interactions using differential equations (Pacala et al., 1996; Pereira and Gordon, 2001; Kang and Theraulaz, 2016). Pacala et al. (1996) developed deterministic and stochastic models showing that the distribution of workers over tasks based only on simple interactions between individuals with limited capacity can reach a stable state that is close to the optimal level. The results of these models further indicate how the rates of interaction can influence the efficiency of a colony to track

environmental fluctuations. The interaction rate may be associated with colony size and regulated by workers to balance the speeds between information transfer and environmental changes. Colonies of larger size may respond to environmental changes faster than those of smaller size, and furthermore, how well a colony can adapt to environmental perturbations is determined by workers' strategies of how to react to environmental stimuli and social interactions (Pereira and Gordon, 2001).

Social inhibition models are used to study the interactions between workers of different ages in honeybees (Beshers et al., 2001) and wasps (Naug and Gadagkar, 1999). It is assumed that younger workers are inhibited to forage outside the nest by interactions with older foragers (Beshers et al., 2001; Huang and Robinson, 1992, 1996; Naug and Gadagkar, 1999). This inhibition opposes the effect that intrinsically pushes younger workers to forage. With this mechanism, a balance between workers engaged in in-nest tasks and outside foraging can be achieved, independently of the initial condition of numbers of in-nest workers and foragers, and keep stable under environmental perturbations (Beshers et al., 2001; Naug and Gadagkar, 1999).

2.3.3   Space

Similar to social interaction, another alternative modelling perspective to inherent differentiation in workers' task choice is explicitly assuming that workers and tasks in a colony are spatially arranged. The foraging-for-work model (Franks and Tofts, 1994; Tofts, 1993; Tofts and Franks, 1992) shows that heterogeneity in task allocation can emerge from a colony of identical workers, given that task demands are distributed non-randomly in space. In this model, workers are assumed to randomly seek a task to perform, continue to perform the task if it has been done successfully or move to a different location if no task needs to be performed at the current position. Individual task engagement is directly driven by whether a task is encountered, which makes task allocation predicted by this model flexible to changes of task needs. The foraging-for-work model can theoretically generate age polyethism in which young workers are close to brood area and old workers are near the nest entrance (Tofts and Franks, 1992; Tofts, 1993; Tripet and Nonacs, 2004).

The spatial task-encounter hypothesis assumes that short-term specialisation can result from spatial variation of task demands (Johnson, 2010), which is supported by biological experiments conducted in scenarios of task allocation of foraging and brood care in ant colonies (Robinson et al., 2009). The foraging-for-work model can be combined with the frequent-task-quitting mechanism, which randomises the location of workers who become insensitive to task demands for some period (Johnson, 2009). The frequent-task-quitting, found in colonies of *Apis mellifera* (Johnson, 2002), has an opposing effect to the foraging-for-work mechanism, which allocates workers to areas with high task demands. This coupled model can explain an equilibrium in which workers switch between tasks and locations, independently of their spatial distribution in the nest, and can adapt to dynamic environments (Johnson, 2009).

2.3.4   Integration of Different Concepts

The process involved in a worker's response to a task-associated stimulus can be divided
into two parts (Bonabeau et al., 1996):

(a) Sampling the stimulus;

(b) Decision-making on whether or not to perform the task once (a) is done.

Most response-threshold models ignore the first part and only focus on individual response
to task needs (Bonabeau et al., 1996; Theraulaz et al., 1998; Duarte, Pen, Keller and
Weissing, 2012; Castillo-Cagigal et al., 2014; Lichocki et al., 2012; Gautrais et al., 2002).
There are some studies that attempted to address both (a) and (b) by combining the
response threshold with other factors such as social interaction (Fewell and Bertram, 1999;
Bertram et al., 2003; Kang and Theraulaz, 2016) and spatial distribution (Richardson
et al., 2011). In general, these studies demonstrate that the integrated models can predict
behavioural patterns closer to empirical evidence and achieve greater colony performance
than the models only with the response-threshold mechanism.

2.4   Limitations and Future Research

Following the review in Section 2.3, we identify several limitations of models in the litera-
ture. First, we find that the questions on how the factor of time may influence workers' task
selection tend to be ignored in most models. Then for a single individual worker, the pro-
cesses of responding to task-related stimuli require further specification and clarification.
Moreover, the factor of social interaction needs to be explored from a self-organisational
perspective. Social insect colonies are potentially examples of efficient and flexible or-
ganisations shaped by the optimising processes of natural selection (Charbonneau and
Dornhaus, 2015a). The efficiency and flexibility of mechanisms of task allocation need to
be further explored in addition to behavioural patterns.

2.4.1   The Factor of Time

Most models of task allocation in social insects do not specify on what timescales the
focal mechanistic processes take effect. However, it is crucial to figure out the temporal
range that each factor applies to, in order to compare and integrate different factors, and
ultimately, to achieve a relatively complete picture of mechanisms for task allocation. In
general, the influence of genes, body size or larval development tends to be long-term and
stable over individual lifetime, followed by the medium-term effect from age, which is still
much longer than the moment-to-moment impact of interaction between workers and their
environments. Even though this seems relatively clear in empirical studies, theoretical ap-
proaches tend to ignore the timescales of the relevant processes or factors.

For example, the fixed-threshold model (Bonabeau et al., 1996) assumes the timescales
are relatively short without further specification or quantification. The models that follow

up the fixed-threshold model, for instance, the threshold-reinforcement model (Theraulaz et al., 1998), tend to ignore the timescales of additional factors such as individual experience. This makes it difficult to further expand the response-threshold mechanism with other factors such as social interaction, which is also assumed to occur on short timescales (Gordon, 2002, 2016). As the relative timescales among responding to environmental stimuli, learning by individual experience and interacting with other nest mates for an individual worker are not specified, studies on how individual properties and social communication interact and contribute to workers' task decisions can be difficult to move forward.

The answers to the question of how an individual worker in a colony selects a task are related to both causation and ontogeny in Tinbergen's four questions (see Section 1.2). As developmental variation is continuous, it is necessary to find out the mechanistic processes at different timescales in order to understand the proximate causation for task allocation (Tinbergen, 1963; Bateson and Laland, 2013; Naug, 2016). A practical approach is to specify the time window for the influence of each factor and attempt synthesis of different factors based on the associated time windows. To build a clear framework, we propose a bottom-up approach based on timescales, following the assumption that at the moment-to-moment term, the number of acting factors can be minimised, which may generate preliminary and more reliable results.

The effect of time on individual task selection and coordination of workers at the group level is overlooked by most models of task allocation in social insects. The question of whether task engagement of an individual worker depends on time is hardly explored, while it is suggested that the dynamics of human activities and behaviours of some other animals are time-dependent (Barabási, 2005; Reynolds, 2011). How actions of a large number of workers are coordinated is a major question for social insect colonies (Camazine et al., 2001). As individual workers are physically separated units, coordination of both their spatial and temporal dynamics is significant to the overall function of a colony (Johnson, 2009). There are a number of studies that have explored spatial distribution of workers and tasks in a colony (see Sections 2.2.2 and 2.3.3). However, most models simply assume that all workers in a colony simultaneously encounter, perform and quit tasks at discrete time-steps (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012; Cornejo et al., 2014). Little work has investigated the dynamics of temporal patterns in task engagement across workers.

2.4.2 The Stimulus-Response Dynamics

Our understanding of the stimulus-response dynamics at the individual level is not sufficient. Most studies consider that individual task engagement follows the response-threshold mechanism. However, there are several ambiguities or inconsistencies involved in different implementations and analyses of the response-threshold concept. Some studies implicitly treat response threshold and response probability as the same property that

describes the process in which workers respond to task needs (Jeanne, 2016; Naug, 2016). Some simply regard either response threshold or response probability (Page Jr. and Mitchell, 1998; Gordon, 2002; Duong and Dornhaus, 2012) as the only determinant in the whole responsive process for an individual worker. Most models assume that response probability is dependent on response threshold (Robinson, 1992; Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002), while empirical studies explicitly describe response probability and response threshold as two independent parameters (Jeanson and Weidenmüller, 2014; Weidenmüller, 2004; Westhus et al., 2013; Duong and Dornhaus, 2012). The reason behind this may be that the response-threshold models tend to ignore the process of how task demands are encountered or sampled by individual workers (Bonabeau et al., 1996; Lichocki et al., 2012) and that both response threshold and response probability are hard to measure in experiments (Beshers and Fewell, 2001).

Apart from response threshold and response probability, response duration, the time interval during which a worker tends to perform a task once engaged, is also an important component involved in the processes of task allocation (Johnson, 2002; Weidenmüller, 2004; Westhus et al., 2013). The assumptions made in theoretical models tend to be simplified as either that response duration depends on the necessity of performing a task, or that workers quit from a task with certain probability after a constant time period. Overall, response threshold, response probability and response duration are all likely to act as significant parameters in task allocation. Currently, the way we understand the stimulus-response dynamics at the individual level has not reached a well-quantified level. Further research needs to pay more attention to the relations between the three components mentioned above, and to clarify how they are influenced by other factors such as environmental stimuli and individual experience.

2.4.3   Social Interaction

The models of task allocation based on social interaction tend to lack self-organisational properties (Beshers and Fewell, 2001). As reviewed in Section 2.3, most studies focus on the response-threshold models, specifying workers' internal properties that can be influenced and modulated by their developmental histories (Jeanne, 2016), such as social interactions between workers. However, the models that include both response threshold and social interaction appear to only describe numbers of workers engaged in different tasks at the colony level without a specification on individual-level task selection (Fewell and Bertram, 1999; Bertram et al., 2003; Kang and Theraulaz, 2016). Similarly, the models based on an alternative framework in which workers are assumed to be identical and can interact with each other do not provide a mechanism of how a worker selects a task at the individual level. It will be interesting to see how social interaction can be integrated into the stimulus-response dynamics at the individual level and the outcomes of the colony-level behavioural patterns in future research. A first step towards this would be to ask if there exists a framework that is only based on social interaction and specifies the mechanistic processes of individual-level task selection.

2.4.4 Colony Efficiency and Flexibility

The efficiency for the mechanistic processes of task allocation in social insects is not sufficiently explored. There are a few models that quantitatively evaluated colony efficiency of certain mechanisms for evolutionary analysis (Waibel et al., 2006; Tarapore et al., 2009; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012; Duarte, Scholtens and Weissing, 2012). However, on worker-life timescales, the efficiency evaluation can be inconsistent with the stimulus system (Lichocki et al., 2012). In this case, the stability of stimulus dynamics may be a more appropriate measurement of colony efficiency (Jeanson and Lachaud, 2015; Castillo-Cagigal et al., 2014). Future research needs to further investigate how colony efficiency is connected with individual behavioural programs and productivity in well-established scenarios with different types of tasks.

Social insect colonies naturally live in dynamic environments. Most models (reviewed in Section 2.3) assume that task allocation is responsive to environmental conditions (Charbonneau and Dornhaus, 2015a). However, the question of how well and how fast task allocation based on these models can adapt to environmental changes is not sufficiently explored in a quantitative manner (Pereira and Gordon, 2001; Diwold et al., 2009). A number of studies introduced environmental perturbations by changing colony size or composition (Bonabeau et al., 1996; Gordon et al., 2006; Pinter-Wollman et al., 2012; Beshers et al., 2001). Others manipulated the variation of some abstract task demands that workers may directly respond to (Wakano et al., 1998; Johnson, 2009). Future experiments need to be designed based on more specific and measurable task-related stimuli such as temperature and food availability (Westhus et al., 2013; Bertram et al., 2003; Fewell and Bertram, 1999). Much more research is required to understand how the mechanistic processes of colony-level task allocation can adapt to environmental fluctuations from a self-organisational perspective.

2.5 Conclusion

In this chapter, we reviewed empirical and theoretical studies of mechanisms of task allocation in social insects. Empirical studies identify the factors that determine task allocation in social insects as internal and external, which can interact with each other within a colony. Based on these factors, current models are used to explain and simulate the underlying processes of how colony-level patterns of task allocation can emerge from behaviour rules at the individual level. We made several suggestions on what questions future work may need to address. To gain a comprehensive view of task allocation, further research may integrate different factors into one modelling framework and be aware of the relative timescales that each factor applies to. Theoretical models need to particularly focus on temporal dynamics involved in individual task selection and worker-worker coordination. The process of how workers respond to environmental contexts needs to be specified and quantified with clearly identified parameters that can be empirically measured. Moreover, the effect of worker-worker interaction demands further attention. Colony efficiency needs

to be quantitatively explored together with behavioural rules in well-defined scenarios with different tasks and so does the flexibility of task allocation in dynamic environments.

Chapter 3

Individual Behaviour – A Time-Resolved Model

3.1   Introduction

To further our understanding of mechanisms of task allocation, we consider the role of timescales in exploring the question of how workers dynamically interact with task-associated stimuli. There may be different opinions on the priorities of what timescale to start with. Here following a bottom-up approach, we focus on the moment-to-moment timescale at which the number of acting factors can be minimised and thereby potentially leading to more easily verifiable outcomes. As workers' task allocation develops over time, particularly on short timescales, temporal dynamics are likely to have a strong effect on behavioural patterns at both individual and colony levels. In this study, we regard individual-level task allocation in social insects as the processes that explicitly involve the effect of time on workers' behaviours.

Most established experimental methods (O'Donnell and Foster, 2001; Weidenmüller et al., 2002; Weidenmüller, 2004; Gardner et al., 2007; Duong and Dornhaus, 2012; Cook and Breed, 2013; Jandt and Dornhaus, 2014; Cook et al., 2016) do not allow for sufficiently precise and flexible control of task-associated stimuli. This study explores thermoregulation, a crucial task for brood development in a colony (Heinrich, 2004; Goulson, 2010; Jones and Oldroyd, 2007). Elicited by high temperature, alate workers can fan their wings in a stationary position to cool down the nest (Jones and Oldroyd, 2007). This provides an ideal chance to empirically study the stimulus-response dynamics: The stimulus intensity is temperature, which is comparatively simple to measure and control; Wing fanning, which is the response, can be clearly distinguished from other behaviours during experiments.

The existing experiments that aim to investigate the influence of temperature on workers' response tend to involve temperature ramps (O'Donnell and Foster, 2001; Weidenmüller et al., 2002; Weidenmüller, 2004; Westhus et al., 2013). As a result, these experiments confound the effects of temperature and elapsed time. The results and discussions drawn from

these studies implicitly assume a priori that workers' task engagement is time-independent. However, it is not certain that the observed behavioural patterns result from the effect of temperature rather than the elapsed time, as in this case, temperature develops over time. Therefore, it is necessary to decouple the effects of temperature and elapsed time by setting up constant temperature in experiments. To the best of our knowledge, this has not been done before.

Most theoretical models (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Duarte, Pen, Keller and Weissing, 2012; Lichocki et al., 2012; Cornejo et al., 2014) simply assume that workers' activities in a colony simultaneously happen at discrete time-steps and do not capture a fine-grained, time-resolved picture of individual actions. In order to take timing patterns into account, stochastic processes (Gardiner, 2004) are needed to describe task allocation at the individual level, because in general, the timing of actions for an individual worker is uncertain. If we take account of the effect of time in a model of task allocation, each variable in the model needs to be treated as a function of time in principle.

For example, if we integrate the temporal influence into the response-threshold models (reviewed in Section 2.3.1), workers' response probability becomes time-dependent. As a result, we use a rate function $\lambda(t)$ to represent the instantaneous response probability per unit time at a given time t. For the fixed-threshold model, if stimulus intensity s does not change over time t, then $\lambda(t)$ is constant for any t. There are two important implications of the response-threshold models: (1) The fixed-threshold model assumes that a worker's probability to engage in a task increases with the task-associated stimulus intensity; (2) The threshold-reinforcement model indicates that a worker's probability to engage in a task increases with her repeated task performance. According to these implications, we can derive the following hypotheses:

(1) $\lambda(t)$ is proportional to the stimulus intensity;

(2) $\lambda(t)$ increases with repeated task engagement.

Motivated by the above hypotheses, we first explore the effects of stimulus and individual experience on workers' task selection using a set of experiments in bumblebee fanning. Typically, these experiments set up constant levels of temperature in order to decouple the effects of stimulus and elapsed time by the equipment which makes it possible to precisely measure and control the stimulus intensity (Westhus et al., 2013). We also analyse the influence of individual efficiency based on another set of experiments with a similar set-up. For the data arising from both sets of experiments, we perform survival analysis (Kleinbaum and Klein, 2012; Liu, 2012), as well as traditional analysis, which is only used for comparison.

Survival analysis is a collection of statistical tools to analyse time-dependent stochastic processes. The basic objectives of survival analysis include estimating the rate function

which gives the instantaneous probability per unit time for an event to occur at a certain time-point provided that the event has not occurred before this time-point, and assessing the effect of covariates on the time-interval until the event occurs. Here a covariate can be, for instance, the stimulus intensity such as nest temperature. Only a few studies have applied survival analysis for experimental data of task allocation in social insects. Jeanson et al. (2005) used survival curves which give the probability that an event has not occurred until a certain time-point to analyse the duration of workers' task performance. The Cox proportional hazards model (Cox, 1972), a popular semi-parametric model for survival data, was adopted to analyse the inter-task intervals in bumblebees (Meyer et al., 2015)[1] and ants (Leighton et al., 2017).

Based on our analysis of the experimental data, we develop a time-resolved model of task allocation, which captures the timing of individual actions as a fundamental component. Then we simulate and verify our model with the empirical data. Finally, we discuss and compare our results with the existing empirical studies and models.

3.2 Biological Experiments

There are two sets of biological experiments used in this study. The first set of experiments was designed to study the effects of stimulus and individual experience on workers' task allocation. In these experiments, brood temperature, which is regarded as the stimulus for the task of fanning, was kept constant over time in order to decouple the effects of stimulus and time; Individual experience is quantified as the position in the sequence of uninterrupted fanning periods for each bumblebee worker. The second set of experiments was used to test the influence of individual efficiency on task allocation. In general, workers' perception of rewards from performing a task is expected to encourage them to engage in the task more strongly. This expectation was tested by this set of experiments in which the brood temperature can be changed by workers' fanning. Here perception of individual efficiency is regarded as the perceived decrease of brood temperature.

3.2.1 The Effects of Stimulus and Individual Experience

The first set of experiments was conducted by Anja Weidenmüller and her colleagues in the Neurobiology Lab at the University of Konstanz, Germany. Young colonies of the bumblebee *Bombus terrestris* were obtained from a commercial breeder (Biobest, Belgium) and housed in wooden two-chamber nest boxes at 22°C room temperature, 50% RH and under a 12h:12h light:dark cycle. Colonies were provided with ad libitum sucrose solution in the 'foraging' part of the nest boxes, and fed on defrosted, fresh honeybee-packed pollen every second day directly into the nest chambers.

The experimental set-up consisted of a circular test arena (diameter 7.3 cm, height 4.9 cm) made of Plexiglas (illustrated in Figure 3.1). The wall of the test arena was equipped

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[1]Part of this paper is also included in this chapter.

with ventilation holes circumventing the chamber 0.5 cm above ground. The floor of the arena had two indentations alongside the wall where sugar and water were provided during experiments and a central hole through which a brood dummy protruded. The brood dummy consisted of an aluminium cone (diameter 1 cm) to mimic the size and shape of natural bumblebee brood. The base of the brood dummy was attached to a water-filled aluminium heating plate which was connected to a water bath. A thermocouple ran along the longitudinal axis of the dummy, ending in the tip. In this way, the temperature of the brood dummy could be precisely measured and controlled.
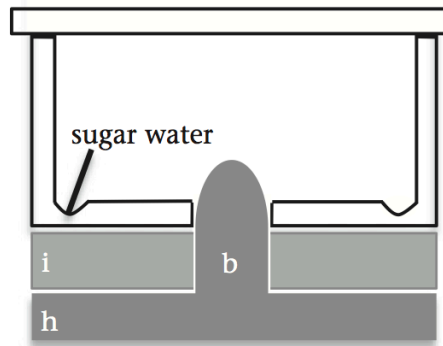
Figure 3.1: The test arena set-up: (b) brood dummy; (h) heating plate; (i) insulation (Westhus et al., 2013).
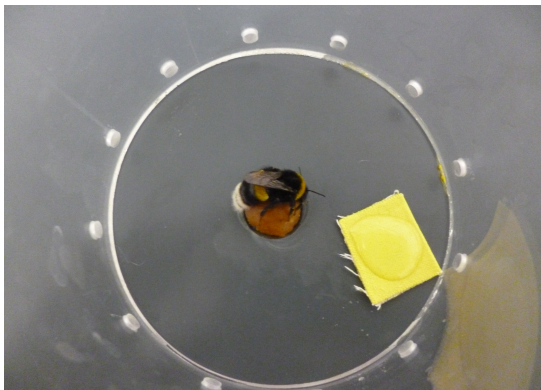
(a) A bumblebee worker in the test arena   (b) A bumblebee worker on the brood dummy

Figure 3.2: Bumblebee workers during experiments (photos by Lasse Kling).

Two aluminium heating plates were placed directly next to each other and covered with one insulating Styrofoam board, through which two brood dummies protruded. Each plate was connected to a separate water bath and was used to heat one brood dummy. One water bath (and the associated brood dummy) was set to 32°C and the other was set to either 42°C or 47°C, depending on the experiment, as in general, bumblebee workers do not actively respond to the demand of the fanning task when the temperature of brood dummy falls below 42°C (Anja Weidenmüller, personal communication). Each brood

dummy was covered with fresh Parafilm and a thin layer of canopy wax that had been removed from the mother colony of the tested workers and frozen at -20°C in order to spread the colony odour. The top of the brood dummy was additionally covered with wax that had been taken directly from the brood of the same colony in order to provide the necessary olfactory stimuli. The amount of brood wax used for each brood dummy was controlled according to the amount in brood areas of natural colonies. The thermocouples measuring brood dummy temperature were connected to a recoding device (NI cRIO-9074 and NI 9213, National Instruments, Germany) using a program (*ShortRun*, created with National Instruments LabVIEW^{TM} 2010, Version 10.0.1, by Stefanie Neupert) to record time, temperature and occurrences of fanning behaviour (via a keyboard).

Individual bumblebee workers were positioned onto brood dummies (see Figure 3.2) at either 42°C or 47°C and logged their fanning activities every second over a 30-minute period. 40 workers from three colonies were tested, 20 at 32°C and 42°C, another 20 at 32°C and 47°C. At the beginning of each test, the test arena was offered a 32°C brood dummy, reflecting the optimum brood temperature (Weidenmüller et al., 2002). For each experiment, a single worker was picked up gently by her wings from the brood area of her colony under red light using forceps and placed directly on the brood dummy in the test arena. The test arena was closed with a Plexiglas lid and the worker was left undisturbed for a 10-minute acclimatisation phase. The worker's fanning behaviour was then continuously observed and recorded for 10 minutes. Next, the test arena with the worker was carefully lifted from the brood dummy and placed on the other, adjacent brood dummy, which now protruded centrally into the test arena and had a temperature of either 42°C or 47°C. The fanning behaviour of the worker on this second brood dummy was recorded for another 20 minutes. Sucrose solution was offered ad libitum. At the end of each experiment, the worker was marked and returned to her colony. Test arenas and brood dummies were cleaned and new wax was prepared before the next experiment.

3.2.2 The Effect of Individual Efficiency

The second set of experiments was conducted by Lena Kreuzer and Anja Weidenmüller in the Neurobiology Lab at the University of Konstanz, Germany. Young colonies of the bumblebee *Bombus terrestris* were purchased from a commercial breeder (Biofa AG, Münsingen, Germany) and housed in wooden-nest boxes at 22°C room temperature, 45% RH and under a 12h:12h light:dark cycle. These wooden boxes ($26 \times 40 \times 10$ cm^3) were divided into two chambers (nest and food) with four ventilation holes (diameter 3.6 cm), covered by wire mesh. The bumblebees were fed daily with apiInvert in the food chamber and every other day with pollen directly in the nest chamber. Bumblebee workers were used only once and each was marked with a tag glued to the thorax by shellack after use.

The set-up of the test arena in these experiments is similar to that used for the experiments described in Section 3.2.1. In addition, the temperature of the aluminium pin (brood dummy) was controlled by a PID regulator, rather than by the water bath. A

voltage generator (Voltcraft VLP-2403) provided constant voltage power of 7.5 V and in the middle of the aluminium pin there was a peltier element. A change of temperature could be immediately generated by an electrical current or could result in a change of an electrical current. In this way workers' fanning could cause a decrease in temperature of brood dummies, which was simultaneously controlled by the electrical generator. The temperature change triggered by workers' fanning was limited within 2°C from the pre-set temperature to guarantee that both workers who experienced fanning efficiency and those who did not were exposed to an equal mean temperature over the whole trial. The water bath was set at a constant temperature of 26°C to make sure that the energy loss kept the same through the underside for all trials. The temperature on the top of the aluminium pin was measured via a thermocouple, connected to a recording device (NI cDAQ-9174, National Instruments, Germany) running a program (*BumblebeeState_035*, written with National Instruments LabVIEW^TM 2011, Version 11.0, by Stefanie Neupert) to record time, temperature and occurrences of fanning behaviour (via a keyboard).

Bumblebee workers were tested under two different conditions of efficiency:

(1) Closed loop – brood temperature was kept at a pre-set level without any influence from workers' fanning;

(2) Open loop – workers could decrease brood temperature by their own fanning.

Individual workers were positioned in the test arenas under either closed-loop or open-loop condition and their fanning activities were recorded every milli-second. 43 workers were tested: 23 for the closed loop and 20 for the open loop. At the beginning of each experiment, a single selected worker was carefully removed from her colony using forceps beneath infra-red light and settled in the test arena with a brood dummy at 32°C for a 10-minute acclimatisation phase. Then the brood dummy was set to a sequence of temperatures following 39°C, 44°C, 39°C and 44°C. Each temperature phase lasted for 7 minutes after being adjusted to a stable level (less than 0.05°C fluctuation). Particularly, if the test was designed for the open-loop condition, the switch between different temperature phases was executed under the closed-loop condition and once the temperature reached a stable level, the open-loop condition applied for the 7-minute observation period. ApiInvert was provided during these experiments. At the end of each experiment, the worker was labelled and placed back to her colony. Test arenas and brood dummies were cleaned and new wax was prepared before the next experiment.

3.3   Results and Analysis

We perform survival analysis in addition to traditional analysis for the empirical data from both sets of experiments (see Section 3.2). Traditional analysis does not take account of the influence of time and is only used for comparison with survival analysis.

3.3.1   The Effects of Stimulus and Individual Experience

The experiments were conducted with different *constant* temperatures $T = 42°C$ and $T = 47°C$. There were 32 bumblebee workers who showed fanning behaviour after being positioned on the second brood dummy (14 for $T = 42°C$, 18 for $T = 47°C$). A small number of workers did not fan at all (6 for $T = 42°C$, 2 for $T = 47°C$). The reasons behind may be complicated and are beyond the scope of this research. Our analysis is implicitly conditioned on the 32 workers who fanned at least one second during the last 20 minutes of experiments. Those who did not show any fanning activity during this period are excluded from our analysis.

Traditional Analysis

The total fanning time and the number of uninterrupted fanning periods are measured for each individual worker (see Figure 3.3). The results suggest that there is no significant difference of workers' total fanning time between $T = 42°C$ and $T = 47°C$ (Mann-Whitney U-test: $P = 0.246$; illustrated in Figure 3.3(a)). Similarly, the number of workers' uninterrupted fanning periods does not appear to significantly differ between $T = 42°C$ and $T = 47°C$ (Mann-Whitney U-test: $P = 0.447$; illustrated in Figure 3.3(b)). Therefore, the magnitude of stimulus, measured as brood temperature, does not have a statistically significant effect on bumblebee workers' engagement in the fanning task. At each time-point, the proportion of fanning workers is also measured (see Figure 3.4), which tends to oscillate and appears not to monotonically change with time. Thus workers' experience of previous task performance does not appear to significantly influence later decision-making on allocation of the fanning task if we discard the initial transient period ($t < 200$).

(a) Total fanning time

(b) Total uninterrupted fanning periods
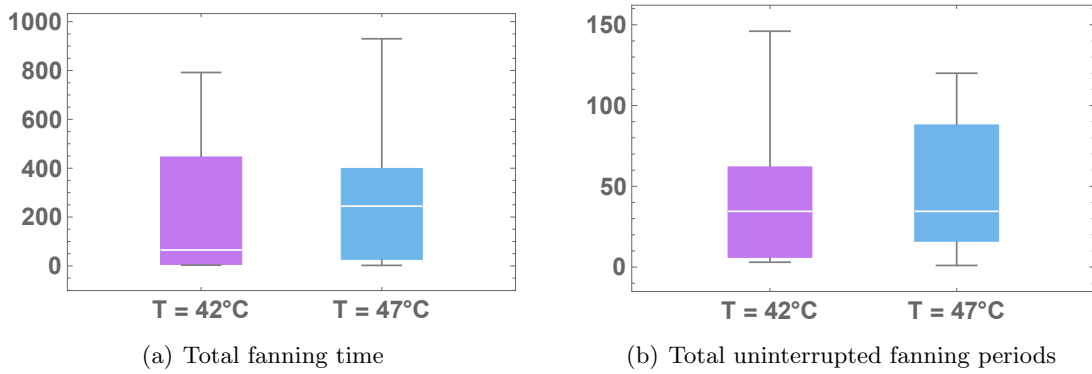
Figure 3.3: Box-and-whisker plots of the total fanning time and the number of uninterrupted fanning periods for workers with $T = 42°C$ and $T = 47°C$.

Survival Analysis

For an individual worker i in an experiment at temperature T, we denote the start time of the j-th uninterrupted fanning period of worker i by $s_{i,j}$ and the corresponding end time by $q_{i,j}$. Two sequences $S_i = \cup_j s_{i,j}$ and $Q_i = \cup_j q_{i,j}$ are recorded, representing the start and

Fanning Proportion
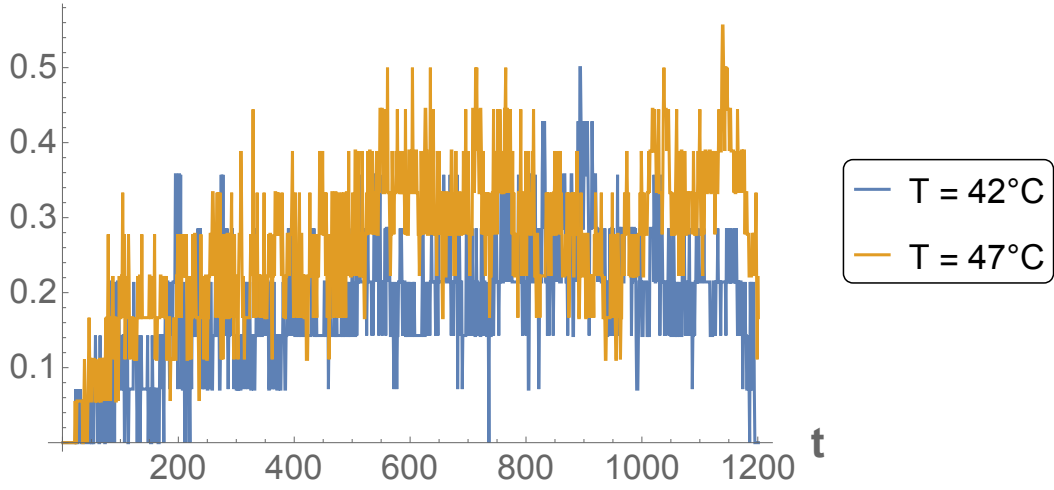
Figure 3.4: Proportion of fanning workers over time t.

end time-points of all uninterrupted fanning periods with one-second resolution. Then for worker i at temperature T, the interval of the subsequent uninterrupted fanning periods between position j and position $j+1$ is $\sigma_{i,j}^{T} = s_{i,j+1} - q_{i,j}$ and the duration of the j-th un-interrupted fanning period is $\omega_{i,j}^{T} = q_{i,j} - s_{i,j}$. The inter-fanning interval $\sigma_{i,j}^{T}$ and fanning duration $\omega_{i,j}^{T}$ for all i, j, T contain the event and covariate data used to analyse the rate functions $\lambda(t)$ and $\mu(t)$ respectively, where $\lambda(t)$ represents the instantaneous probability per unit time of a worker to start fanning given that she is not fanning at time t, and $\mu(t)$ represents the instantaneous probability per unit time to stop fanning given that she is fanning at time t. Any inter-fanning interval or fanning duration continuing at the end of experimental period is right-censored. To understand the effects of stimulus and individual experience, we need to know whether the brood temperature T and the position j in the sequence of uninterrupted fanning periods have a significant impact on $\lambda(t)$ and $\mu(t)$.

We use the Cox proportional hazards model (Kleinbaum and Klein, 2012; Liu, 2012) to analyse the effect of covariates on the rate function $\lambda(t)$. This model assumes that the rate function can be expressed as

$$\lambda(t) = \lambda_0(t)e^{\sum_i \beta_i X_i}$$

where X_i is a time-independent covariate with coefficient β_i and $\lambda_0(t)$ is the baseline rate function that depends on time t. The coefficient β_i quantifies the effect of covariate X_i on $\lambda(t)$. To check the value of β_i, we need two sets of event data between which only the values of X_i are different, without specifying the baseline rate function $\lambda_0(t)$. Here the proportional hazards assumption, which means that any covariate X_i does not depend on time t for all i, has to be verified. For each covariate X_i, the outcome of the Cox model can be reflected by a P-value, which represents the statistical significance of X_i, or by a relative risk or hazard ratio, which gives e^{β_i}.

We take the multiset of inter-fanning intervals $\Sigma = \cup_{i,j}\sigma_{i,j}^{T}$ as event data, and the temperature T and the position j in the sequence of uninterrupted fanning periods as covariates. To test the proportional hazards assumption for a covariate, we verify whether the Schoenfeld residuals (Schoenfeld, 1982), the difference between the observed covariate values and the expected value, are correlated with the event times, represented by the ranks of inter-fanning intervals. Here the proportional hazards assumption applies to both covariates T and j, because the Schoenfeld residuals of T are hardly correlated with the ranks of inter-fanning intervals (Pearson's correlation coefficient: 0.016; illustrated in Figure 3.5(a)), and so are the Schoenfeld residuals of j (Pearson's correlation coefficient: 0.035; illustrated in Figure 3.5(b)).

(a) Brood temperature

(b) Individual experience

Figure 3.5: The Schoenfeld residuals over the ranks of inter-fanning intervals for different covariates (with a linear regression line).

The results of the Cox model show that the brood temperature T does not significantly influence $\lambda(t)$ (Wald statistic: $P = 0.496$; illustrated in Figure 3.6(a)), nor does the position j in the sequence of uninterrupted fanning periods (illustrated in Figure 3.6(b)). Particularly for the covariate j, although the Wald statistic ($P = 4.12\mathrm{e}{-11}$) implies that the influence of j may be significant, the relative risk resulting from the regression is 1.005 (with confidence interval $[1.004\ldots1.007]$), which approximates to 1 and indicates extremely small influence of j.

Similarly, for the rate function $\mu(t)$, we use the Cox model with input of the multiset of fanning durations $\Omega = \cup_{i,j}\omega_{i,j}^{T}$ as event data and T, j as covariates. Here the proportional hazards assumption applies to both T and j as well since the Schoenfeld residuals are barely correlated with the ranks of fanning durations for either T (Pearson's correlation coefficient: -0.039; illustrated in Figure 3.7(a)) or j (Pearson's correlation coefficient: 0.081; illustrated in Figure 3.7(b)). The results of the Cox model indicate that $\mu(t)$ is not significantly affected by the brood temperature T (Wald statistic: $P = 0.838$; Figure 3.8(a)) or by the position j in the sequence of uninterrupted fanning periods (illustrated in Figure 3.8(b)). Although the Wald statistic ($P = 0.019$) suggests that j may have a significant effect, the relative risk resulting from the regression is 0.998 (with confidence interval $[0.997\ldots1.000]$), which approximates to 1 and indicates that j almost has no influence on $\mu(t)$.

(a) Brood temperature   (b) Individual experience
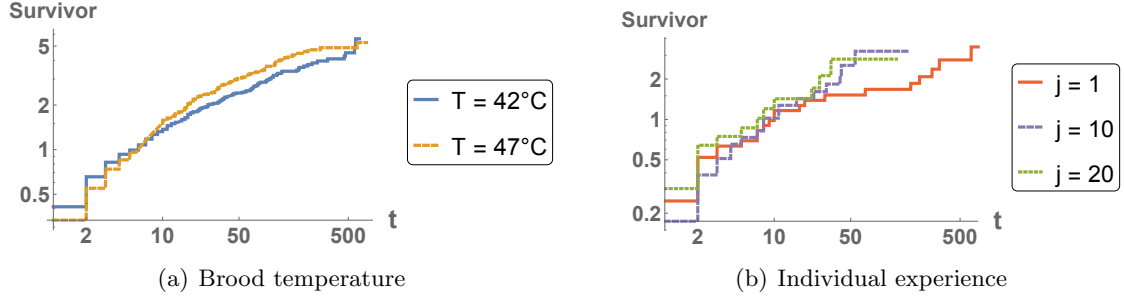
Figure 3.6: Log(-log) survival curves of inter-fanning intervals stratified by different co-variates in log-scaled time t: (a) The inter-fanning intervals are partitioned into two strata based on the brood temperature T; (b) The inter-fanning intervals are partitioned into multiple strata based on the position j in the sequence of uninterrupted fanning periods and we only give three representatives here, as the curves of the remaining strata look similar and are omitted for clarity. For both (a) and (b), the effects of the covariates T, j respectively seem insignificant, otherwise the difference of survival curves between strata would be much more obvious.

(a) Brood temperature   (b) Individual experience
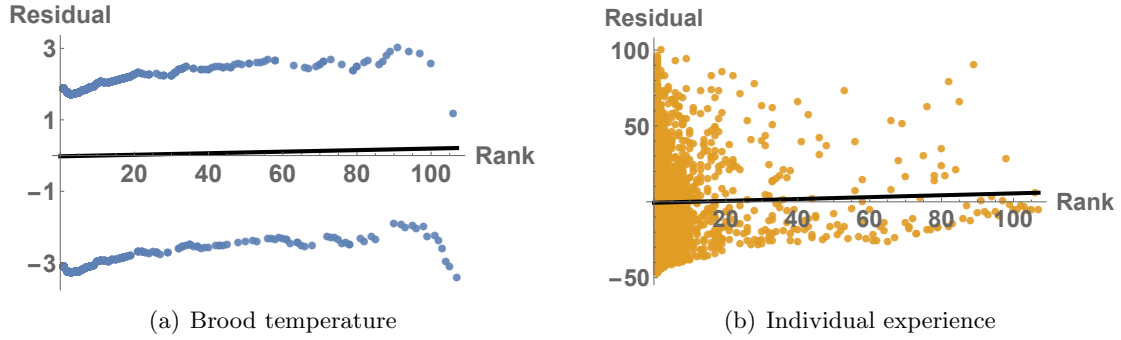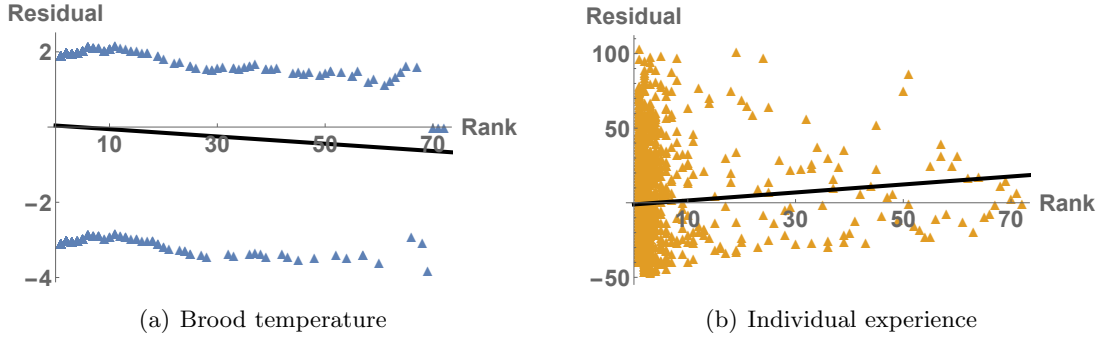
Figure 3.7: The Schoenfeld residuals over the ranks of fanning durations for different covariates (with a linear regression line).

(a) Brood temperature   (b) Individual experience
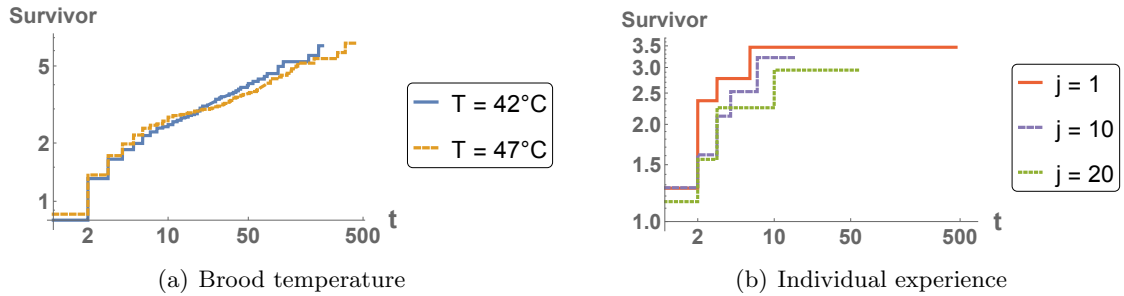
Figure 3.8: Log(-log) survival curves of fanning durations stratified by different covariates in log-scaled time t: (a) The fanning durations are partitioned into two strata based on the brood temperature T; (b) The fanning durations are partitioned into multiple strata based on the position j in the sequence of uninterrupted fanning periods and we only give three representatives here, as the curves of the remaining strata look similar and are omitted for clarity. For both (a) and (b), the effects of the covariates T, j seem insignificant, otherwise the difference of survival curves between strata would be much more obvious.

Overall, based on the results of the Cox proportional hazards models, neither the brood temperature T nor the position j in the sequence of uninterrupted fanning periods appears to have a significant influence on the allocation of workers to the task of fanning, which is quantified by the rate functions $\lambda(t)$ and $\mu(t)$. The conclusion of survival analysis is consistent with that of traditional analysis, suggesting that neither stimulus intensity nor individual experience significantly influences workers' task allocation. At this point, we would like to ask what factors may have a strong effect on workers' decision-making in task selection on the moment-to-moment timescale. To answer this question, we analyse the empirical data from the set of experiments for individual efficiency in Section 3.3.2.

3.3.2 The Effect of Individual Efficiency

The second set of experiments was conducted with different conditions on whether workers' fanning can decrease brood temperature (open loop) or not (closed loop). There were 41 bumblebee workers who performed the fanning task after the 10-minute acclimatisation phase: 19 for the open loop and 22 for the closed loop. Each experiment was set with a sequence of temperatures (39°C – 44°C – 39°C – 44°C), which was designed for other experimental purposes that are out of the scope of this study. Here we stratify the data of workers' fanning activities based on the pre-set temperature (39°C or 44°C) to exclude the potential effect of the temperature, as the temperature at 39°C may be a level below which individual fanning behaviour is actively stimulated (Anja Weidenmüller, personal communication).

Each bumblebee worker experienced the same temperature for two stable periods separated by a period of different temperature. However, we do not consider the impact of the position in the sequence of phases with the same temperatures on the fanning data, due to the possible influence of transitions between two different temperatures. For this set of experiments, we analyse the effect of individual efficiency (open loop or closed loop) on the rate functions $\lambda(t)$ and $\mu(t)$. A few workers did not show fanning behaviour at all or kept fanning all the time during a 7-minute experimental phase, rather than frequently starting or stopping the fanning task. The relevant data-points are excluded from our analysis as the reasons behind may be complicated and are beyond the scope of this research.

Traditional Analysis

The total fanning time (see Figure 3.9) and the number of uninterrupted fanning periods (see Figure 3.10) are measured for individual workers in each phase at both temperatures. There is no statistically significant difference of workers' total fanning time between the open-loop and closed-loop conditions in Phase 1 of 39°C (Mann-Whitney U-test: $P = 0.151$; illustrated in Figure 3.9(a)), Phase 2 of 39°C (Mann-Whitney U-test: $P = 0.877$; illustrated in Figure 3.9(b)), Phase 1 of 44°C (Mann-Whitney U-test: $P = 0.275$; illustrated in Figure 3.9(c)) or Phase 2 of 44°C (Mann-Whitney U-test:

$P = 0.479$; illustrated in Figure 3.9(d)). Similarly, the difference of number of work-
ers' uninterrupted fanning periods between the open-loop and closed-loop conditions does
not appear to be significant in Phase 1 of 39°C (Mann-Whitney U-test: $P = 0.251$; illus-
trated in Figure 3.10(a)), Phase 2 of 39°C (Mann-Whitney U-test: $P = 0.979$; illustrated
in Figure 3.10(b)), Phase 1 of 44°C (Mann-Whitney U-test: $P = 0.962$; illustrated in
Figure 3.10(c)) or Phase 2 of 44°C (Mann-Whitney U-test: $P = 0.101$; illustrated in
Figure 3.10(d)). Therefore, individual efficiency does not appear to have a significant
influence on bumblebee workers' allocation of the fanning task.

(a) 39°C, Phase 1   (b) 39°C, Phase 2

(c) 44°C, Phase 1   (d) 44°C, Phase 2
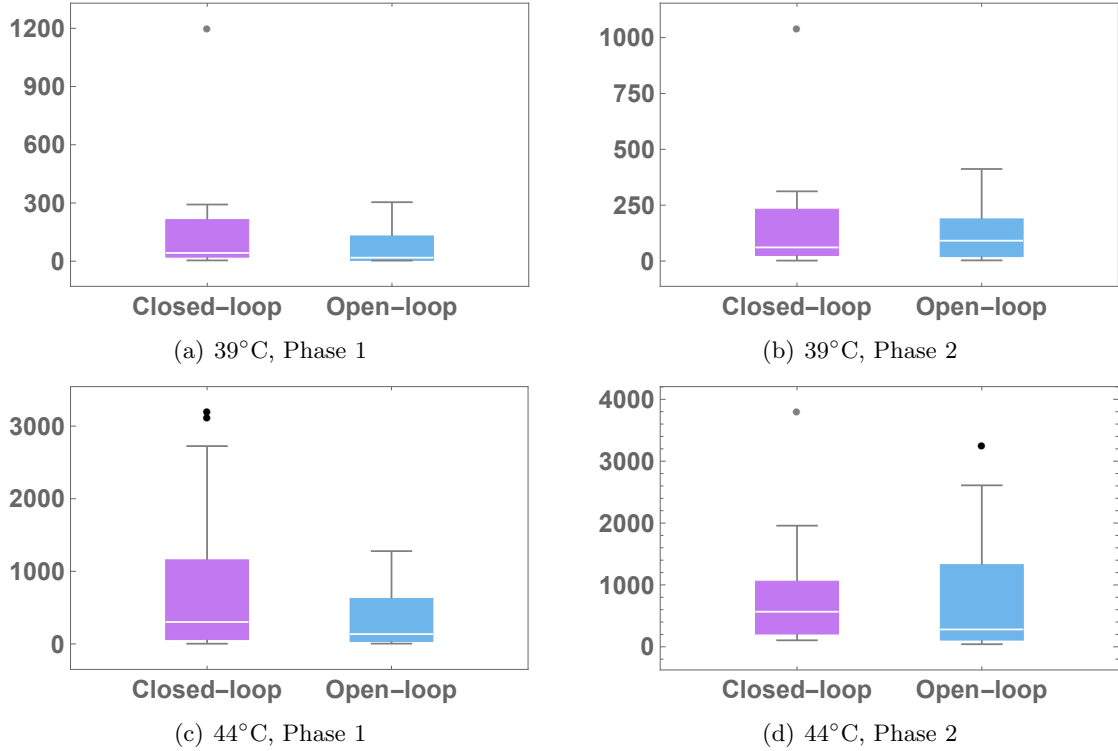
Figure 3.9: Box-and-whisker plots of the total fanning time for workers under the open-
loop and closed-loop conditions. Workers are categorised by the pre-set temperature and
the experimental phase.

Survival Analysis

Similar to Section 3.3.1, for all individual workers, we compute the inter-fanning intervals
Σ and fanning durations Ω, which are regarded as event data for the rate functions $\lambda(t)$
and $\mu(t)$ respectively. Any inter-fanning interval or fanning duration continuing at the
end of a temperature phase is right-censored. We put each event data-point for both Σ
and Ω into strata based on the associated temperature (39°C or 44°C) and consider the
efficiency condition E (open-loop or closed-loop) as the only covariate. Then we apply the
Cox proportional hazards model to both Σ and Ω in addition to graphical approaches.

For the rate of task engaging $\lambda(t)$, as illustrated in Figure 3.11, the survival curve un-
der the closed loop seems to be slightly above that under the open loop for both 39°C and

(a) 39°C, Phase 1

(b) 39°C, Phase 2

(c) 44°C, Phase 1

(d) 44°C, Phase 2
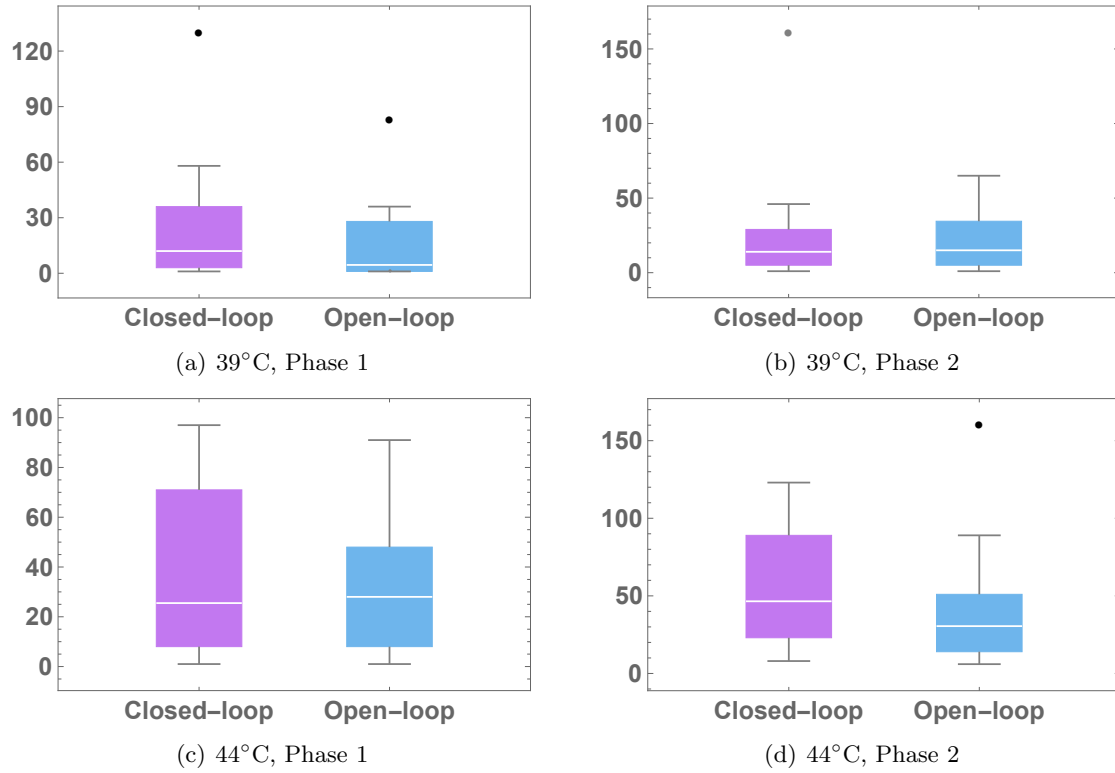
Figure 3.10: Box-and-whisker plots of the number of uninterrupted fanning periods for workers under the open-loop and closed-loop conditions. Workers are categorised by the pre-set temperature and the experimental phase.

44°C. To test this observation, we then use the Cox proportional hazards model. Here the proportional hazards assumption applies to E as the Schoenfeld residuals of E are barely correlated with the ranks of inter-fanning intervals for both 39°C (Pearson's correlation coefficient: 0.025; illustrated in Figure 3.12(a)) and 44°C (Pearson's correlation coefficient: 0.028; illustrated in Figure 3.12(b)). The results of the Cox model show that individual efficiency, regarded as the decrease of brood temperature, has a significant negative influence on $\lambda(t)$ for both 39°C (Wald statistic: $P = 0.009$; Relative risk: 0.850; Confidence interval $[0.753 \ldots 0.960]$) and 44°C (Wald statistic: $P = 8.12\mathrm{e}{-5}$; Relative risk: 0.862; Confidence interval $[0.801 \ldots 0.928]$).

(a) 39°C

(b) 44°C
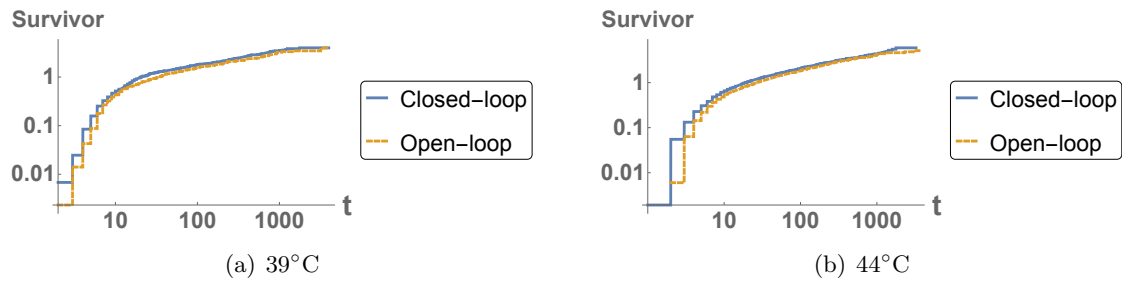
Figure 3.11: Log(-log) survival curves of inter-fanning intervals stratified by the covariate of individual efficiency in log-scaled time t for different temperatures.

For the rate of task quitting $\mu(t)$, a cursory visual inspection of Figure 3.13 suggests that

(a) 39°C   (b) 44°C
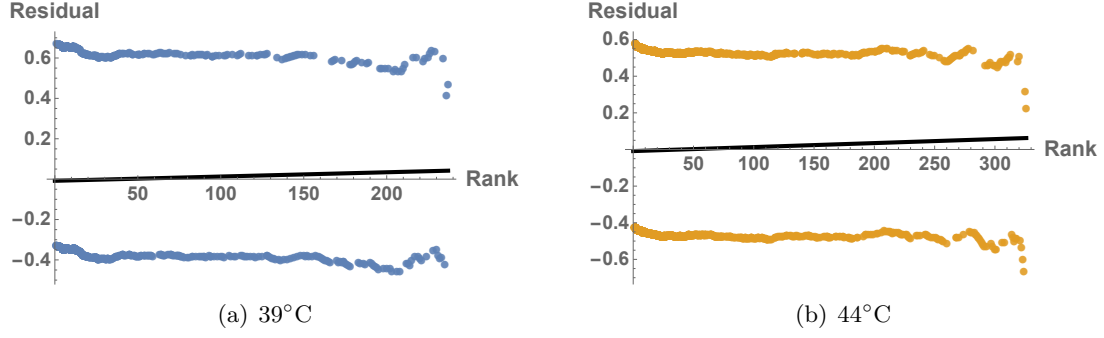
Figure 3.12: The Schoenfeld residuals of the covariate of individual efficiency over the ranks of inter-fanning intervals for different temperatures (with a linear regression line).

the effect of individual efficiency E seems not significant, as there is no obvious difference of survival curves between the open loop and closed loop for both temperatures. Then we use the Cox proportional hazards model to test this observation. The proportional hazards assumption applies to E as the Schoenfeld residuals of E are hardly correlated with the ranks of fanning durations for 39°C (Pearson's correlation coefficient: 0.014; illustrated in Figure 3.14(a)) and for 44°C (Pearson's correlation coefficient: 0.008; illustrated in Figure 3.14(b)). The results of the Cox model indicate that individual efficiency E has a significant positive effect on $\mu(t)$ for 39°C (Wald statistic: $P = 0.004$; Relative risk: 1.191; Confidence interval $[1.056 \ldots 1.343]$) and 44°C (Wald statistic: $P = 0.040$; Relative risk: 1.080; Confidence interval $[1.004 \ldots 1.162]$), which is, however, not revealed by the coarse-grained survival curves.

(a) 39°C   (b) 44°C
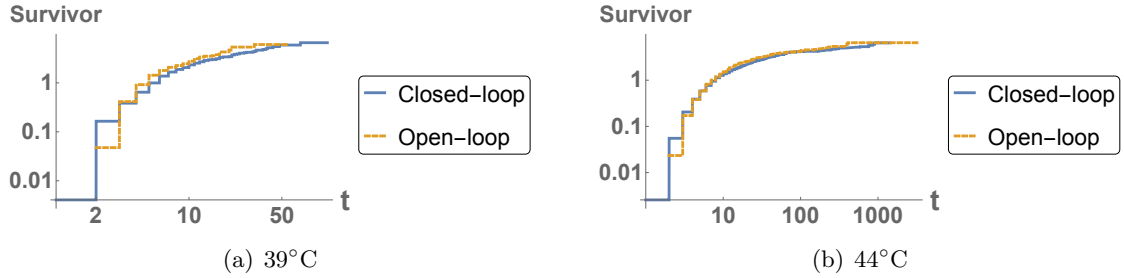
Figure 3.13: Log(-log) survival curves of fanning durations stratified by the covariate of individual efficiency in log-scaled time t for different temperatures.

Overall, according to the results of the Cox proportional hazards models for both $\lambda(t)$ and $\mu(t)$, individual efficiency appears to have a significant negative influence on the allocation of workers to the task of fanning. Survival analysis specifies the processes of task allocation at the level of unit time whereas traditional analysis only describes the aggregate behaviours over the whole experimental period. As demonstrated by our analysis for the effect of individual efficiency, we can use survival analysis to identify the results that cannot be detected by traditional analysis as the latter ignores the temporal influence. Then we build an agent-based model to capture the effect of time and facilitate a fine-grained view of task allocation in social insects.

(a) 39°C

(b) 44°C
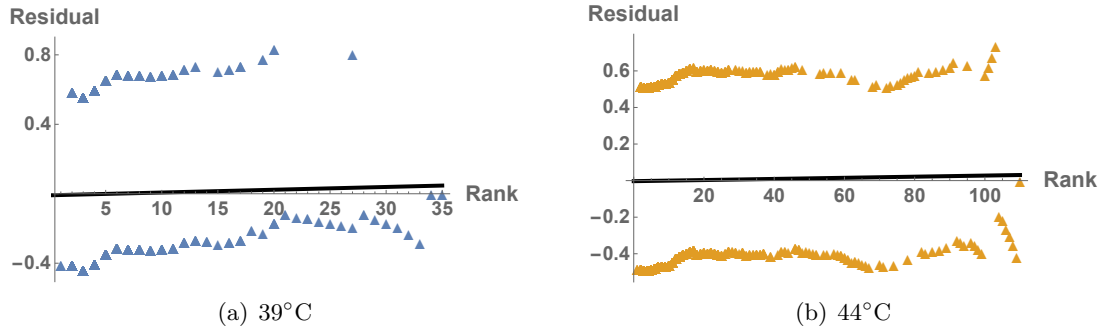
Figure 3.14: The Schoenfeld residuals of the covariate of individual efficiency over the ranks of fanning durations for different temperatures (with a linear regression line).

3.4 A Time-Resolved Model of Task Allocation

Whether or not to engage in a task, such as fanning, is a decision that is repeatedly assessed by each individual worker. The experimental observations show that even at a constant temperature, workers assess the brood temperature several times before a decision to fan is made. Such an assessment can be indicated by their antennation of the brood dummy (Anja Weidenmüller, personal communication). Typically, workers tend to fan for a short while before they stop and re-assess the situation (see Figure 3.15). The process of how workers assess or gather the information necessary to decide whether to engage in tasks implies the importance of the timing patterns for task allocation. However, this is not handled in the established response-threshold models (Bonabeau et al., 1996; Theraulaz et al., 1998; Jeanson et al., 2007; Lichocki et al., 2012).
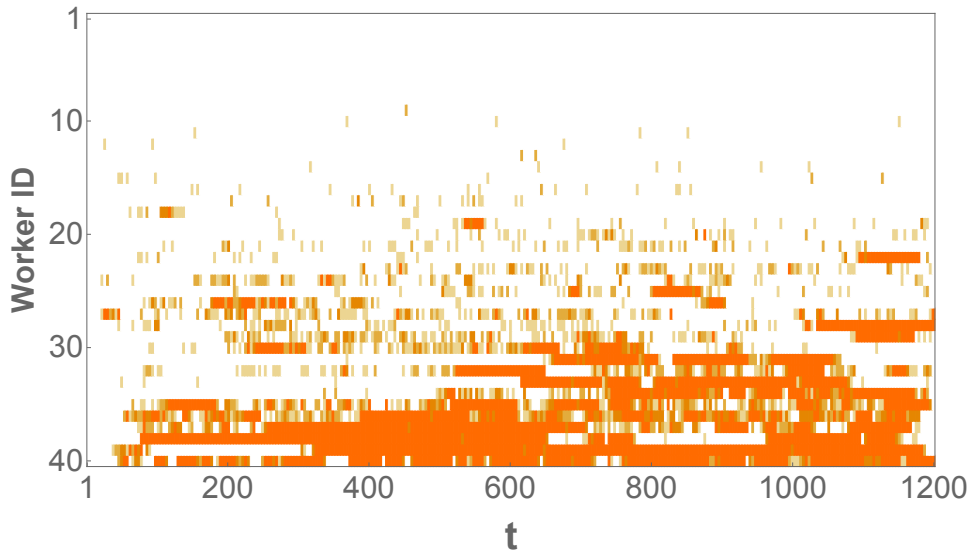
Figure 3.15: Fanning activities of bumblebee workers at a constant brood temperature (either 42°C or 47°C) over time t. Workers are sorted in ascending order from top to bottom by their total fanning time. Each row represents a single worker. Each column represents the time interval of one second. Fanning activity is visible through the gradient of shading. Darker areas indicate more active fanning periods. White boxes represent inactivity or any activity other than fanning.

To describe these complex timing patterns, we propose an explicitly time-resolved model of task allocation. This model gives the underlying processes of how workers select and perform tasks at the individual level. As illustrated in Figure 3.16, allocating an individual worker i to a task is a three-step process that involves polling or encountering task-related stimuli. When worker i is ready to take up a new task, she first decides which task k to execute according to the task-polling probabilities $p_1, p_2, ..., p_k$. She then tests whether the level of the task-related stimulus s_k is above her threshold θ_k: If so, i starts to engage in task k; Otherwise, i repeats the polling process mentioned above. Once engaged in task k, worker i executes k for a certain amount of time after which she enters a refractory resting period. Stopping executing task k and Stopping resting after performing k are two stochastic events with the rate functions $\mu_k(t)$ and $\lambda_k(t)$ respectively. After the completion of one such task cycle, worker i is immediately free to engage in another task or to resume the same task as before.
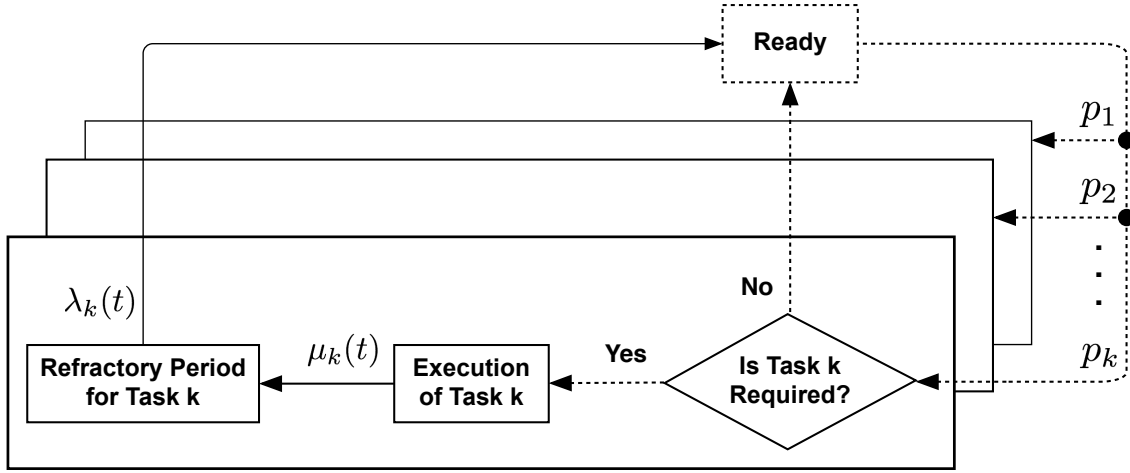
Figure 3.16: The time-resolved model of task allocation for a single worker and multiple tasks.

Unfortunately, it is exceedingly difficult to simultaneously set up and precisely control multiple tasks in biological experiments. As a first step, most experiments set up and observe only a single task. For workers in the experiments used for our analysis, in between the performance of the controlled task, there may exist other behaviours, such as self-grooming and wandering, as well as possibly unobservable ones. To verify the time-resolved model with the empirical data, we thus reduce the conceptual model (illustrated in Figure 3.16) to only distinguish between a known, observable task A and a task collection B, a set of alternative behaviours that potentially exist during experiments (see Figure 3.17). We simulate this model (see Algorithm 1) based on the Gillespie next reaction method (Gillespie, 1976, 1977), a Monte Carlo algorithm statistically faithful for simulating dynamic systems in which stochastic effects are involved in individual actions and coordinations. Based on our simulations, we verify our time-resolved model with the empirical data at the group level and in turn explain the empirical data at the individual level by the time-resolved model.
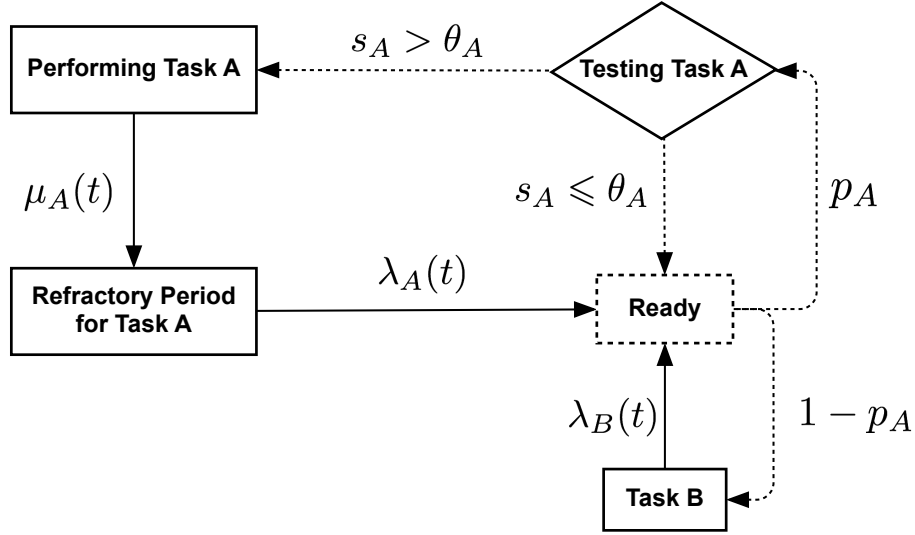
Figure 3.17: The simplified time-resolved model of task allocation for a single worker and for a single observable task. Task A refers to the fanning task controlled in experiments. Task $B = \{B_1, ..., B_{k-1}\}$ is a lumped meta-task that represents a mixture of possible behaviours.

Algorithm 1 Simulation algorithm for the time-resolved model of task allocation

---

1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
3:     $state(w_i) \leftarrow B$
4:     $rate(w_i) \leftarrow \lambda_B$
5:     (* initialise worker w_i *)
6: **end for**
7: **while** $t < t_{end}$ **do**
8:     $H \leftarrow \sum_i rate(w_i)$ (* $i = 1, 2, ..., N$ *)
9:     $\Delta t \sim Exponential(H)$ (* draw next event interval *)
10:     $t \leftarrow t + \Delta t$
11:     select w_i according to probabilities $p(w_i) = rate(w_i)/H$
12:     **if** $state(w_i) = A$ **then**
13:         $state(w_i) \leftarrow R$
14:         $rate(wi) \leftarrow \lambda_A$
15:         (* w_i starts her refractory period after performing Task A *)
16:     **else**
17:         $r \leftarrow random(0, 1)$
18:         **if** $r < p_A(w_i) \wedge s_A > \theta_A$ **then**
19:             $state(w_i) \leftarrow A$
20:             $rate(w_i) \leftarrow \mu_A$
21:             (* w_i starts to perform Task A *)
22:         **else**
23:             $state(w_i) \leftarrow B$
24:             $rate(w_i) \leftarrow \lambda_B$
25:             (* w_i starts to be engaged in Task B *)
26:         **end if**
27:     **end if**
28: **end while**

For workers' behaviours at the group level, we first compare the distribution of lumped inter-fanning intervals Σ from the empirical data (see Section 3.2.1) with our simulation result, as well as the fitted exponential and Weibull distributions (see Figure 3.18). We find that the result of our simulation can be better mapped to the empirical data (Kullback-Leibler divergence: 0.074) than either the exponential distribution (Kullback-Leibler divergence: 6.367) or the Weibull distribution (Kullback-Leibler divergence: 1.794). The inter-fanning intervals are clearly not drawn from an exponential distribution, as would be expected from the fixed-threshold model (Bonabeau et al., 1996), or from a decreasing Weibull distribution, which would be predicted by the threshold-reinforcement model (Theraulaz et al., 1998). Instead, the distribution of inter-fanning intervals is power-law-like as is also recognisable from the straight negative slope in the log-log scaled histogram (Akaike, 1974).[2]
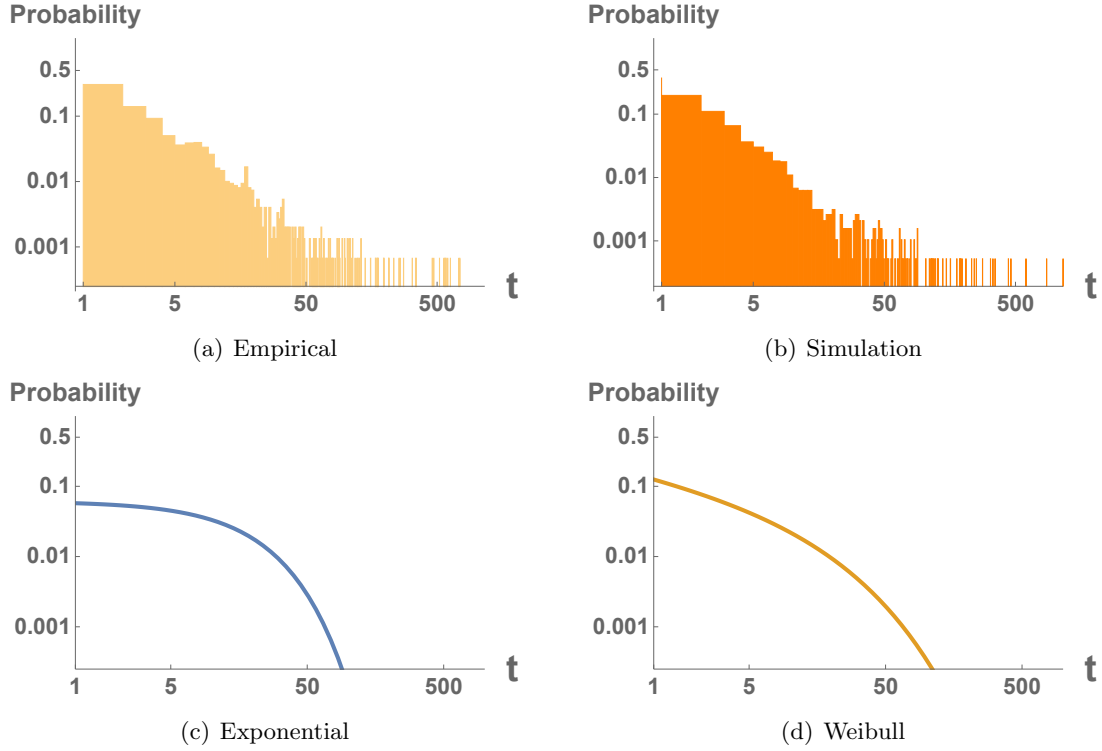
Figure 3.18: Distributions of lumped inter-fanning intervals of workers in a log-log scale: (a) Empirical data; (b) Simulation results ($N = 25$, $t_{end} = 1200$, $\theta_A = 32$, $s_A = 42$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0, 1.25)$, $\lambda_B \sim \mathbf{U}(0, 1)$, $p_A \sim \mathbf{U}(0, 1)$); (c) The probability density function of event times from the exponential distribution fitted to the empirical data with rate $\lambda = 0.061$; (d) The probability density function of event times from the Weibull distribution fitted to the empirical data with shape $\alpha = 0.602$ and scale $\beta = 8.659$. Both fitted exponential and Weibull distributions are obtained by the maximum likelihood estimation (implemented by *EstimatedDistribution* in Mathematica, Version 11.1, Wolfram Research Inc.). Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

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[2]Here for simplicity, we refer to this as power-law-like as it is usually difficult to reliably identify *discrete* empirical data as an exact power-law (Clauset et al., 2009).

Similarly, we then compare the distribution of lumped fanning durations Ω from the empirical data (see Section 3.2.1) with our simulation result, as well as the fitted exponential and Weibull distributions (see Figure 3.19). The result of our simulation is the closest to the empirical data (Kullback-Leibler divergence: 0.066) compared with the exponential distribution (Kullback-Leibler divergence: 8.526) or the Weibull distribution (Kullback-Leibler divergence: 2.673). Here the distribution of fanning durations is also power-law-like rather than exponential (Akaike, 1974), which indicates that the timing patterns cannot be ignored and that the oversimplified assumption about the task-quitting process in the fixed-threshold and threshold-reinforcement models (Bonabeau et al., 1996; Theraulaz et al., 1998) does not apply here.
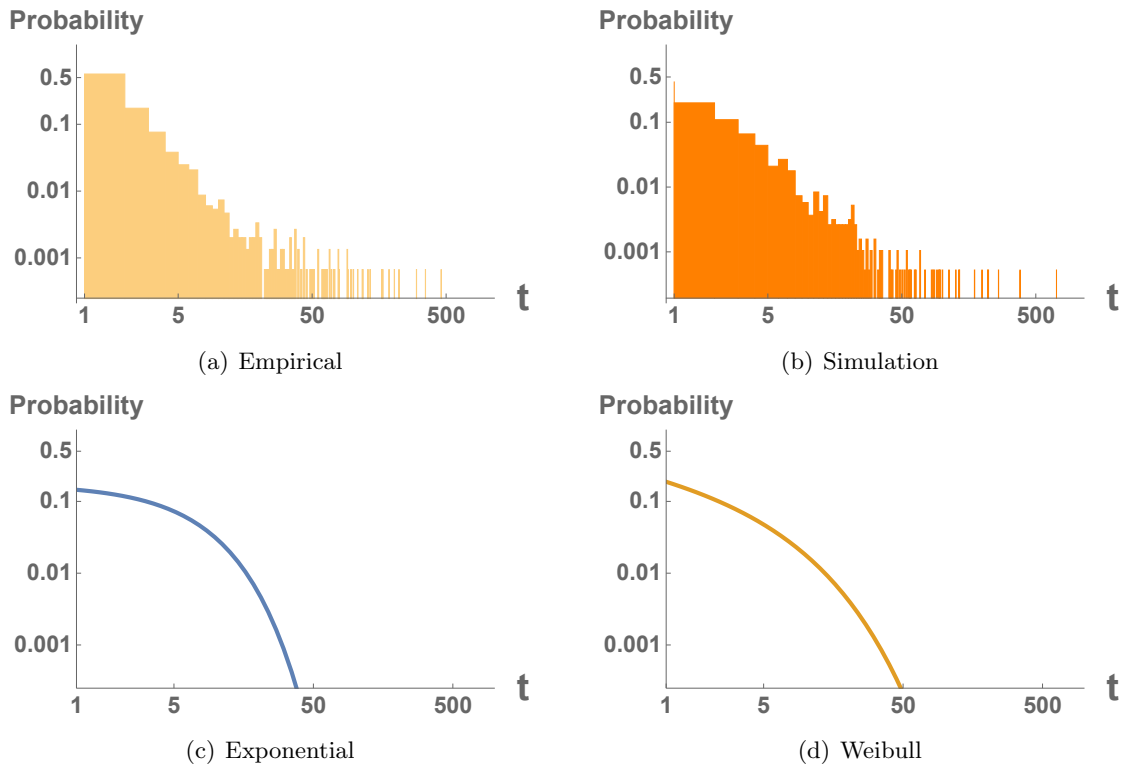
Figure 3.19: Distributions of lumped fanning durations of workers in a log-log scale: (a) Empirical data; (b) Simulation results ($N = 25$, $t_{end} = 1200$, $\theta_A = 32$, $s_A = 42$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0, 1.25)$, $\lambda_B \sim \mathbf{U}(0, 1)$, $p_A \sim \mathbf{U}(0, 1)$); (c) The probability density function of event times from the exponential distribution fitted to the empirical data with rate $\lambda = 0.172$; (d) The probability density function of event times from the Weibull distribution fitted to the empirical data with shape $\alpha = 0.668$ and scale $\beta = 3.496$. Both fitted exponential and Weibull distributions are obtained by the maximum likelihood estimation (implemented by *EstimatedDistribution* in Mathematica, Version 11.1, Wolfram Research Inc.). Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

Our time-resolved model also can explain the empirical data at the individual level even though there is a large variation in both distributions of inter-fanning intervals and fanning durations across workers in the experiments. Here for the distribution of inter-fanning

intervals, we illustrate two typical cases (see Figure 3.20): Some workers exhibit a power-law-like statistics in their inter-fanning intervals (Figure 3.20(a)) while the distribution of inter-fanning intervals of others resembles an exponential distribution (Figure 3.20(b)).

(a) Power-law-like (Worker 31)   (b) Exponential (Worker 15)

Figure 3.20: Distributions of inter-fanning intervals for two representatives of individual bumblebee workers from the experiments in a log-log scale.

As illustrated in Figure 3.17, the inter-fanning intervals consist of both the refractory periods for Task A and the time on performing Task B, which is assumed to be a mixture of potential behaviours. The ratio between the refractory-A period and the Task-B period depends on the value of p_A. For a worker with large p_A, her inter-fanning intervals almost exclusively contain the refractory period for A and thus follow an exponential distribution with rate $\lambda_A(t)$ (see Figure 3.21(c)). Alternatively, the behaviour of a worker with small p_A are dominated by Task B, which is mixed of Poisson processes with different rates. Therefore, as illustrated in Figure 3.21(a), the inter-fanning intervals of this worker follow a power-law-like distribution, because a mixture of Poisson processes with different rates can generate event intervals from a power-law distribution (Hidalgo R., 2006).

(a) Power-law-like ($p_A = 0.5$)   (b) Intermediate ($p_A = 0.8$)   (c) Exponential ($p_A = 1.0$)
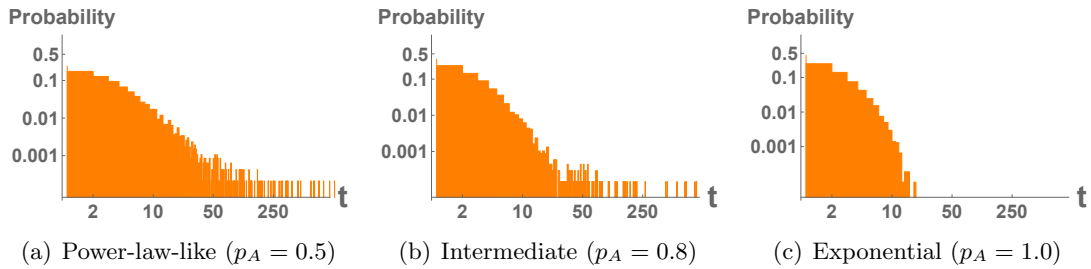
Figure 3.21: Distributions of inter-fanning intervals for three representatives of individual workers from the simulation results in a log-log scale with $N = 1$, $t_{end} = 100000$, $\theta_A = 32$, $s_A = 42$, $\lambda_A = 0.575$, $\mu_A \sim \mathbf{U}(0, 1.25)$, $\lambda_B \sim \mathbf{U}(0, 1)$, p_A varying from 0.5 to 1. Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

Similarly, for the distribution of fanning durations, the empirical data also indicate a large differentiation across workers. As illustrated in Figure 3.22, the distributions of fanning durations for some workers are power-law-like (see Figure 3.22(a)) and for some others are

exponential-like (see Figure 3.22(b)). In our time-resolved model, a worker's fanning durations are determined by the rate $\mu_A(t)$ (see Figure 3.17). The fanning durations of a worker with constant $\mu_A(t)$ follow an exponential distribution (illustrated in Figure 3.23(b)); For a worker with varying $\mu_A(t)$ over a sequence of fanning periods, illustrated in Figure 3.23(a), the distribution of her fanning durations tends to be power-law-like, as a Poisson process with varying rates over a certain period can result in power-law distributed event intervals (Hidalgo R., 2006; Malmgren et al., 2008).

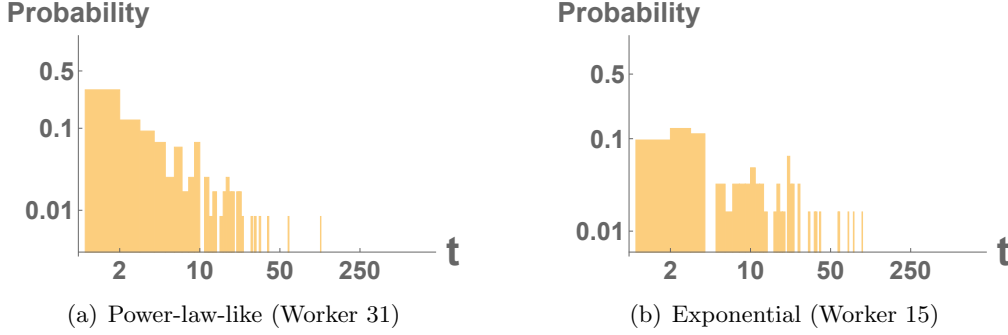(a) Power-law-like (Worker 6)   (b) Exponential-like (Worker 31)
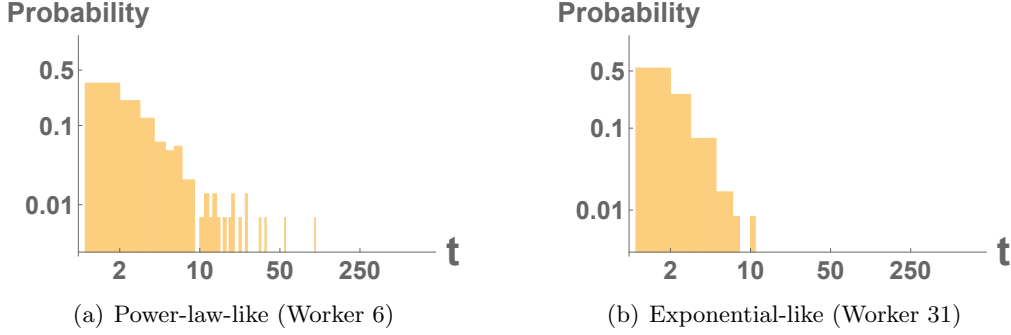
Figure 3.22: Distributions of fanning durations for two representatives of individual bumblebee workers from the experiments in a log-log scale.

(a) Power-law-like ($\mu_A \sim \mathbf{U}(0, 1.25)$)   (b) Exponential ($\mu_A = 0.5$)
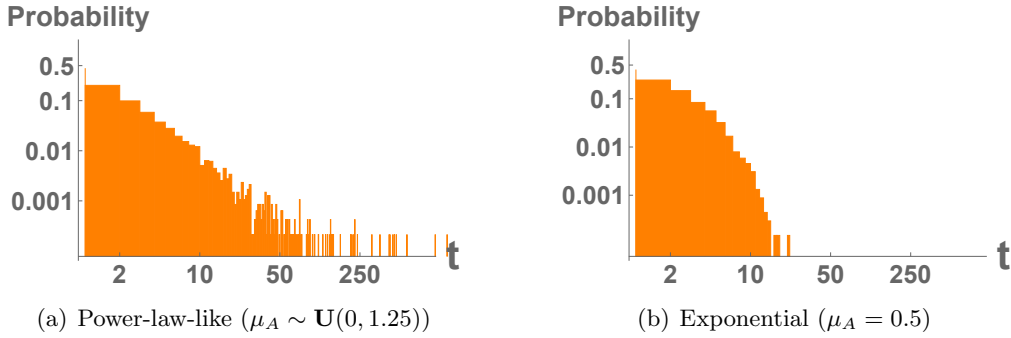
Figure 3.23: Distributions of fanning durations for two representative of individual workers from the simulation results in a log-log scale with $N = 1$, $t_{end} = 100000$, $\theta_A = 32$, $s_A = 42$, $\lambda_A = 0.575$, $\lambda_B \sim \mathbf{U}(0, 1)$, $p_A = 0.5$. Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

Here we do not directly compare our model with the set of experimental data for individual efficiency (see Section 3.2.2), as this set of experiments is also designed for other purposes which are out of scope of this study.

3.5   Discussion

This research focuses on the allocation of the fanning task for individual bumblebee workers at the moment-to-moment timescale. On this timescale, the influence of time on workers' activities cannot be ignored (see Section 3.4). Compared with the existing models in the literature, one of the core features of our time-resolved model is explicitly characterising

workers' ongoing behaviours in task allocation as time-dependent stochastic processes. For a particular task such as fanning, there are two stochastic processes involved: (1) A worker is about to engage in the task with some rate if she is in a refractory period; (2) A worker is about to stop with another rate if she is performing the task. Both processes can be measured in empirical studies by the time period until the target event occurs, such as inter-fanning intervals and fanning durations.

At the group level, our time-resolved model is substantially better fitted with the empirical data for both task-engaging and task-quitting processes than the fixed-threshold model or the threshold-reinforcement model (see Section 3.4). Most response-threshold models assume that all workers in a colony simultaneously encounter, start and stop performing tasks at discrete time-steps (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012; Cornejo et al., 2014). The temporal dynamics of task engagement across workers are oversimplified in these models, which, therefore, cannot match the empirical data used in this study. The response-threshold models of task allocation were implemented in a time-sequential manner assuming asynchronous actions among workers in a few studies (Page Jr. and Mitchell, 1998; Jeanson et al., 2007), but unfortunately, this has barely been followed up by other studies.

One of the core interests in current research on task allocation is to investigate what are the primary sources that cause task specialisation or differentiation in workers' task preference (Gordon, 2016). Most studies regard inherent inter-individual variation in response to similar environmental conditions as the main cause (Jeanson and Weidenmüller, 2014) while it is also suggested that task specialisation can emerge from a colony of identical workers with self-reinforcement by individual experience (Theraulaz et al., 1998) or spatial variation of localised task demands (Tofts and Franks, 1992; Johnson, 2010). This study suggests that variation in workers' task selection may also result from the time delays among workers in perceiving and assessing task-related stimuli (Pacala et al., 1996).

The empirical data suggest that workers' behavioural patterns of task engagement tend to follow power-law-like distributions, with sequences of bursty periods intervened by much longer events (see Section 3.4). Power laws are widespread in natural and social systems and have been investigated across various disciplines (Newman, 2005). There are a variety of possible mechanisms proposed to explain how power-law distributions may arise in different contexts (Barabási, 2005; Newman, 2005). One of the most popular candidates is the priority-based queuing mechanism originally proposed for human activities (Barabási, 2005), which has also been applied to animal behaviours (Reynolds, 2011; Wearmouth et al., 2014). It shows that when an individual chooses among multiple tasks based on the parameter of some perceived priority, the waiting times of the tasks in the queue maintained by the individual can follow a power-law distribution (Barabási, 2005). One of the key components that cause the power-law output in the queuing model is the variation of

task-associated priorities, which are randomly generated and determine the corresponding waiting times. This is similar to the mechanism on how a power-law-like distribution can be generated in our time-resolved model of task allocation even though the latter does not include any queuing process. Motivated by the ubiquity of power laws, it will be interesting to see how the mechanisms in different systems may be related and connected to each other in future research.

For an individual worker, our time-resolved model assumes that the process of engaging in a task is separate from the process of checking the task-associated stimulus. This corresponds to the empirical evidence that response probability and response threshold are independent parameters in thermoregulation of bumblebees (Jeanson and Weidenmüller, 2014; Weidenmüller, 2004; Westhus et al., 2013; Duong and Dornhaus, 2012) and honeybees (Cook and Breed, 2013). However, in most models, the response probability is assumed to correlate with the response threshold (Robinson, 1992; Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002). The reason behind this inconsistency may be that these response-threshold models ignore the process of how workers encounter or sample task-related stimuli. As a result, it is difficult to verify these models with quantitative experimental data.

Our survival analysis assumes the rate, which is a function of time and represents an instantaneous probability per unit time, as the main characteristics for the processes of workers' task allocation. Most empirical studies in the literature measure the response probability in traditional approaches as the proportion of trials in which a worker shows the target behaviour (Weidenmüller, 2004; Duong and Dornhaus, 2012; Ravary et al., 2007) or the proportion of workers that show the target behaviour for a given condition (O'Donnell and Foster, 2001; Cook and Breed, 2013; Westhus et al., 2013). However, at least on the moment-to-moment timescale, the results of these experiments may not reflect the exact response probability or likelihood of task engagement, which is an inherent property of individual workers (Duong and Dornhaus, 2012; Weidenmüller, 2004) and can develop over time. The improper measurement of the response probability may be the reason why empirical studies tend to use an additional parameter, response threshold, to characterise the variation in workers' task responsiveness at the individual level. However, workers' response thresholds may be a by-product of their response probabilities as those with large response probabilities in a given time-interval are likely to be observed to respond at low stimulus intensity and thus have small response thresholds (Duong and Dornhaus, 2012).

To the best of our knowledge, the experiments used for our analysis are the first to decouple the effect of time and the effect of stimulus on workers' task allocation. Our analysis indicates that the *absolute* value of stimulus, regarded as brood temperature, does not have a significant effect on workers' fanning engagement on the moment-to-moment timescale.

This result contrasts with most response-threshold models (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012), which predict that the response probability tends to increase with the absolute stimulus intensity. This leads to the question – how the perceived stimulus is assessed by individual workers. Some empirical study suggests that the *rate of temperature increase* has a significant influence on workers' decisions of fanning engagement (Westhus et al., 2013). However, it is difficult to guarantee that the result is caused by the rate of temperature increase rather than the elapsed time as the brood temperature is set to increase with time during experiments (Westhus et al., 2013).

Our time-resolved model adopts the simplest possible assumption that workers start performing the task if the perceived brood temperature exceeds a certain threshold value (see Figure 3.17). This deterministic threshold decision-making can be found to correspond with specific neurons in some insect species (Christoph Kleineidam, personal communication) and is fully sufficient for colony homeostasis since a group of workers work as a closed-loop control system (for a detailed discussion, see Section 5.2.1). The main objective here is to cool down the colony. Commencing this task does not require an assessment of the absolute value of temperature, the rate of temperature increase or any other complex function. Particularly, the magnitude of temperature can determine the number of workers required in fanning, which is irrelevant from the individual-level decision-making on whether or not to engage.

We show that individual experience, measured as the position in the sequence of uninterrupted fanning periods, does not appear to strongly influence workers' fanning behaviour on the moment-to-moment timescale. This conclusion is in contradiction to the hypothesis drawn from the threshold-reinforcement model (Theraulaz et al., 1998; Gautrais et al., 2002) that the response probability of a worker for a task tends to increase with repeated task performance. The effect of individual experience on how workers respond to task-related stimuli has been mainly studied in theoretical models, with scarce and inconsistent support from empirical evidence (Jeanson and Weidenmüller, 2014). This may be due to difficulties with precise measurement and manipulation of stimulus intensities (Jeanson and Weidenmüller, 2014) or improper identification and analysis of target behaviours (Duong and Dornhaus, 2012; Westhus et al., 2013). Based on our analysis, we find that individual experience hardly affects the process of either task engaging or task quitting on the moment-to-moment timescale. Interestingly, this is concluded from the Cox model in which the statistical test suggests that the effect of individual experience is significant whereas the impact coefficient resulting from the regression is extremely small (see Section 3.3.1). The reason behind may be that the timescale is too short for individual experience to take effect and further research may need to explore whether our conclusion is valid for a longer timescale.

Our analysis points out that individual efficiency, measured as temperature decrease

caused by workers' task performance, has a significant negative influence on their fanning behaviour on the moment-to-moment timescale (see Section 3.3.2). However, it is generally expected that workers are more likely to perform the tasks from which they have received rewards (Oster and Wilson, 1978; Plowright and Plowright, 1988), with support of empirical evidence in ant foraging (Tripet and Nonacs, 2004; Ravary et al., 2007). The reason behind this contradiction may lie in the difference of task types. Workers in a colony tend to reduce the stimulus to the lowest possible level for a maximising task such as foraging, while for a homeostatic task such as fanning, it is adequate to maintain the stimulus within a narrow range (Duarte et al., 2011). In the experiments used for our analysis, bumblebee workers who have received rewards from the fanning task tend to engage less in fanning and may be more likely to perform other tasks that are more urgent or demanding, such as foraging. Therefore, the negative effect of individual efficiency on workers' engagement in homeostatic tasks may be part of the feedback rules in task allocation and contribute to the overall colony-level homeostasis and performance across different tasks.

Based on the empirical data, our time-resolved model of task allocation describes the refractory periods as time intervals between task execution for individual workers. Refractory periods have been quantified by recent studies as the cost of task switching – a potential disadvantage of non-specialisation (Jeanson and Lachaud, 2015; Leighton et al., 2017). Frequent task quitting that connects task execution to a refractory period can be an important principle to balance flexibility and efficiency in task allocation (Johnson, 2002, 2009). Based on this principle, workers can adapt to changes of task demands by adjusting their activity levels while remaining specialised rather than by switching between tasks (Jeanson et al., 2007). Inter-individual variation in the rates of task engaging from the refractory period may account for elitism and specialised inactivity (Pinter-Wollman et al., 2012; Charbonneau and Dornhaus, 2015b,a). It may need to be further explored how the functional roles of refractory periods contribute to the organisation of social insects.

3.6 Conclusion

In this chapter, we took account of the factor of time and explored mechanisms of task allocation in bumblebees on the moment-to-moment timescale. We performed survival analysis for the data from two sets of experiments in which the task-associated stimulus can be precisely measured and controlled. Surprisingly, we find that neither stimulus intensity nor individual experience appears to have a strong effect on workers' task engagement. This contrasts with most established empirical studies (O'Donnell and Foster, 2001; Weidenmüller et al., 2002; Weidenmüller, 2004; Westhus et al., 2013) and most theoretical models (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012), which do not account for the influence of time. Our results also indicate that individual efficiency has a negative influence on workers' task engagement, in contrast to the general expectation that workers' perception of rewards from performing a task tends to encourage them to engage in the task more

strongly. Then we built a time-resolved model of task allocation which was verified with the empirical data, suggesting that the influence of time cannot be ignored. Overall, our exploration of temporal dynamics facilitate a fine-grained analysis of empirical data and consequently improves our understanding of the underlying mechanisms of task allocation.

Chapter 4

Social Behaviour –
Game-Theoretical Models

4.1 Introduction

The majority of studies of mechanisms of task allocation in social insects focus on the influence of internal factors (reviewed in Chapter 2). In contrast, the effect of social interaction on task allocation is less well-studied (see Section 2.4.3), even though the factor of social interaction is widely investigated in other behaviours such as foraging and colony migration (Grüter and Leadbeater, 2014). Recent studies focus on the idea that task allocation can be regarded as a set of distributed processes driven by the interactions between individuals and their environmental contexts (Gordon, 2016). However, communication between individual workers in an insect colony is complex. Due to difficulties in experimental control and measurement of social behaviours, theoretical approaches have the potential to guide empirical work and play a leading role in exploring the influence of social interaction on task allocation.

To study the impact of social interaction on task allocation from a self-organisational perspective, we propose a framework based on game theory. Game theory is the mathematical toolbox for interdependent decision-making and has been widely applied in biological problems (Izquierdo et al., 2012; McGill and Brown, 2007; Dugatkin and Reeve, 1998; Broom and Rychtář, 2013). Here a *game* formalises an interaction among a group of individuals, called *players* (Nowak and Sigmund, 2004; Izquierdo et al., 2012). Players take actions based on their behavioural characteristics, called *strategies* (Nowak and Sigmund, 2004; Izquierdo et al., 2012; Broom and Rychtář, 2013). How successful a player's strategy is represented by a *payoff*, which depends on the strategy of this player and those of others who interact with the player (Nowak and Sigmund, 2004; Izquierdo et al., 2012; Broom and Rychtář, 2013).

Classical game theory was initially developed as a branch of game theory for analysing how rational players should behave to maximise their payoffs (von Neumann and Morgenstern, 1944; Izquierdo et al., 2012). In such a game, each player does not know exactly

others' strategies but assumes other players are rational (Broom and Rychtář, 2013). The outcome of the game is the so-called *Nash equilibrium*, one of the fundamental concepts in game theory, at which no player could improve her expected payoff by only changing her own strategy (Izquierdo et al., 2012). Classical game theory is a static approach which only focuses on possible equilibria without specifying how steady states are reached, which leads to a limited applicability (Izquierdo et al., 2012; Broom and Rychtář, 2013).

Evolutionary game theory is a branch of game theory used to study the dynamics of population exposed to evolutionary pressures (Gintis, 2009; Izquierdo et al., 2012). In general, the evolutionary dynamics include the processes of selection (with replication) and mutation (Izquierdo et al., 2012). Players' payoffs in evolutionary game theory can translate into Darwinian fitness, which determine how the frequencies of strategies in the population vary over time (Nowak and Sigmund, 2004; Izquierdo et al., 2012). Particularly, adaptive dynamics, a subset of evolutionary game theory, has been developed and is applied increasingly to understand the long-term consequences of small mutations with the key feature of linking population dynamics to evolutionary dynamics (Brännström et al., 2013; McGill and Brown, 2007; Nowak and Sigmund, 2004; Broom and Rychtář, 2013).

From a perspective of abstract modelling, the selection-mutation process in adaptive dynamics can be understood and re-interpreted as an imitation-innovation process on learning timescales (Izquierdo et al., 2012): Both selection and imitation are essentially a frequency-dependent process of strategy copying; Mutation and innovation describe slight perturbation which occurs in population with low chance. This leads to the scope of learning game theory, another branch of game theory, which studies the dynamics of a group of individuals who adjust their strategies by learning over time (Izquierdo et al., 2012). In this study, we focus on learning game theory, as task allocation in social insects occurs on worker-life timescales. Typically in learning game theory, the mechanism that determines how individual strategies develop over time is not limited to the imitation-innovation process but can be diverse, depending on the specific ecological contexts involved.

Game theory was used by an early study (Wahl, 2002) to investigate the evolutionary dynamics of specialisation in the context of division of labour for co-viruses. The models in this study demonstrate how individual strategies, simplified as generalists, specialists or parasites, can evolve. However, these models do not capture enough ecological details for exploring individual lifetime dynamics in social insects. A recent study by Kanakia et al. (2016) applied a game-theoretical approach to study task allocation in swarm robotic systems. This study focuses on how the stimulus-response dynamics can be implemented in an engineering system of simple agents without direct communication. As a result, it ignores the influence of social interaction between individuals, which is the key concern here.

In this chapter, we use learning game theory to explore how social interactions between

self-organised workers lead to particular behavioural patterns of task allocation, which refer to specialisation (see Section 1.1). We first develop a simple game of task allocation in Section 4.2. Based on this task-allocation game, we build three models integrated with other assumptions that determine the dynamics of workers' strategies over time: social learning (in Section 4.3), individual reinforcement (in Section 4.4) and task recruitment (in Section 4.5). Each of these models indicates a mechanistic process for which some evidence may exist in real scenarios. The model integrated with social learning assumes that workers have a relatively complex learning ability and can be analysed by the framework of adaptive dynamics. However, the assumptions made in this model about individual cognitive ability need to be empirically tested, even though recent studies show that insect workers can achieve seemingly complex social learning (Hunt and Chittka, 2015; Alem et al., 2016). Alternatively, the other two models do not assume complex learning ability. The outcomes of all three models are investigated by agent-based simulations with different environmental contexts.

4.2 A Task-Allocation Game

We assume that workers in a colony need to perform two types of tasks (A and B): Task A represents a homeostatic task, such as thermoregulation to maintain nest temperature within certain bounds; Task B refers to a maximising task, such as foraging to support the energy cost of the colony. Both tasks have to be properly carried out for the survival of the colony. For example, poor maintenance of nest temperature can slow down the development of the brood and some brood may not survive if there is a shortage of food intake.

Workers are assumed to interact with each other in a small group of size n, due to their physical or spatial limitations. Empirical studies suggest that individual task preference can be determined by an inherent response probability (Duong and Dornhaus, 2012; Jeanson et al., 2005; Gordon, 2010). Accordingly, for a worker i, her task preference is represented by a strategy $x_i \in [0,1]$, which indicates the probability that she selects Task A; Conversely, the probability for worker i to perform Task B is $1 - x_i$. In each time-period, x_i can also be regarded as the proportion of effort that worker i puts in Task A on average and the average proportion of effort that she spends on Task B is then $1 - x_i$.

Therefore, based on her and other workers' strategies in the game, worker i receives her payoff

$$\Pi_i(X) = B(X) - C(x_i)$$

where $X = \{x_j | j = 1, 2, ..., n\}$, $B(X)$ and $C(x_i)$ are the benefit and cost for worker i respectively. In the game, workers' payoffs are the key component which can be regarded as their perception of rewards and penalties of task engagement influenced by social interactions with others. Here the benefit $B(X)$ is shared by all workers $j = 1, 2, ..., n$ in the game and the cost $C(x_i)$ only applies to individual worker i.

The overall benefit $B(X)$ is assumed as

$$B(X) = B^A(X) \cdot B^B(X)$$

where $B^A(X)$, $B^B(X)$ are the benefits of Task A, Task B respectively. Here $B^A(X)$ is considered as a discount of $B^B(X)$, which reflects, for instance, how much food is collected (Task B) given that the brood temperature is well regulated (Task A). In order to achieve a large $B(X)$, the workforce needs to be properly balanced between both tasks. As a homeostatic task, Task A needs to be controlled at a certain level. Under performing or over performing Task A can reduce $B^A(X)$. We use a simple way to model

$$B^A(X) = -\frac{4}{n^2} \cdot (\sum_{j=1}^{n} x_j)^2 + \frac{4}{n} \cdot \sum_{j=1}^{n} x_j.$$

Here $B^A(X)$ is assumed to achieve the maximum value, which is normalised between 0 and 1, when half of the workforce in the game is engaged in Task A and to be 0 when none or all of workers in the game are engaged (illustrated in Figure 4.1(a)). As Task B is a maximising task, which implies, for example, the more food is collected, the more brood can survive, $B^B(X)$ is simply assumed to be linear:

$$B^B(X) = \frac{1}{n} \cdot b \left(\sum_{j=1}^{n} (1 - x_j) \right)$$

where b is the benefit of Task B per unit cost of Task B (illustrated in Figure 4.1(b)), which can represent the quality of food resources, for example.

(a) Task A ($n = 10$)   (b) Task B ($n = 10$, $b = 20$)
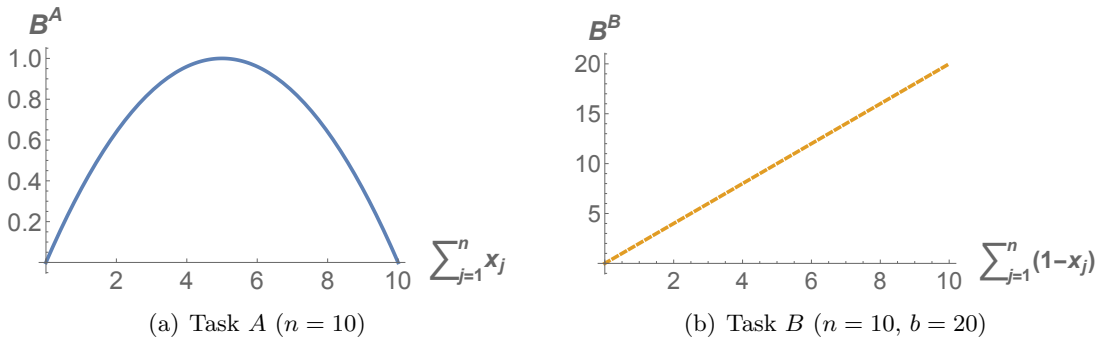
Figure 4.1: An example of the benefit functions for Task A and Task B.

The overall cost $C(x_i)$ is simply given by

$$C(x_i) = C^A(x_i) + C^B(x_i)$$

where $C^A(x_i)$, $C^B(x_i)$ are the costs of Task A, Task B respectively. Here we assume the cost of a homeostatic task to be linear in individual effort (illustrated in Figure 4.2(a)) and thus define

$$C^A(x_i) = r \cdot x_i$$

where r is the cost of Task A per unit cost of Task B, which can indicate how costly Task B (foraging) is, given that the cost of Task A (a maintenance task) is relatively small and stable in comparison with Task B. We assume that $C^B(x_i)$ is marginally decreasing with the effort in Task B, indicating some possible scenarios in which foragers initially need to spend more effort exploring their neighbourhood and once they become familiar with the surrounding areas of food resources, the cost for them tend to be less than the initial stage (illustrated in Figure 4.2(b)). As a result, we simply assume

$$C^B(x_i) = -(1 - x_i)^2 + 2(1 - x_i).$$

Here the cost of Task B for a worker who engage fully in Task B per time-period is assumed to be 1 unit.

(a) Task A ($r = 1$) (b) Task B
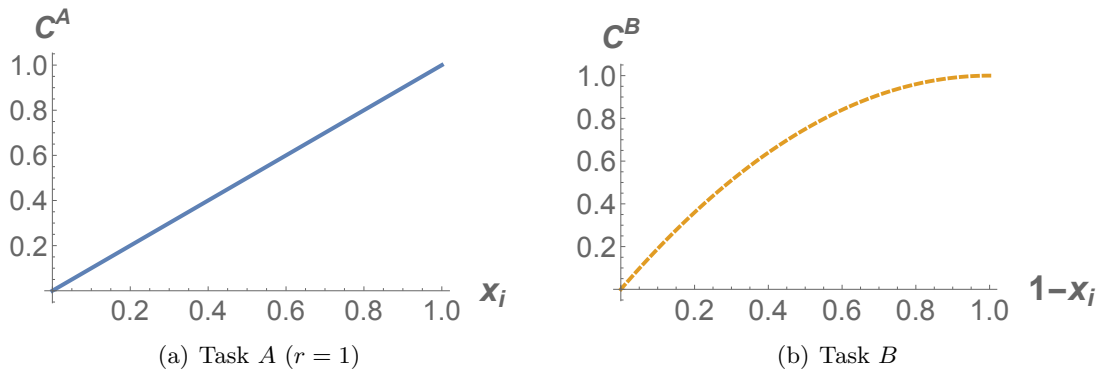
Figure 4.2: An example of the cost functions for Task A and Task B.

To simulate this task-allocation game, we set up a colony of size $N \gg n$ with a range of environmental conditions represented by b and r. The strategy of each worker in the colony is initialised as 0.5, indicating that there is no intrinsic inter-individual differentiation of strategies among workers.

4.3 Social Learning

Based on the framework described in Section 4.2, we build a model of task allocation integrated with social learning. Here social learning refers to the process that a worker can estimate and learn another worker's strategy by direct communication. In this model, each worker is assumed to behave as follows:

 (i) Evaluate her payoff based on her and others' strategies in the game;

 (ii) Select a worker with randomness in proportion to the associated payoffs across all workers and copy her strategy;

 (iii) Innovate her strategy slightly with a small chance and then continue with Step (i).

The detailed algorithm for the simulations of this model is given by Algorithm 2.

Algorithm 2 Simulation algorithm for the model with social learning

---
1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
3:     $x_i \leftarrow 0.5$ (* initialise the strategy of w_i *)
4: **end for**
5: uniformly select and partition workers in the colony into multiple games of size n
6: **while** $t < t_{end}$ **do**
7:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
8:         $\Pi_i \leftarrow B(X) - C(x_i)$ (* w_i evaluates her payoff in the game g of workers with strategies $X = \{x_j | w_j \in g\}$ *)
9:     **end for**
10:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
11:         select w_k randomly according to probabilities $p(w_k) = e^{\alpha \Pi_k} / \sum_k e^{\alpha \Pi_k}$
12:         (* $k = 1, 2, ..., N$ *)
13:         $x_i \leftarrow x_k$
14:         (* w_i selects a worker w_k and copies her strategy *)
15:     **end for**
16:     $m \sim Binomial(N, \beta)$
17:     select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
18:     **for** worker $w_i \in M$ **do**
19:         $x'' \sim Normal(x_i, \gamma)$
20:         $x_i \leftarrow x''$
21:         (* w_i innovates her strategy *)
22:     **end for**
23: **end while**

The results of our simulations for social learning are illustrated in Figure 4.3. Here the behavioural patterns of task allocation at the colony level are divided into being inviable, strong specialisation and weak specialisation:

- Inviable – The average payoff of workers in a colony is not positive, indicating imbalanced allocation of workforce between Task A and Task B;

- Strong specialisation – The workforce of a colony splits into different groups each of which tends to focus only on one task;

- Weak specialisation – All workers in a colony adopt similar strategies.

In practice, the region diagram in Figure 4.3 is obtained through the results at the steady state shown in Figure A.1. Those colonies with the non-positive mean of workers' payoffs are classified under being inviable (according to Figure A.1(a)). The other colonies are tentatively classified under strong specialisation if the standard deviation of workers' strategies exceeds a certain level (set as 0.2 here) or weak specialisation otherwise (based on Figure A.1(b)). However, a large standard deviation of workers' strategies cannot guarantee strong specialisation, as a colony with a wide span of workers' strategies may belong to weak specialisation and correspond to a large standard deviation as well. To capture the span of workers' strategies, we verify the above temporary region classification by the

Shannon entropy

$$H = -\sum_{i=1}^{N} P(x_i) \ln \left(P(x_i) \right)$$

where $P(x)$ is the probability mass function for workers' strategies in the colony. As shown in Figure A.1(c), the entropies of workers' strategies in colonies with large standard deviation are smaller than those with small standard deviation, which in turn confirms the above temporary region classification.
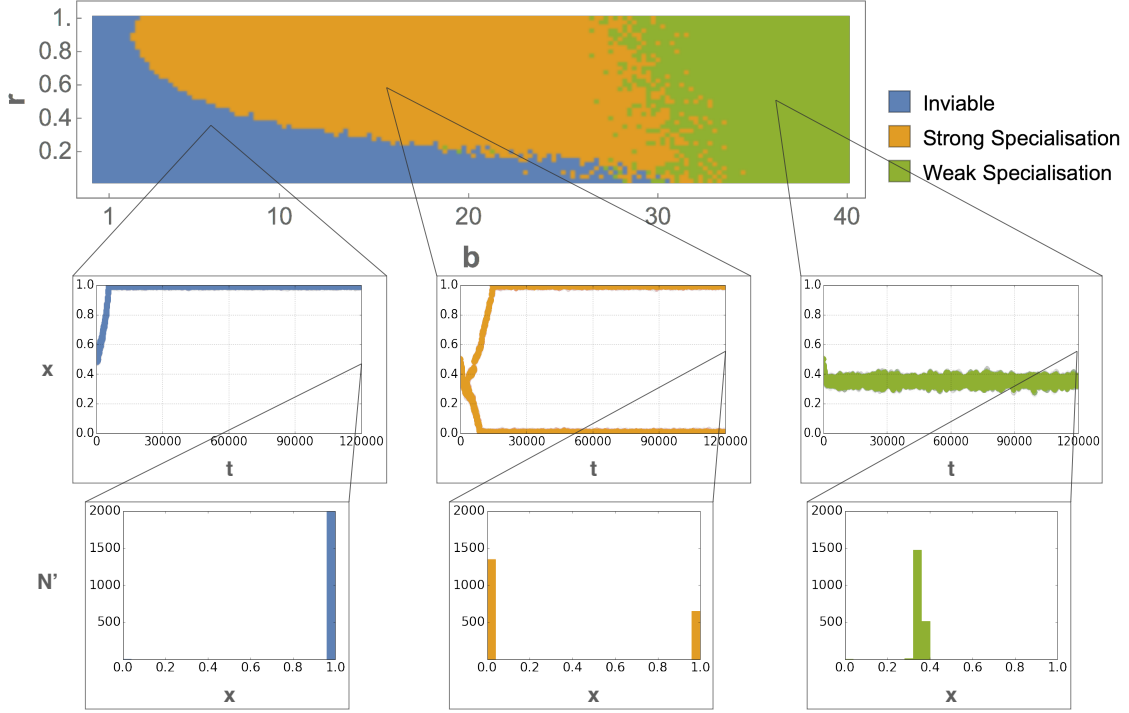
Figure 4.3: Behavioural patterns of the model with social learning. The upper region diagram describes the patterns of task allocation of colonies based on the model with social learning in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). The middle line of inset figures show three typical cases of how workers' strategies x in a colony develop over time t: being inviable ($b = 5, r = 0.4$), strong specialisation ($b = 10, r = 1$) and weak specialisation ($b = 35, r = 0.2$), followed by three lower inset histograms, each of which corresponds to the above colony at the last time-period, where N' represents the number of workers within a certain range of strategies.

We find that colony-level task specialisation can emerge from the interaction dynamics between workers and their environments alone (see strong specialisation in Figure 4.3). Under a certain range of environmental conditions, colonies initially consist of workers with identical strategies and then separate their workforce into different groups in each of which workers specialise into a single task, which is only influenced by social interactions between workers. One of the core interests in the study of task allocation is to investigate what are the primary sources that can cause variation in workers' task preference (Gordon,

2016). Most studies regard inherent inter-individual differentiation in response to similar environmental conditions as the main cause (Jeanson and Weidenmüller, 2014), while it is shown that task specialisation can emerge from a colony of identical workers with experience-based reinforcement (Theraulaz et al., 1998) or spatial variation of localised task demands (Tofts and Franks, 1992; Johnson, 2010). The results of the model with social learning, which does not involve any inherent inter-individual differentiation, show that an alternative source of variation in task preference can be social interactions between workers.

We also find that different environmental conditions (characterised by b and r) can cause obvious variation of behavioural patterns of task allocation, even though the underlying mechanisms are the same. As shown in Figure 4.3, strong specialisation tends to emerge in those environments with poor food resources (when b is small). As the quality of food resources in the environment improves (when b is large), workers in a colony are less likely to specialise into tasks and tend to behave with similar strategies. Our task-allocation game (described in Section 4.2) is similar to a continuous Snowdrift game (Doebeli et al., 2004), in which the benefit is shared by all individuals, and the costs tend to be different across individuals, depending on their strategies adopted. Both games can be used to explore features of cooperation and illustrate a principle called "Tragedy of the Commune" (Doebeli et al., 2004). This principle describes that in a group, individuals contribute to and reap a common good and some individuals may make high levels of investment while some invest less or nothing, leading to some steady states that are not always uniform.[1] The results of our model with social learning indicate a new perspective for how task allocation can change with environmental conditions based on the factor of social interaction, as an alternative to the response-threshold models (reviewed in Section 2.3.1).

From a perspective of abstract modelling, the process described by the model with social learning is similar to the evolution of continuous Snowdrift games and can be analysed by the framework of adaptive dynamics. Here we give a mathematical analysis for the model with social learning based on the work by Doebeli et al. (2004). In a game of size n, with $n-1$ type-I workers of strategy x and 1 type-II worker of strategy y ($x, y \in [0,1]$), the growth rate of the type-II worker is

$$f_x(y) = \Pi\Big(y, (n-1)x\Big) - \Pi\Big(x, (n-1)x\Big)$$

where $\Pi\Big(y, (n-1)x\Big)$ is the payoff of the type-II worker in this game and $\Pi\Big(x, (n-1)x\Big)$ is the payoff of a type-I worker in a game with all type-I workers of size n. Thus, the

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[1] "Tragedy of the Commune" is subtly different from what is commonly known as "Tragedy of the Commons" (Hardin, 1968). "Tragedy of the Commons" refers to the case that defection is always the optimal strategy for an individual, which leads to over-exploiting the common resource, while "Tragedy of the Commune" means that a mixed strategy of cooperation and defection is optimal and thus cooperation and defection can stably coexist.

selection gradient is

$$D(x) = \left.\frac{\partial f_x(y)}{\partial y}\right|_{y=x} = \frac{4b}{n}\left(3x^2 - 4x + 1\right) + 2x - r.$$

Then the singular strategy (solution of $D(x^*) = 0$) is

$$x^* = \frac{8b - n \mp \sqrt{16b^2 - 16bn + n^2 + 12bnr}}{12b}.$$

Both strong specialisation and weak specialisation require the condition that there exists such $x^* \in [0, 1]$ that x^* is convergency stable

$$\left.\frac{dD(x)}{dx}\right|_{x=x^*} = \frac{8b}{n}(3x^* - 2) + 2 < 0.$$

In addition to the above condition, strong specialisation emerges if

$$\left.\frac{\partial^2 f_{x^*}(y)}{\partial y^2}\right|_{y=x^*} = \frac{8b}{n^2}(3x^* - 2) + 2 > 0$$

and weak specialisation requires

$$\left.\frac{\partial^2 f_{x^*}(y)}{\partial y^2}\right|_{y=x^*} = \frac{8b}{n^2}(3x^* - 2) + 2 < 0.$$

In other cases such as when x^* is convergency unstable, colonies tend to become inviable based on our payoff function (see Section 4.2), as one task out of the two is abandoned.

The behavioural patterns of task allocation based on the above analysis are illustrated in Figure 4.4, which are similar to those based on the model with social learning in Figure 4.3. Compared to the mathematical analysis, the behavioural patterns of our model involve more scenarios of being inviable, especially when r is small. This can be attributed to the fact that workers' payoffs tend to decrease with the value of r in strongly specialised colonies (see Figure A.1(a), details explained in Section 5.3.1). Therefore, when r is small, the balance of colony workforce allocated between Task A and Task B is fragile and the random effects involved in simulations can break this balance of task allocation, leading to more inviable situations.

4.4 Individual Reinforcement

Based on the framework described in Section 4.2, we build a model of task allocation integrated with individual reinforcement. Here individual reinforcement is achieved by the process that workers assess and improve their strategies by making comparison with their previous strategies in their memories (Izquierdo et al., 2012). In this model, each worker is assumed to behave as follows:

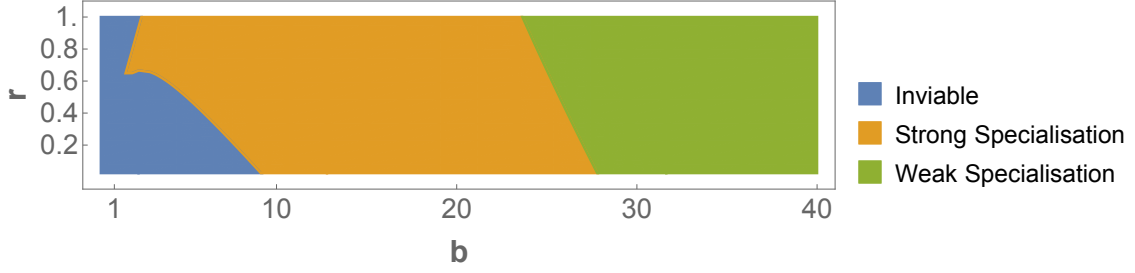(i) Evaluate her payoff based on her and others' strategies in the game;

Figure 4.4: Behavioural patterns predicted by adaptive dynamics. The above diagram describes the patterns of task allocation of colonies based on the mathematical framework of adaptive dynamics in a range of values for parameters b and r (given $n = 10$), which are involved in the functions for payoff evaluation (see Section 4.2).

(ii) Memorise her strategy and associated payoff;

(iii) Innovate her strategy slightly with a small chance;

(iv) Revert to her previous strategy if her current payoff is worse and then continue with Step (i).

The detailed algorithm of the simulations of this model is given by Algorithm 3.

The results of the simulations for individual reinforcement are illustrated in Figure 4.5. Similar to social learning (see Section 4.3), the region diagram in Figure 4.5 is obtained through the results at the steady state shown in Figure A.3, according to the mean payoff (see Figure A.3(a)), the standard deviation (see Figure A.3(b)) and the Shannon entropy (see Figure A.3(c)). Particularly for the model with individual reinforcement, all viable colonies behave with strong specialisation, identified by the large standard deviations of workers' strategies and confirmed by the small variation of the entropies. Our simulations indicate that workers who adjust their strategies based only on their own exploration tend to strongly specialise in different tasks. There is no weak specialisation compared to the model with social learning (see Figure 4.3) as here, no strategy copying is involved between workers.

Experience-based reinforcement is likely to influence workers' decision-making in task selection (Jeanson and Weidenmüller, 2014). Most studies focus on how individual experience is accumulated through encountering task-associated stimuli or engaging in tasks (Jeanson and Weidenmüller, 2014). An individual worker can receive the information about task demands by not only perceiving the task-related stimuli but also through interacting with other workers (Beshers and Fewell, 2001). Empirical evidence suggests that workers' task preference is correlated with their recent interaction history (Gordon and Mehdiabadi, 1999). However, how social experience (experience obtained through social interactions) can modulate workers' task preference is scarcely explored. Our model with individual reinforcement provides one potential underlying mechanism that can explain this question as workers' payoffs may represent their recent interaction history. The results of this

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Algorithm 3 Simulation algorithm for the model with individual reinforcement

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1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
3:      $x_i \leftarrow 0.5$ (* initialise the strategy of w_i *)
4: **end for**
5: uniformly select and partition workers in the colony into multiple games of size n
6: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
7:      $\Pi_i \leftarrow B(X) - C(x_i)$ (* w_i evaluates her payoff in the game g of workers with strategies $X = \{x_j | w_j \in g\}$ *)
8: **end for**
9: **while** $t < t_{end}$ **do**
10:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
11:          $x_i' \leftarrow x_i$
12:          $\Pi_i' \leftarrow \Pi_i$
13:          (* w_i memorises her previous strategy and payoff *)
14:      **end for**
15:      $m \sim Binomial(N, \beta)$
16:      select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
17:      **for** worker $w_i \in M$ **do**
18:          $x'' \sim Normal(x_i, \gamma)$
19:          $x_i \leftarrow x''$
20:          (* w_i innovates her strategy *)
21:      **end for**
22:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
23:          $\Pi_i \leftarrow B(X) - C(x_i)$
24:      **end for**
25:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
26:          **if** $\Pi_i < \Pi_i'$ **then**
27:              $x_i \leftarrow x'$ (* w_i reverts to her pervious strategy *)
28:          **end if**
29:      **end for**
30: **end while**
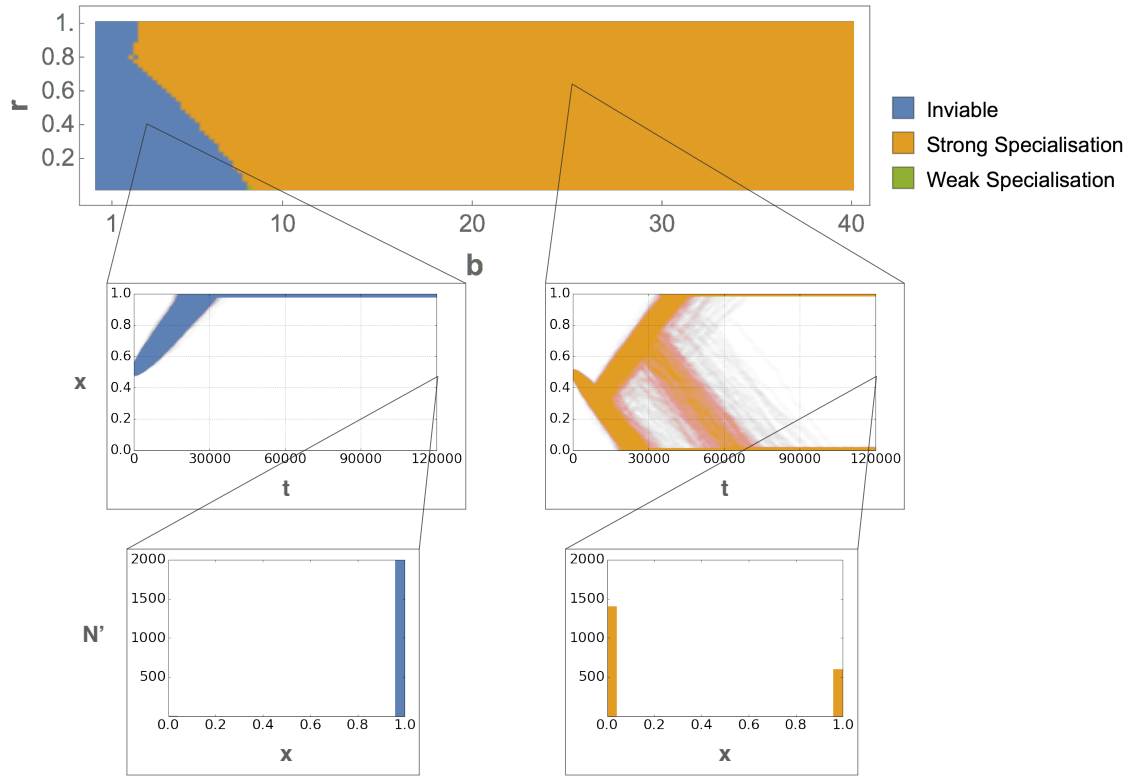
Figure 4.5: Behavioural patterns of the model with individual reinforcement. The upper region diagram gives the patterns of task allocation of colonies based on the model with individual reinforcement in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). The middle line of inset figures show two typical cases of how workers' strategies x in a colony develop over time t for being inviable ($b = 4, r = 0.3$) and strong specialisation ($b = 25, r = 0.8$), followed by two histograms of workers' strategies, each of which corresponds to the above colony at the last time-period, where N' represents the number of workers within a certain range of strategies.

model are also consistent with empirical evidence that the presence of social experience may promote task specialisation (Jeanson et al., 2008).

4.5 Task Recruitment

Based on the framework described in Section 4.2, we build a model of task allocation integrated with recruitment. Here task recruitment assumes that workers simply follow the tasks performed by other workers without relying on complex cognitive ability, which is widely explored and well supported by empirical studies on social insects (Gordon, 1996, 2010). In this model, workers perform only one task depending on their strategies at each time-period in contrast with social learning and individual reinforcement. Therefore, the proportion of effort that each worker puts in Task A at one time-period is either $x' = 1$ if she performs Task A or $x' = 0$ if she performs Task B, which is then used as input for payoff evaluation. Subsequently, the tasks that workers are recruited to further modify their strategies. We assume that each worker behaves as follows:

(i) Select a task (A or B) with randomness based on her strategy;

(ii) Evaluate her payoff based on her and others' allocated tasks in a game;

(iii) Select a worker with randomness in proportion to the associated payoffs across all workers and follow the task that the selected worker performs;

(iv) Modify her strategy based on the task she follows in Step (iii):

$$x_i \leftarrow \begin{cases} \rho + (1 - \rho)x_i & \text{if } x'_i = 1, \\ (1 - \rho)x_i & \text{otherwise} \end{cases}$$

where ρ is a constant between 0 and 1;

(v) Innovate her strategy slightly with a small chance and then continue with Step (i).

The detailed algorithm for the simulations of this model is given by Algorithm 4.

The results of the simulations for task recruitment are illustrated in Figure 4.6. Similar to social learning (see Section 4.3), the region diagram in Figure 4.6 is obtained through the results at the steady state shown in Figure A.4. Particularly for task recruitment, all viable colonies behave with weak specialisation, which are identified by the small standard deviations of workers' strategies (see Figure A.4(b)) and confirmed by the small variation of the entropies (see Figure A.4(c)). Our simulations show that workers in a colony based on the model with task recruitment are unlikely to specialise in tasks, in contrast to individual reinforcement (see Figure 4.5). Compared to the model with social learning (see Figure 4.3), the patterns of task allocation based on task recruitment tend to be uniform – only weak specialisation, as in this model, workers are characterised by the tasks they perform in the interactions between each other rather than their strategies, and consequently, their strategies tend to be bounded to a level determined by the ratio of workers engaged in Task A and Task B at the steady state.

Algorithm 4 Simulation algorithm for the model with task recruitment

1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
3:     $x_i \leftarrow 0.5$ (* initialise the strategy of w_i *)
4: **end for**
5: uniformly select and partition workers in the colony into multiple games of size n
6: **while** $t < t_{end}$ **do**
7:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
8:         $r \leftarrow random(0, 1)$
9:         **if** $r < x_i$ **then**
10:             $x_i' \leftarrow 1$ (* w_i selects Task A *)
11:         **else**
12:             $x_i' \leftarrow 0$ (* w_i selects Task B *)
13:         **end if**
14:     **end for**
15:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
16:         $\Pi_i \leftarrow B(X') - C(x_i')$ (* w_i evaluates her payoff in the game g of workers with allocated tasks $X' = \{x_j' | w_j \in g\}$ *)
17:     **end for**
18:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
19:         select w_k randomly according to probabilities $p(w_k) = e^{\alpha \Pi_k} / \sum_k e^{\alpha \Pi_k}$
20:         (* $k = 1, 2, ..., N$ *)
21:         $x_i' \leftarrow x_k'$
22:         (* w_i selects a worker w_k and follows her task *)
23:         **if** $x_i' = 1$ **then**
24:             $x_i \leftarrow \rho + (1 - \rho)x_i$
25:         **else**
26:             $x_i \leftarrow (1 - \rho)x_i$
27:         **end if**
28:     **end for**
29:     $m \sim Binomial(N, \beta)$
30:     select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
31:     **for** worker $w_i \in M$ **do**
32:         $x'' \sim Normal(x_i, \gamma)$
33:         $x_i \leftarrow x''$
34:         (* w_i innovates her strategy *)
35:     **end for**
36: **end while**
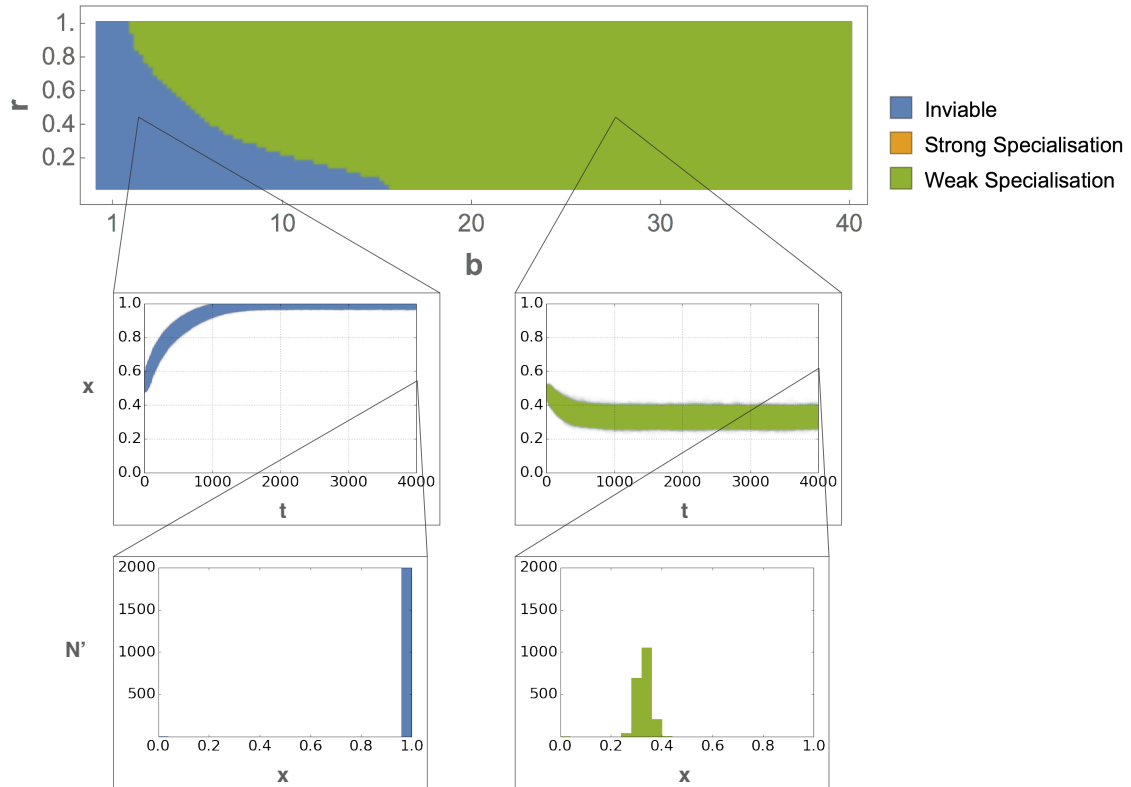
Figure 4.6: Behavioural patterns of the model with task recruitment. The upper region diagram gives the patterns of task allocation of colonies based on the model with task recruitment in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). The middle line of inset figures show two typical cases of how workers' strategies x in a colony develop over time t for being inviable ($b = 4, r = 0.3$) and weak specialisation ($b = 25, r = 1$), followed by two histograms of workers' strategies, each of which corresponds to the above colony at the last time-period, where N' represents the number of workers within a certain range of strategies.

4.5.1   Integration with Experience-based Reinforcement

We integrate the experience-based reinforcement (individual experience and social experience separately) into the model of task allocation with recruitment. In these integrated models, workers are assumed to accumulate and reduce their own experiences through performing and not-performing the related tasks. Here in the task-recruiting process – Step (iii) of the model with task recruitment, each worker can not only follow the task performed by another worker but also select a task based on her experiences of previous task engagement. Workers' task decisions are made in proportion to their accumulated experiences of previous task performance and the current payoffs of other workers. Here the difference between the reinforcement by individual experience and social experience is: For individual experience, workers' experiences are accumulated depending on their own learning rates, which are assumed to be different across workers in a colony; For social experience, workers' experiences increase by the evaluation of social interactions, represented by their payoffs. The detailed algorithms for the simulations of the models with reinforcement by individual experience and social experience are given by Algorithm 5 and Algorithm 6 respectively in Appendix A.3.1.

As illustrated in Figure 4.7, the results of the models integrated with task recruitment and experience-based reinforcement suggest that strong specialisation can occur under certain environmental conditions in contrast to the model only with task recruitment (see Figure 4.6). The fact that task selection depends on experiences influenced by previous task performance leads to a positive feedback loop in addition to the process of task recruitment. This positive feedback loop can make workers' accumulated experiences for one task exceed the magnitude of recruitment signals from other workers, leading to strong specialisation in certain environments. Interestingly, the environmental conditions in which strong specialisation occurs appear to be different between individual experience and social experience.

For the reinforcement by individual experience (see Figure 4.7(a)), the behavioural patterns are similar to those of the model with social learning (see Figure 4.3) – strong specialisation tends to emerge in the environments when b is small. As the magnitude of the recruitment signal is proportional to b, workers' own accumulated experiences tend to outweigh the recruitment signals from others, thereby becoming specialised in one task, when b is small. When b is large, workers are more likely to follow others' tasks due to stronger recruitment signals than their own experiences, the influence of which, however, still exist especially when the difference of costs between Task A and Task B is large (small r). As workers tend to select the task with less cost, in a colony, workers' payoffs for the process of task recruitment are low (see Figure A.4(a)) and the balance of workforce allocated to both tasks is fragile when r is small (for details, see Section 5.3.1). Thus occasionally, the reinforcement by individual experience can make task allocation in the environment with small r out of balance, leading colonies to become inviable (illustrated in Figure 4.7(a)).

However, for the reinforcement by social experience, the environmental conditions in which strong specialisation tends to occur seems to be different from social learning or the reinforcement by individual experience. As indicated in Figure 4.7(b), strong specialisation appears to occur when b and r are relatively large. In these environments, workers' payoffs received in the process of task recruitment are large (illustrated in Figure A.4(a)), which are then accumulated into their own task experiences. Subsequently, workers' accumulated experiences for one task tend to outweigh the recruitment signals from other workers, leading to strong specialisation in colonies which live in the environments with large b and r.

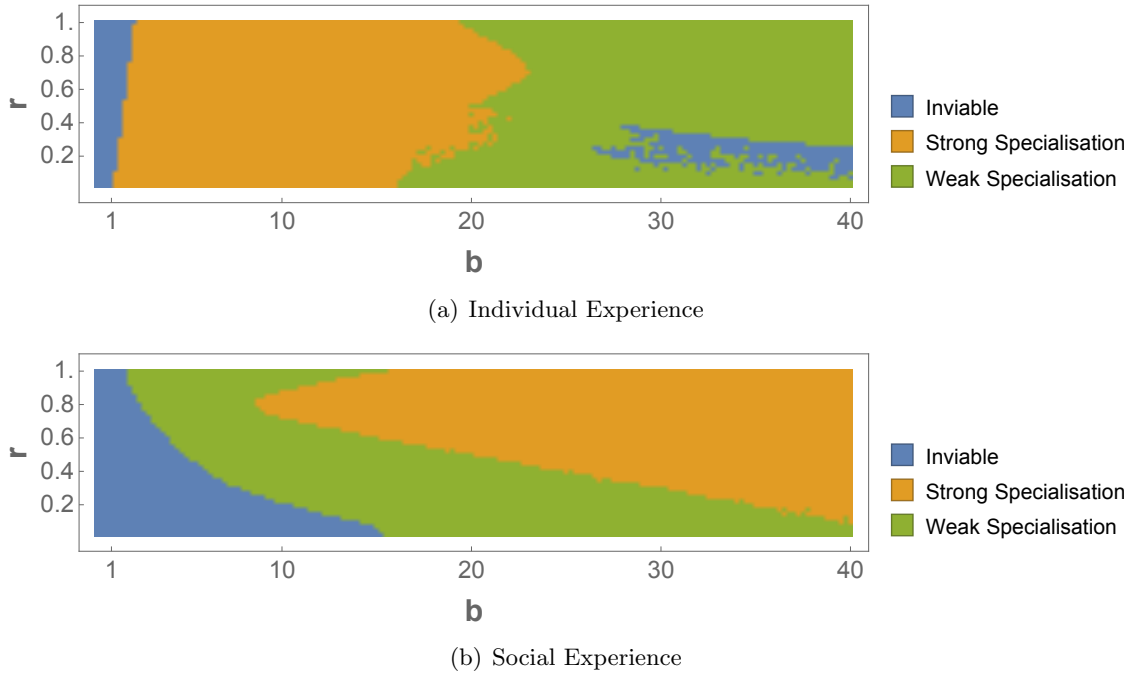(a) Individual Experience

(b) Social Experience

Figure 4.7: Behavioural patterns of the models with task recruitment and experience-based reinforcement. Both region diagrams give the patterns of task allocation of colonies based on the model with task recruitment and experience-based reinforcement in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). These region diagrams are obtained by the same procedure with social learning based on the results at the steady state shown in Figure A.5 and Figure A.6.

4.5.2   Integration with Spatial Fidelity

Apart from individual experience and social interaction, spatial distribution is also widely considered as an important factor that influences task allocation (reviewed in Chapter 2). Here we integrate spatial fidelity into the model with task recruitment. By this we assume that in a colony, each worker tends to show fidelity to some fixed location in the process of task recruitment. As a result, the colony can be divided into multiple task-recruiting groups while the games in which workers interact with each other for payoff evaluation are not restricted to the spatial limitation. The detailed algorithm of the simulations of

this model is given by Algorithm 7 in Appendix A.3.2.

The results of the simulations for the model with task recruitment and spatial fidelity are similar to the model only integrated with task recruitment. As illustrated in Figure 4.8, even though workers within a task-recruiting group tend to behave with similar strategies, the strategies of workers between these groups can differ. However, the colony-level workforce does not split into obviously different specialised groups. Spatial influence on task allocation is mostly studied as to the distribution of task demands (reviewed in Section 2.3.3). Here we use our game-theoretical models to explore how spatial factors may influence social interactions involved in task allocation, motivated by empirical evidence that spatial distribution appears to have a significant effect on interactions between workers in harvester ants (Pinter-Wollman et al., 2011). Further research may explore how variation of patterns and structures of social interaction, caused by spatial distribution or other factors, can influence the results of the model with task recruitment.

Our investigation of the model with task recruitment, which assumes that workers simply follow the tasks performed by others without any complex cognitive ability, is still in an early stage. The task-following process in worker-worker communication is widely observed in social insects and well supported by empirical studies (Gordon, 1996, 2010). There are a considerable number of potential factors and rich contexts that can be involved in or interact with this task-following process. For example, the integration of different types of experience can result in substantially different behavioural patterns (see Figure 4.7). This leads to the question of how workers select tasks based on their experiences and social interactions with others. For this question, most studies focus on workers' decision-making from individual experience and social information use (Grüter and Leadbeater, 2014). Whether and how workers' social experience is accumulated and influence their task preference may need further investigation.

4.6   Discussion

One important question is how we understand that workers in a colony play games or what such a game represents. Due to their physical or spatial limitations, individual workers are likely to sample and respond to local cues that can reflect the global situation (Gordon, 1996). Accordingly, our models assume that the workforce in a colony breaks up into multiple groups or games in which workers interact with each other and evaluate the payoffs for their and others' strategies. Each game happens locally and the behaviour at the colony level is aggregated by these local games. The size of a local group or game may be related to the degree or rate in which workers tend to interact with each other, which can influence the pattern of colony-level task allocation as illustrated by the model with social learning (see Figure 4.9): Weak specialisation arises when workers are involved in small games whereas larger games can lead to strong specialisation. This is consistent with empirical evidence that individuals in larger groups exhibit higher degrees of task specialisation (Holbrook, Kukuk and Fewell, 2013).
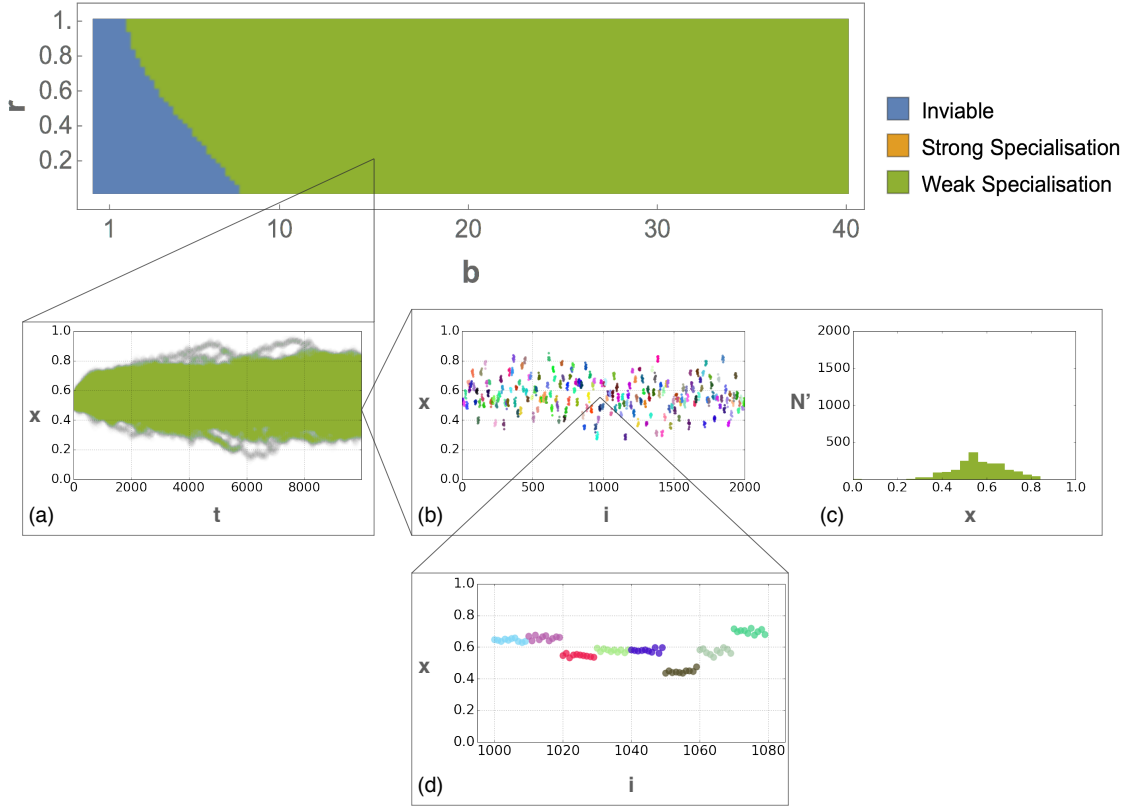
Figure 4.8: Behavioural patterns of the model with task recruitment and spatial fidelity. The upper region diagram gives the patterns of task allocation of colonies based on the model with task recruitment and spatial fidelity in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the same procedure with the original task recruitment (see Section 4.5) based on the results at the steady state shown in Figure A.7. The lower inset figures show a typical case of weak specialisation ($b = 30$, $r = 0.1$): The figure (a) describes how workers' strategies x in the colony develop over time t; The histogram (c) indicates the number of workers N' within a certain range of strategies x in the colony at the last time-period; The plot (b) gives the strategy x for each worker i in the colony at the last time-period – particularly in this plot, workers in the same recruiting group are listed together in line and represented by the same colour, demonstrated by the inset figure (d).
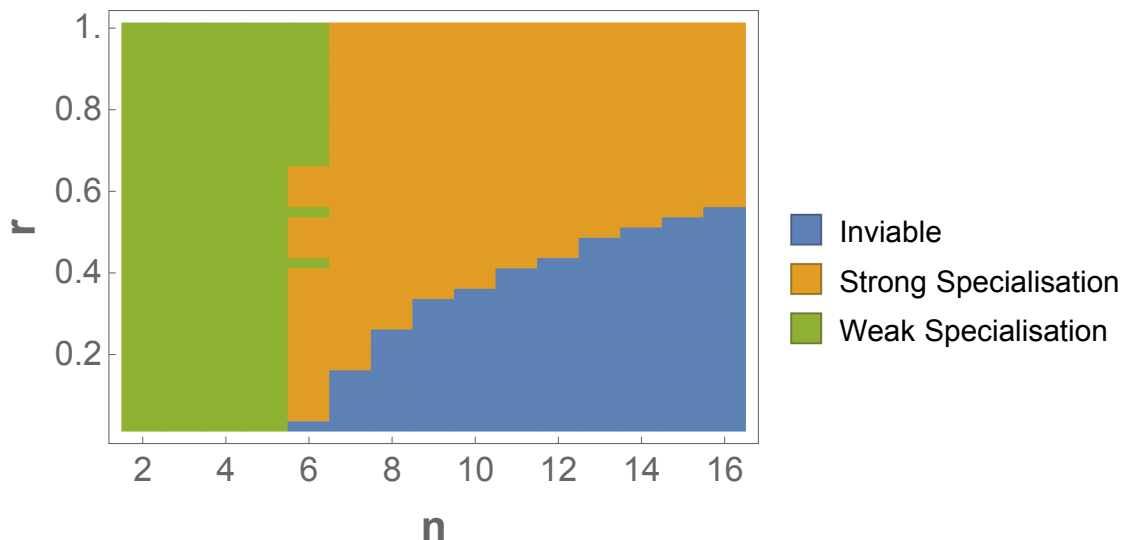
Figure 4.9: Behavioural patterns of the model with social learning for different game sizes. This region diagram describes the patterns of task allocation of colonies based on the model with social learning in a range of values for parameters n and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the same procedure with the region diagram in Figure 4.3, based on the results at the steady state shown in Figure A.2.

Another interesting question is how the strategies of workers in a colony can develop over time. The model with individual reinforcement simply assumes that workers can improve their strategies separately based on their short-term memories of previous strategies and payoffs. In both models with social learning and task recruitment, those workers with large payoffs could be more active to communicate with others or these workers could be more readily to be perceived by others. In general, workers are assumed to be able to move globally across the colony and communicate with others after receiving their payoffs. Spatial movement such as walking around is widely observed in empirical studies and is likely to influence task allocation in social insects (Gordon, 2002; Charbonneau et al., 2013; Seeley, 1982; Johnson, 2003; Cartar, 1992). In the model with task recruitment, workers can recognise the tasks that others perform simply by chemical cues or antennal contact in the task-following process (Gordon, 1996; Gordon and Mehdiabadi, 1999). However, in the model with social learning, the process of strategy copying between workers seems not straightforward and may assume that workers require complex cognitive ability, such as some type of concept learning studied in bumblebees (Giurfa, 2015). One possibility may be that workers infer and estimate the strategies of the workers that they meet by some fractional concept – For example, an individual worker might perceive the frequency of different tasks performed by another worker through the proportion of the task-associated odours carried by the other worker.

As our task-allocation game is on worker-life timescale, there are potentially more mechanisms in the development of workers' strategies than social learning, individual reinforcement and task recruitment, depending on the ecological contexts. Different mechanisms

of how workers develop their strategies can lead to variation of behavioural patterns of task allocation. For instance, the behavioural pattern of the model with individual reinforcement (see Figure 4.5) is opposite from task recruitment (see Figure 4.6) while the results of social learning (see Figure 4.3) are partially similar to both of the above models. Empirical studies may test which mechanism an insect colony follows by setting up a range of environmental conditions and checking if the colony-level behavioural patterns follow the predictions of our game-theoretical models.

4.7 Conclusion

In this chapter, we applied learning game theory to study the mechanisms of task allocation in social insects. Learning game theory offers an alternative framework to the response-threshold models (reviewed in Section 2.3) for exploring how behavioural patterns of task allocation can emerge from the interactions between workers and their environments. Based on our game-theoretical models, we find that specialisation can be caused by social interactions between workers in a colony alone, in addition to intrinsic inter-individual differentiation, self-reinforcement and spatial variation of task demands suggested by previous studies (Jeanson and Weidenmüller, 2014; Theraulaz et al., 1998; Johnson, 2010). We also find whether specialisation can emerge or not at the colony level can be determined by the environmental conditions as well as by the mechanisms of how workers' strategies develop over time. The components and assumptions involved in our game-theoretical models can provide new insights into the mechanistic processes of task allocation and may also advance our understanding of other topics such as concept learning (Giurfa, 2015) and selective use of social information (Grüter and Leadbeater, 2014).

Chapter 5

Colony Efficiency and Task Allocation

5.1 Introduction

Social insect colonies are examples of potentially efficient and flexible organisations shaped by the optimising processes of natural selection (Charbonneau and Dornhaus, 2015a). Efficiency represents how well the mechanism of task allocation in a colony can perform under certain environmental condition. It can be measured by some proxy such as the quantity of food collected, the amount of time delay or energy cost and the level of demand satisfied (Dukas and Visscher, 1994; Leighton et al., 2017; Jeanson and Lachaud, 2015). Efficiency is related to the adaptive value in Tinbergen's four questions (introduced in Section 1.2) and may shape the evolution of behavioural patterns of task allocation.

In general, it is reasonable to assume that environmental contexts are static on a fairly short timescale. However, when the focal timescale is extended, environmental conditions tend to fluctuate over time in nature. How a colony performs cannot only be measured by the efficiency achieved but also by the ability to adapt to environmental perturbations. Most models of task allocation (reviewed in Section 2.3) explicitly assume that workers' task selection depends on the associated stimulus and thus appear to be reactive to environmental changes to some degree (Charbonneau and Dornhaus, 2015a).

However, as reviewed in Section 2.4.4, most models of task allocation tend to focus on behavioural patterns and typically evaluate the efficiency in terms of a single task. In order to analyse the efficiency at the colony level, it is necessary to take account of scenarios with different tasks. The flexibility of task allocation to environmental changes needs to be quantified with specific tasks and environmental dynamics. Task allocation in social insects is likely to be a trade-off between efficiency and flexibility. For example, colonies usually tend to maintain a large proportion of inactive workers who appear not to be engaged in any task. It prevents the colony from achieving the optimal efficiency when the demand is low; however, when the demand is urgent and high, inactive workers can become active for the survival of the colony (Charbonneau and Dornhaus, 2015a).

In this chapter, we analyse and discuss the efficiency of models of task allocation based on individual behaviour and social behaviour as well as the performance in dynamic environments: For individual behaviour,[1] we evaluate our time-resolved model of task allocation (proposed in Chapter 3) by an extended simulation of collective fanning in a natural bumblebee colony; For social behaviour, we focus on our game-theoretical models of task allocation integrated with different mechanisms that determine how workers' strategies develop over time (proposed in Chapter 4).

5.2 Individual Behaviour

In this section, we further explore and evaluate our time-resolved model of task allocation, which focuses on the influence of within-worker factors. Our evaluation of the time-resolved model is based on the case of a homeostatic task – fanning in bumblebees, from our empirical data (see Chapter 3). We use computer simulations to demonstrate that colony efficiency cannot only be measured by how well homeostasis is achieved but also by how much workforce is left and available to other tasks. We further explore colony performance on a longer timescale when environmental conditions tend to fluctuate. In addition to colony efficiency, we tackle the question of how fast experience-based reinforcement can adapt to environmental fluctuations by simulations.

Our simulations are based on the time-resolved model (see Section 3.4), which is extended to capture the collective fanning in a bumblebee colony. The simulated nest is exposed to ambient temperature and additionally produces internal heat. Standard processes of Newtonian heat conduction are used to approximate the dynamics of nest temperature. For simplicity, we assume that the effect of each worker's effort on decreasing nest temperature is constant over time and identical with the others in the colony.

5.2.1 Efficiency

For a homeostatic task, such as fanning to cool down nest temperature, task performance at the colony level is usually measured as how close the task-related stimulus is maintained to a target level. In nature, bumblebee colonies are able to keep their brood temperature remarkably stable at the ideal level ($32°C$) for most of the time (Weidenmüller et al., 2002). This can be explained by regarding a bumblebee colony and the environmental context as a closed-loop control system because individual actions influence and are influenced by the stimulus intensity (Castillo-Cagigal et al., 2014). In a colony, workers continuously assess the temperature, perform the task for a while if required and then reassess the situation (for details, see Section 3.4). This closed-loop control ensures that collective homeostasis can be achieved regardless of the details of individual decision-making, provided that a sufficient number of workers are available.

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[1]This part includes published work (Meyer et al., 2015)

Consequently, the efficiency of task performance at the colony-level over a certain period cannot only be measured by how well the task demand is satisfied but also by how many workers have been involved in the task. In principle, the total number of workers that have been involved in the fanning task over a long period may vary from the number of workers needed to balance the generated heat, up to the colony size. Within this range, the fewer the workers that are involved in fanning, the more specialised these workers are. This raises the question of whether task specialisation improves colony efficiency. Even though it may be still under discussion that specialisation contributes to task performance at the individual level (Hölldobler and Wilson, 1990; Johnson, 2003; Dornhaus, 2008), specialisation is likely to promote efficient task performance at the colony level through various ways such as reducing costs in task switching (Charbonneau and Dornhaus, 2015a; Leighton et al., 2017). Therefore, the proportion of workers that have been involved in the task over a certain period can also be used to measure colony efficiency.

We demonstrate the above discussion by extended simulations of the time-resolved model of task allocation (for details, see Algorithm 8 in Appendix B). As a first step, we assume that the ambient temperature is constant at a certain level over time. In our simulations, we compare the efficiency of two colonies: One consists entirely of workers with identical task preference, represented by p_A – the probability to select Task A (defined in Section 3.4) and thus has no specialisation in fanning (Task A); The other is comprised of workers with different p_A and those with larger p_A tend to specialise in fanning. The number of workers actively engaged in fanning at any given time tends to be constant with slight fluctuations in order to keep the temperature stable around the ideal level (see Figure 5.1 and Figure 5.2). The simulations confirm that workers can manage to achieve colony homeostasis based on the closed-loop control, no matter whether there is specialisation in the fanning task at the individual level.
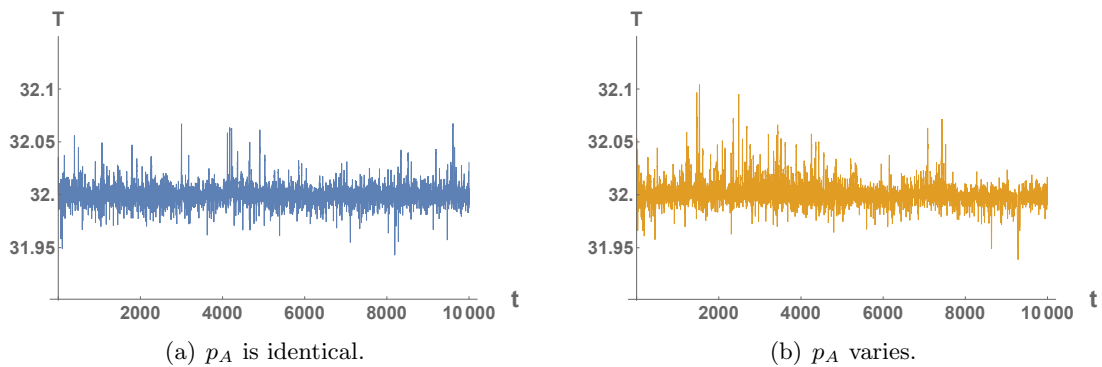

(a) p_A is identical.   (b) p_A varies.

Figure 5.1: Nest temperature T over time t: (a) p_A is identical for all workers in a colony ($p_A = 0.5$); (b) p_A varies among workers in a colony ($p_A \sim \mathbf{U}(0,1)$). For both (a) and (b), simulations are set up with parameters $N = 100$, $\theta_A = 32$, $T_{out} = 30$, $\alpha = 0.1$, $\beta = 0.00333$, $K = 1$, $r = 1/60$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0,1.25)$, $\lambda_B \sim \mathbf{U}(0,1)$. Here $\mathbf{U}(a,b)$ represents a continuous uniform distribution on the interval $[a,b]$.

(a) p_A is identical.

(b) p_A varies.

Figure 5.2: Number of workers actively engaged in fanning over time t: (a) p_A is identical for all workers in a colony ($p_A = 0.5$); (b) p_A varies among workers in a colony ($p_A \sim \mathbf{U}(0,1)$). For both (a) and (b), simulations are set up with parameters $N = 100$, $\theta_A = 32$, $T_{out} = 30$, $\alpha = 0.1$, $\beta = 0.00333$, $K = 1$, $r = 1/60$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0,1.25)$, $\lambda_B \sim \mathbf{U}(0,1)$. Here $\mathbf{U}(a,b)$ represents a continuous uniform distribution on the interval $[a,b]$.
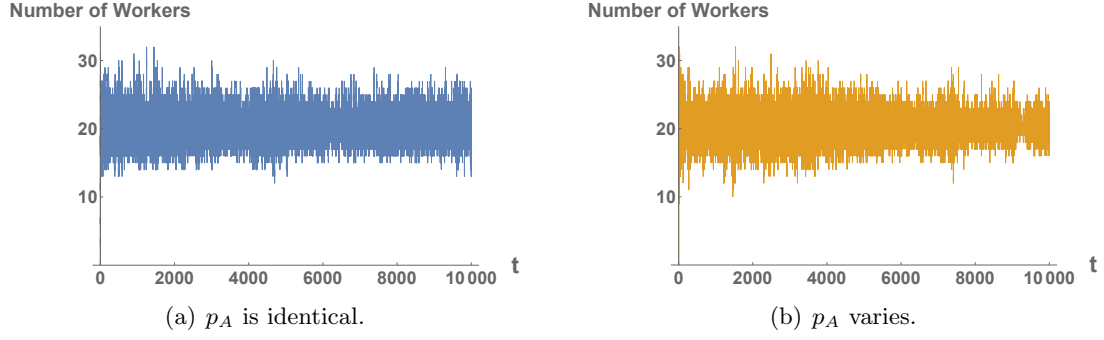
Over our simulation period, however, there seem to be more different workers that have been involved in fanning for the colony with no specialisation than the one with specialisation (see Figure 5.3). In the colony with specialisation, workers with large p_A are engaged in fanning more frequently, thereby reducing the likelihood for those with small p_A to engage (see Figure 5.3(b)), while all workers participate more evenly in the colony with no specialisation (see Figure 5.3(a)). Overall, the colony with specialisation may achieve better efficiency as there is more workforce available to concentrate on other tasks such as foraging, which can lower the costs generated in activities such as monitoring the brood temperature. To satisfy the demands of different tasks in a colony, specialisation is associated with inter-individual variation in workers' task preference, which in turn may have a functional role in enabling the colony to achieve collective homeostasis more efficiently.
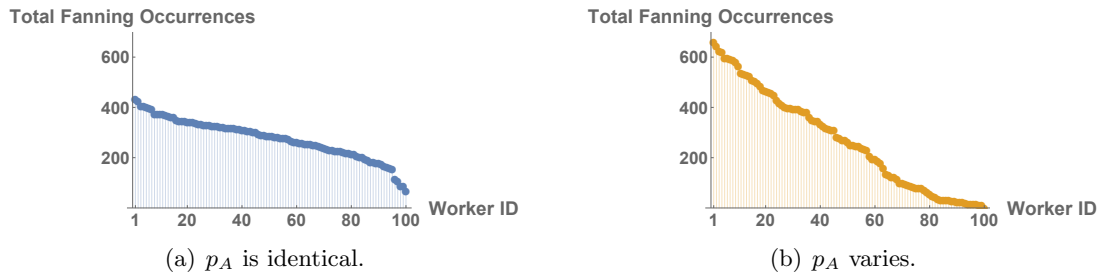

(a) p_A is identical.

(b) p_A varies.

Figure 5.3: Cumulative number of uninterrupted fanning periods for each worker: (a) p_A is identical for all workers in a colony ($p_A = 0.5$); (b) p_A varies among workers in a colony ($p_A \sim \mathbf{U}(0,1)$). For both (a) and (b), simulations are set up with parameters $N = 100$, $\theta_A = 32$, $T_{out} = 30$, $\alpha = 0.1$, $\beta = 0.00333$, $K = 1$, $r = 1/60$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0,1.25)$, $\lambda_B \sim \mathbf{U}(0,1)$. Workers are sorted from left to right in descending order by their total number of fanning periods. Here $\mathbf{U}(a,b)$ represents a continuous uniform distribution on the interval $[a,b]$.

5.2.2 Dynamic Environments

Our time-resolved model describes the dynamics of task allocation on a short timescale, when it is reasonable to assume that environmental conditions do not change. The static environmental context is assumed for the analysis of colony efficiency in Section 5.2.1. However, at longer timescales, environmental conditions tend to dynamically change in nature. Therefore, it is necessary to take into account how quickly a colony can manage to cope with environmental changes, or equivalently, how well colony homeostasis can be maintained when environment conditions fluctuate, in addition to the criteria for colony efficiency discussed in Section 5.2.1.

The results of our data analysis suggest that individual experience does not have a strong influence on bumblebee workers' fanning engagement at the moment-to-moment timescale (see Section 3.3.1). It is entirely possible that the effect of individual experience on task allocation cannot be ignored for a different species, task or on a longer timescale (see Section 2.2.1). Here we integrate the paradigm of reinforcement by individual experience into our time-resolved model of task allocation. Individuals are assumed to derive certain utility from performing a task and accumulate this utility as their task-related experience, which is also gradually forgotten and discounted over time (Weissbuch et al., 2000; Anderson et al., 1992; Camazine et al., 2001).

For an individual i, the cumulative discounted experience for task k is given as

$$E_k^i(j+1) := (1 - \rho) \cdot E_k^i(j) + \rho \cdot U_k^i(j)$$

where $U_k^i(j) \in \mathcal{R}$ is the utility that individual i derives from performing task k at the j-th time-period and $\rho \in [0,1]$ is a discount constant. Then the probability p_A^i to poll for Task A is assumed to be

$$p_A^i = \frac{f(E_A^i)}{f(E_A^i) + f(E_B^i)}.$$

Here $f(x)$ is a monotonically increasing function $f(x) = (m + x)^\gamma$ where m models a residual probability to choose a task with no experience and γ determines how strongly the difference in experiences is emphasised (Sumpter, 2010).

We explore this model using computer simulations (for details, see Algorithm 9 in Appendix B). Two colonies are simulated under the fluctuating environmental conditions that may represent a daily ambient temperature cycle: One colony is parameterised to achieve fast adaptation by strong reinforcement $(U_k^i(j) \in \{0, 20\})^2$ while the other is set with slower adaptation by weak reinforcement $(U_k^i(j) \in \{0, 1\})$.[2] Initially for $t < 500$, the colony with strong reinforcement shows rapid specialisation given that only about 20% of the workforce has been involved in fanning (see Figure 5.5(a)). However, this colony

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[2]For simplicity, the utility of individual task performance is assumed as $U_k^i(j) \in \{0, c\}$ where c is a constant.
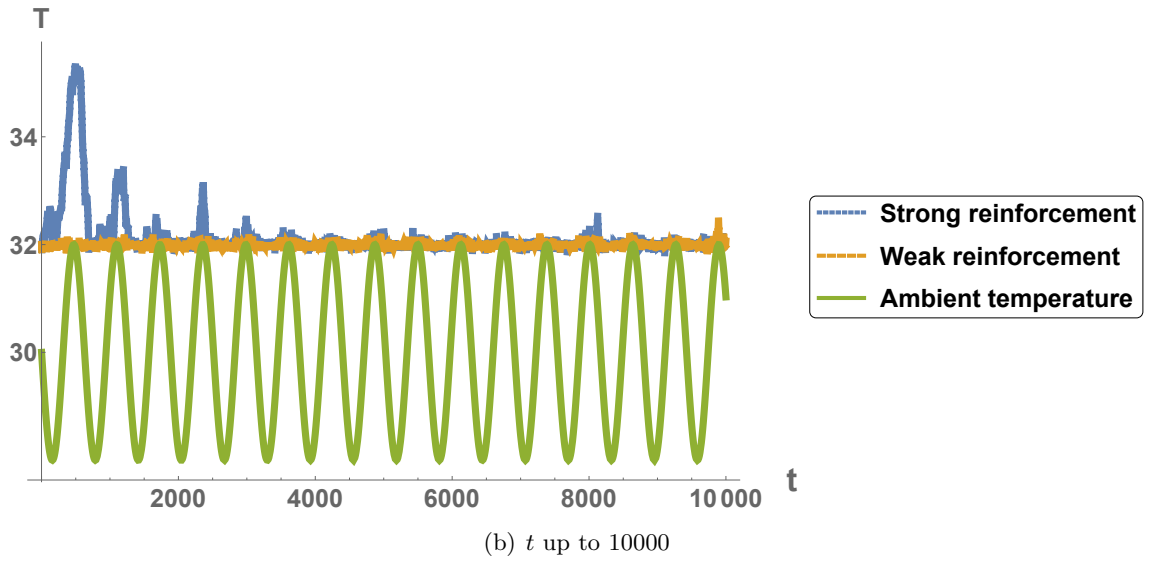
(a) t up to 500

(b) t up to 10000
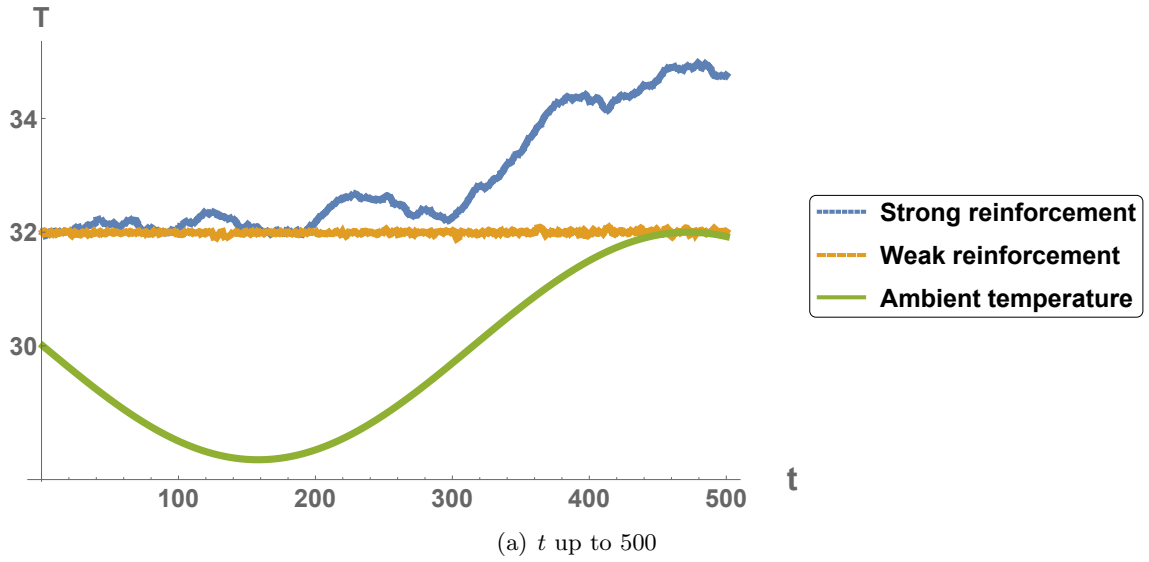
Figure 5.4: Nest temperature T over time t for colonies with strong and weak reinforcement for different time horizons ($N = 100$, $\theta_A = 32$, $\alpha = 0.1$, $\beta = 0.02$, $K = 1$, $r = 1/60$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0, 1.25)$, $\lambda_B \sim \mathbf{U}(0, 1)$, $\rho = 0.05$, $m = 1$, $\gamma = 2$, $E_0 = 0.5$). Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

(a) t up to 500

(b) t up to 10000
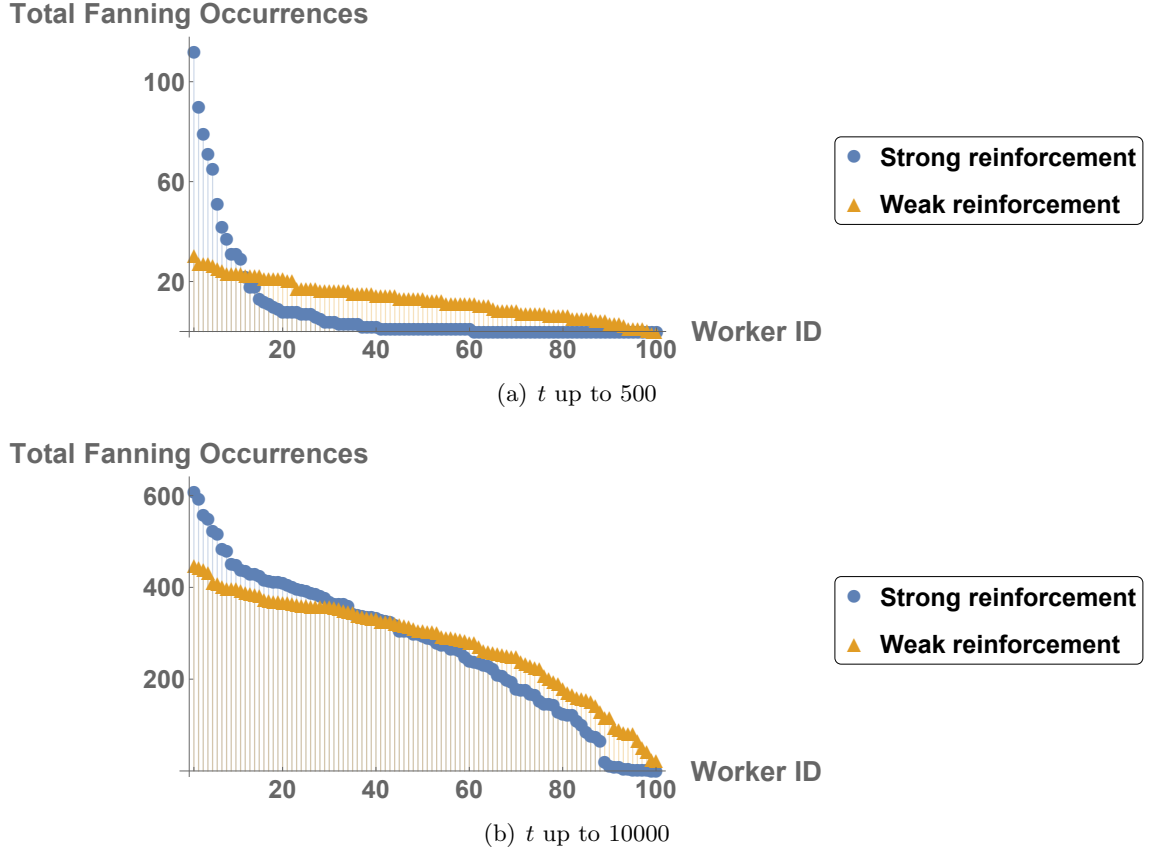
Figure 5.5: Cumulative number of uninterrupted fanning periods for each worker in colonies with strong and weak reinforcement for different time horizons ($N = 100$, $\theta_A = 32$, $\alpha = 0.1$, $\beta = 0.02$, $K = 1$, $r = 1/60$, $\lambda_A = 0.75$, $\mu_A \sim \mathbf{U}(0, 1.25)$, $\lambda_B \sim \mathbf{U}(0, 1)$, $\rho = 0.05$, $m = 1$, $\gamma = 2$, $E_0 = 0.5$). Workers are sorted from left to right in descending order by their total number of fanning periods. Here $\mathbf{U}(a, b)$ represents a continuous uniform distribution on the interval $[a, b]$.

cannot cope with the rising ambient temperature quickly enough ($300 < t < 500$, Figure 5.4(a)). Even though this colony eventually adapts to the environmental fluctuations ($t > 4000$, Figure 5.4(b)), specialisation is lost in the process as shown in Figure 5.5(b), around 90% workers in the colony have been engaged in fanning and their activity levels do not differ as strongly as the initial stage ($t < 500$, see Figure 5.5(a)). On the other hand, the colony with weak reinforcement effectively handles the demand changes all the time (see Figure 5.4) but specialisation has never arisen (see Figure 5.5). For this colony, the reinforcement is indeed rendered ineffective by environmental fluctuations.

We see that a colony with strong reinforcement can specialise fast in task allocation but tends to lose control under environmental fluctuations. On the other hand, a colony with weak reinforcement tends to be flexible in dynamic environments but hardly involves specialisation. This leads to the question of how a trade-off between efficiency (achieved by specialisation) and flexibility in task allocation (Charbonneau and Dornhaus, 2015a) can be achieved. In this case, it can be reasoned by the relationship between the experience-based reinforcement, determined by both effects of positive and negative feedbacks, and the dynamic characteristics of the environment: If the environment changes more slowly than the rate of reinforcement, there can be a long delay from the time when the environmental change occurs until the associated task need is well-satisfied; If the environment fluctuates faster than the reinforcement rate, then task specialisation can barely arise.

Consequently, there are two potential mechanisms of how the trade-off between efficiency and flexibility may be achieved in nature: One is that colonies have evolved under certain environmental conditions through natural selection (Charbonneau and Dornhaus, 2015a); The other is that the rates of workers' positive and negative feedbacks depend on the current environmental conditions (Castillo-Cagigal et al., 2014). A more detailed and exhaustive analysis is unfortunately beyond the scope of this thesis and needs to be kept for future research.

5.3 Social Behaviour

In this section, we evaluate and analyse the game-theoretical models of task allocation, which emphasise the effect of social interaction between individual workers (see Chapter 4). We study how the efficiency achieved by colonies based on these models is related to the behavioural patterns of task allocation as well as how it can be influenced by environmental conditions and the dynamics of workers' strategies over time. As the environment naturally changes over time, we then tackle the question of how the behavioural patterns of task allocation may differ between static and dynamic environments, and discuss how well and how fast colonies based on these models may adapt to variation of environmental conditions.

Game-theoretical models provide a unique opportunity for efficiency analysis as the dynamics of workers' decision-making involve their payoffs, which can be regarded as their

perception of rewards and penalties and may also be linked to the colony-level fitness. Here we consider colony efficiency to be proportional to the mean of workers' payoffs at the steady state. As the optimal achievable payoff changes with environmental conditions (illustrated in Figure 5.6), we quantify the efficiency at the colony level as the ratio between the mean of workers' payoffs at the steady state and the optimal value that can be achieved under the associated environmental conditions (see Figure 5.6). Therefore, the efficiency achieved by colonies based on our game-theoretical models ranges from 0 to 1.[3]
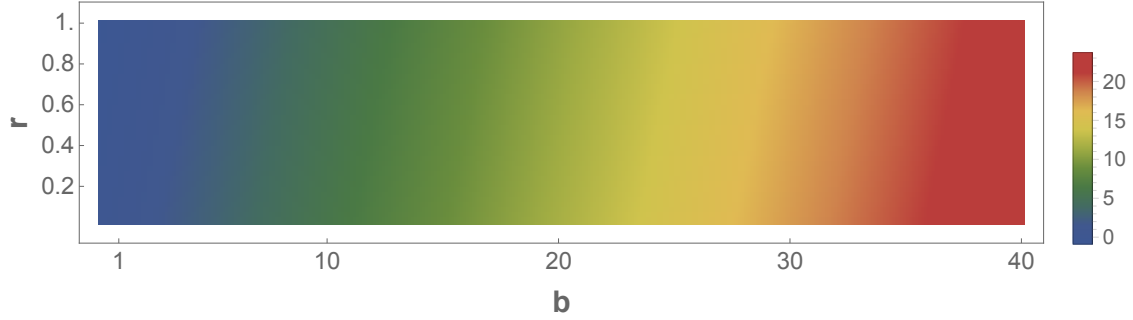

Figure 5.6: Optimal payoffs achieved in a game ($n = 10$). This diagram gives the optimal payoff that a worker can achieve in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). The value for each pair of b and r is obtained by optimising the mean of workers' payoffs in a game of size n using Differential Evolution (Storn and Price, 1997), a stochastic population-based heuristic method for global optimisation (implemented by *differential_evolution* in the package *optimize* of Scipy, Version 0.17.0).

5.3.1 Efficiency

We find that the efficiency achieved by colonies based on the same underlying mechanism of how workers' strategies develop over time can depend on the behavioural patterns and may not be unique over a range of environmental conditions. Variation of environmental conditions can result in different behavioural patterns of task allocation, which correspond to different levels of colony efficiency. For the model with social learning (illustrated in Figure 5.7), colonies associated with weak specialisation can obtain greater efficiency than those with strong specialisation. Here, for weak specialisation, the efficiency achievement tends to keep at the highest level without variation, under different environmental conditions represented by b and r (introduced in Section 4.2), while in the cases of strong specialisation, the efficiency achieved is sensitive to r, the cost ratio of Task A to Task B. This connection between efficiency achievement and behavioural patterns is also indicated by the model integrated with task recruitment and reinforcement by social experience (illustrated in Figure 5.10(b)). For this model, the efficiency achieved by colonies with strong specialisation remains at the largest with almost no differentiation while the efficiency of

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[3]This is the colour scheme used for the efficiency plots of all models in this section (Figure 5.7 – Figure 5.11). For simplicity, the efficiency achieved by any colony with a negative mean payoff is simply treated as 0, indicating being inviable.

colonies with weak specialisation is sensitive to r, in contrast to the model with social learning.
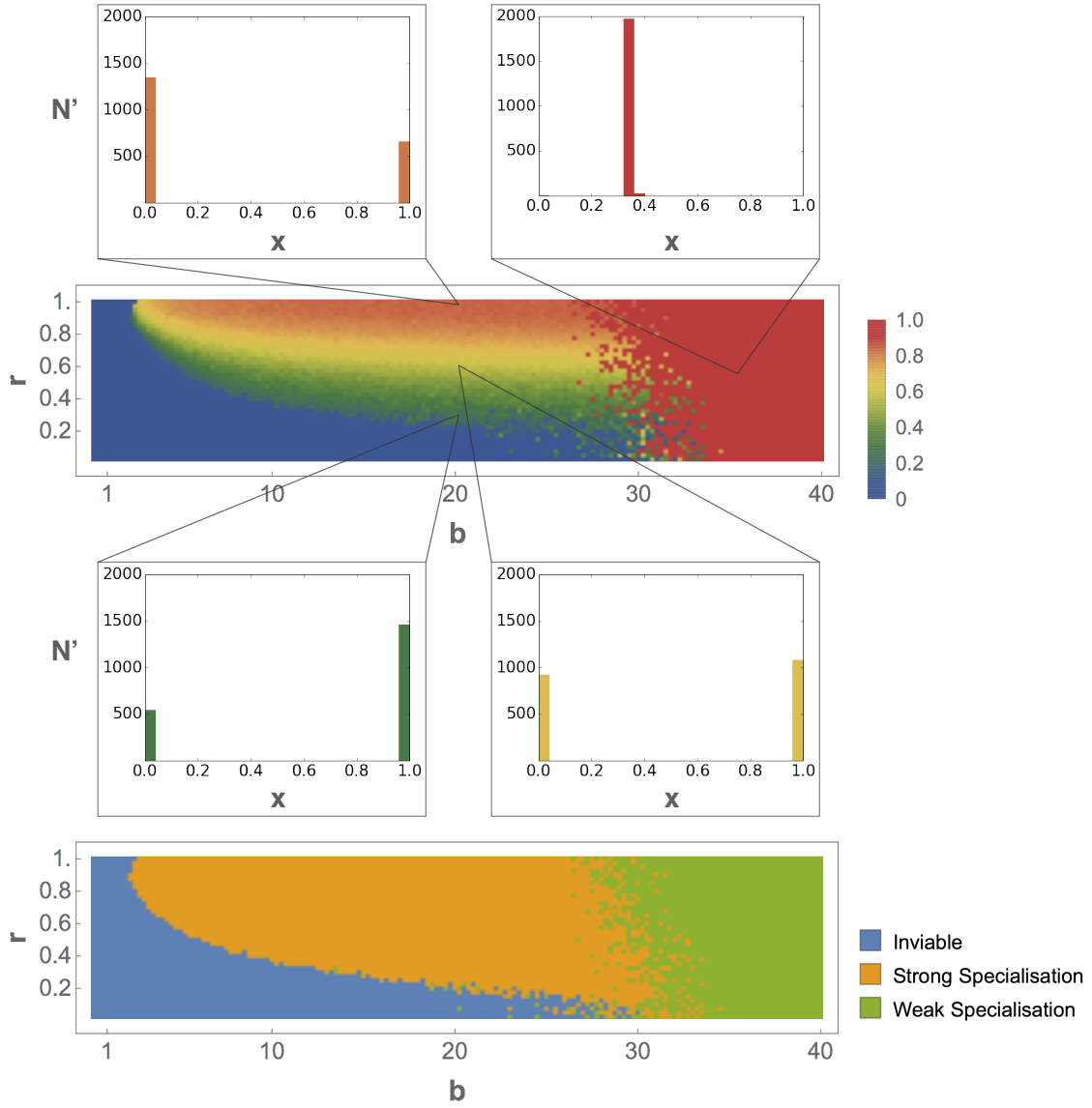

Figure 5.7: Efficiency achievements of the model with social learning. The upper diagram gives the efficiency achieved by colonies based on the model with social learning at the steady state in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the results at the steady state shown in Figure A.1(a) and Figure 5.6. The lower region diagram is explained in Section 4.3 and displayed here as a reference to the associated behavioural patterns. The histograms of workers' strategies x are illustrated for four typical cases: $b = 20$, $r = 0.4$ (lower left); $b = 20$, $r = 0.7$ (lower right); $b = 20$, $r = 1$ (upper left); $b = 35$, $r = 0.5$ (upper right) where N' represents the number of workers within a certain range of strategies.

Not only related to the behavioural patterns, the efficiency achievement of colonies based on the same model tends to be sensitive to the parameter r. This sensitivity of colony efficiency to r occurs not only in the pattern of strong specialisation of the model with

social learning (illustrated in Figure 5.7) but also in weak specialisation of the model with task recruitment (illustrated in Figure 5.8). In both cases, the efficiency achievement gradually decreases with the cost ratio r. This can be attributed to one of the similarities between strong specialisation of social learning and weak specialisation of task recruitment – Workers in a colony have the opportunity to select a single task into which they invest their whole effort at each round of payoff evaluation. This opportunity is offered by the process of strategy copying in strong specialisation of social learning and through task selection in weak specialisation of task recruitment. As workers share a common benefit in games, they tend to adjust their strategies in favour of the task that is less costly in order to achieve better payoffs than others.
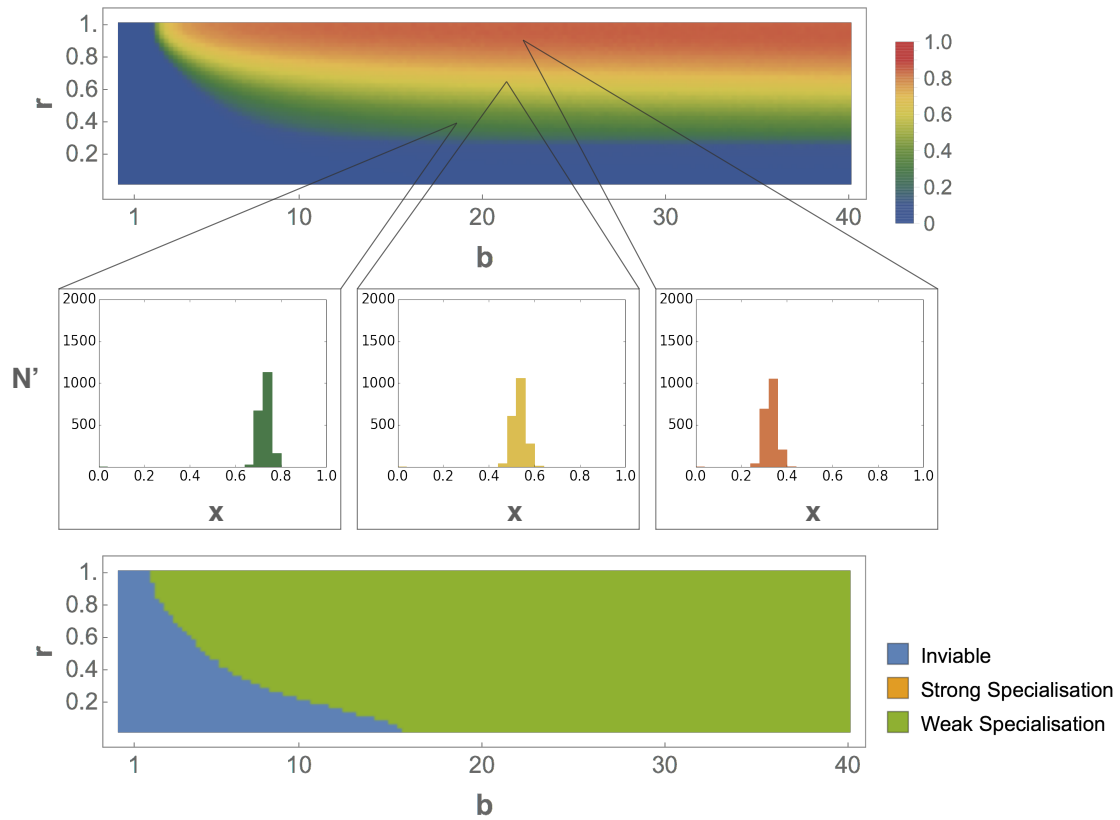

Figure 5.8: Efficiency achievements of the model with task recruitment. The upper diagram gives the efficiency achieved by colonies based on the model with task recruitment at the steady state in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the results at the steady state shown in Figure A.4(a) and Figure 5.6. The lower region diagram is explained in Section 4.5 and displayed here as a reference to the associated behavioural patterns. The histograms of workers' strategies x are illustrated for three typical cases: $b = 25$, $r = 0.4$ (left); $b = 25$, $r = 0.7$ (middle); $b = 25$, $r = 1$ (right) where N' represents the number of workers within a certain range of strategies.

The sensitivity of colony efficiency to the cost ratio between tasks can be moderated by factors such as food resources, spatial effects and experience-based reinforcement. When b (the quality of food resources) is at a high level, colonies based on the model with social

learning tend to show weak specialisation in which workers attempt both Task A and Task B for each game, leading to stable high-level efficiency achievement regardless of the cost ratio r (illustrated in Figure 5.7). For the model with task recruitment, the influence of spatial fidelity appears to make colony efficiency much less sensitive to r, even through spatial fidelity does not show a strong effect on behavioural patterns at the colony level (illustrated in Figure 5.9 compared with Figure 5.8). Besides spatial fidelity, experience-based reinforcement can reduce the sensitivity of colony efficiency to r in the model with task recruitment under a certain range of environmental conditions when workers' accumulated experiences for one task dominate their task selection over recruitment signals from other workers (see Figure 5.10 compared with Figure 5.8). In this case, workers cannot switch between tasks due to their accumulated experiences, which prevents them from reducing their cost, and thus they can increase their payoffs only by improving their benefits. Particularly, the integration with reinforcement by social experience appears to improve the efficiency achievement better than individual experience, as individual experience, which is not related to payoff, can break the process of payoff evaluation, especially when workers' payoffs are at a low level. If the accumulated social experience completely overweighs task recruitment, then this integrated model can approximate to the model with individual reinforcement, for which colony efficiency is almost insensitive to the environmental conditions (illustrated in Figure 5.11).
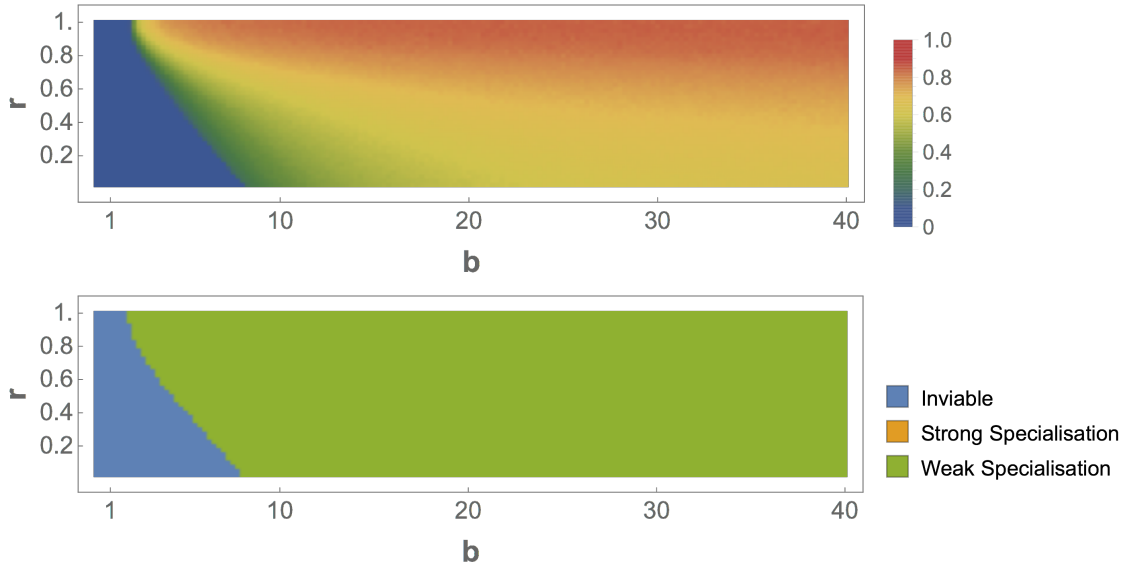

Figure 5.9: Efficiency achievements of the model with task recruitment and spatial fidelity. The upper diagram gives the efficiency achieved by colonies based on the model with task recruitment and spatial fidelity at the steady state in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the results shown in Figure A.7(a) and Figure 5.6. The lower region diagram is explained in Section 4.5.2 and displayed here as a reference to the associated behavioural patterns.

Colony efficiency is not only related to strong or weak specialisation but also depends on

(a) Individual Experience
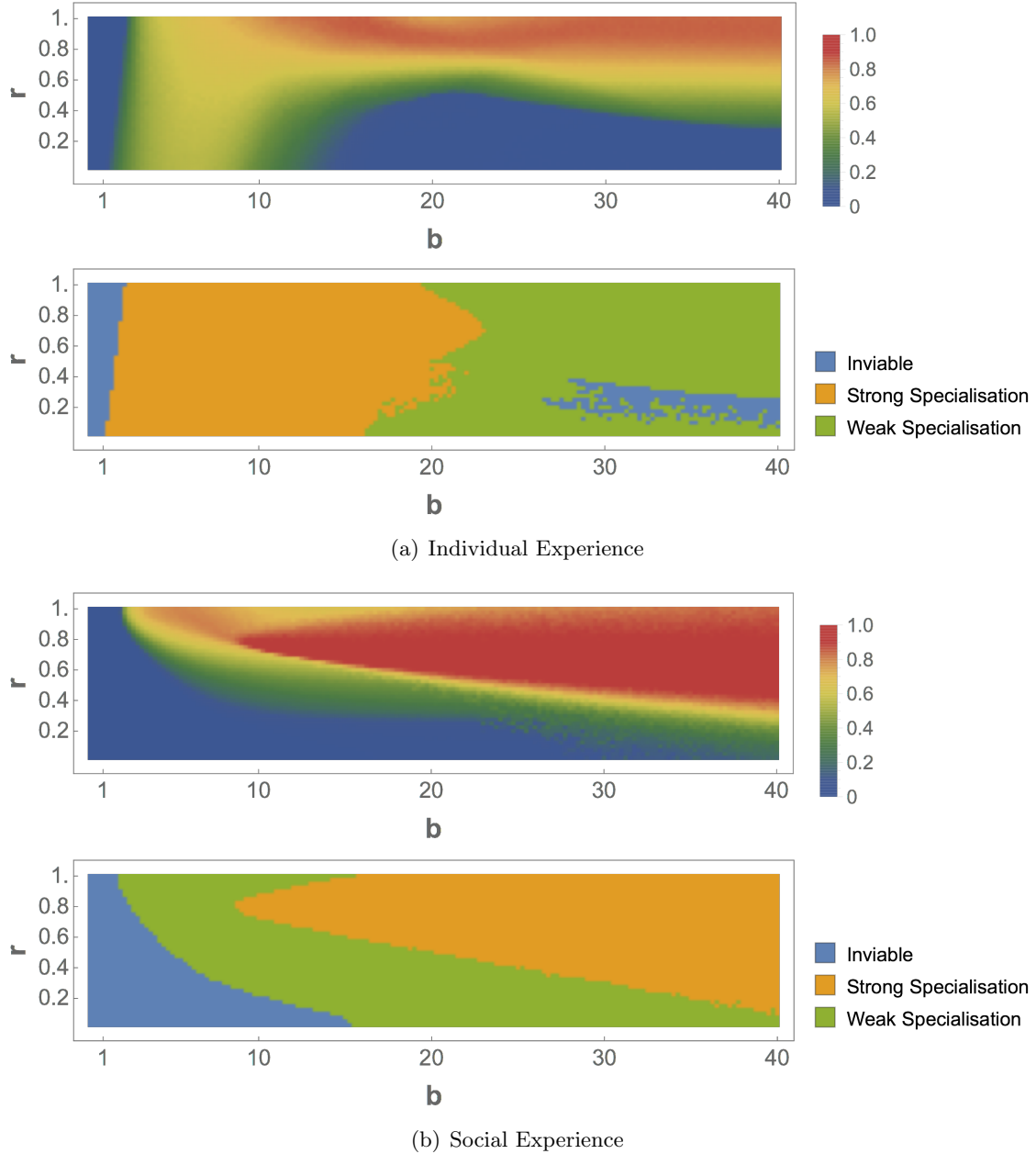

(b) Social Experience

Figure 5.10: Efficiency achievements of the models with task recruitment and experience-based reinforcement. For both (a) and (b), the upper diagrams give the efficiency achieved by colonies based on the models with task recruitment and experienced-based reinforcement at the steady state in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). These diagrams are obtained by Figure A.5(a) and Figure 5.6 for (a) individual experience, Figure A.6(a) and Figure 5.6 for (b) social experience. The lower region diagrams are explained in Section 4.5.1 and displayed here as a reference to the associated behavioural patterns.

the mechanisms that determine how workers' strategies develop over time, since the same behavioural pattern involves different distributions of workers' strategies (see Figure 5.7 – Figure 5.11). Overall, the model with individual reinforcement appears to achieve more consistent and greater efficiency than social learning or task recruitment. The model with task recruitment (see Figure 5.8) is less efficient than the other two models (see Figure 5.7 and Figure 5.11). Integrating spatial fidelity into the model with task recruitment can improve the efficiency in the environments with costly foraging (small r) while reinforcement by social experience may increase the efficiency in the environments with abundant high-quality resources (large b and r). Future empirical and theoretical studies may need to further substantiate the hypotheses drawn from the efficiency analysis of our game-theoretical models in this section.
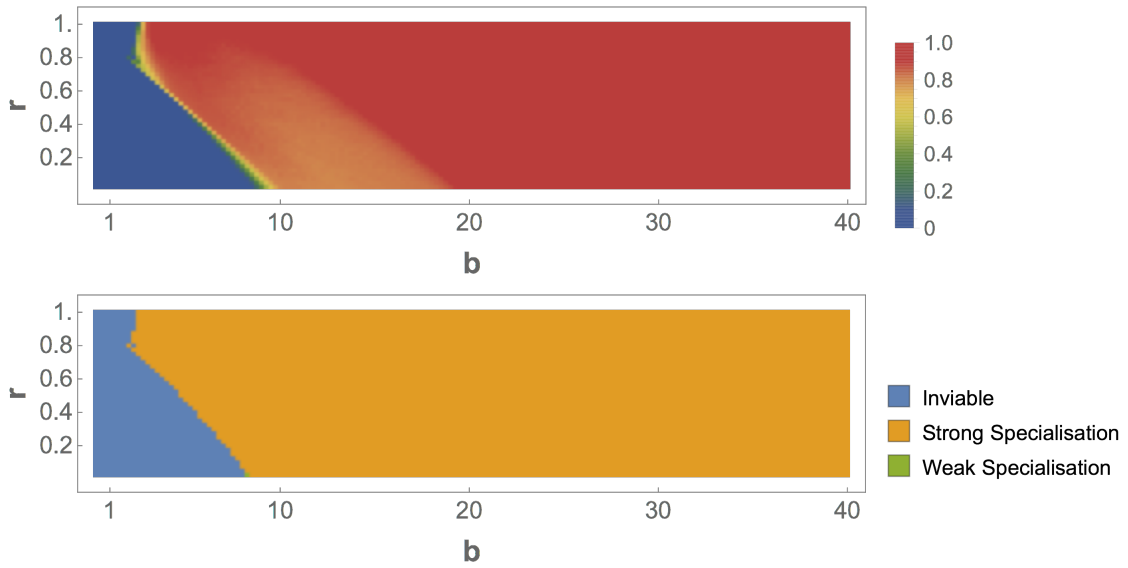

Figure 5.11: Efficiency achievements of the model with individual reinforcement. The upper diagram gives the efficiency achieved by colonies based on the model with individual reinforcement at the steady state in a range of values for parameters b and r, which are involved in the functions for payoff evaluation (see Section 4.2). This diagram is obtained by the results shown in Figure A.3(a) and Figure 5.6. The lower region diagram is explained in Section 4.4 and displayed here as a reference to the associated behavioural patterns.

5.3.2   Dynamic Environments

Most of our game-theoretical models suggest that the environmental contexts (static) determine the efficiency that a colony can achieve as well as the behavioural patterns (see Section 5.3.1). Surprisingly, we find that when the environment changes over time, the history of previous environmental conditions can strongly influence the behavioural patterns of task allocation at the colony level, in addition to the current environmental condition, which is only assumed that colonies can respond to by most models in the literature. The

behavioural pattern after adapting the environmental change depends on the environmental condition before the change happens because these patterns cannot always transfer between each other. This is illustrated with an example of the model with social learning (see Figure 5.12). When the food quality becomes worse (b gets smaller), the pattern of task allocation changes from weak specialisation to strong specialisation, which then keeps stable and do not change back to weak specialisation even though the food quality improves to the initial level. Here strong specialisation, which appears to be more stable, cannot be converted to weak specialisation.

In Figure 5.12(c), after b switches back to the initial value ($t > 40000$), the efficiency achieved by the colony is at a lower level than that before the first environment change ($t < 20000$), since strong specialisation is associated with less efficiency in the model with social learning (see Figure 5.7). However, although weak specialisation achieves better efficiency than strong specialisation at the steady state, it is possible that colonies with strong specialisation may adapt to environmental fluctuations faster than those with weak specialisation. To adapt to the environmental variation, strongly-specialised colonies adjust the ratio of workers in different task groups by strategy copying between workers, while weakly-specialised colonies depend on exploration and innovation of the strategy space by a small proportion of workers. In the dynamics of game theory, the process of innovating new strategies is generally assumed to take a much longer time than strategy imitation (Broom and Rychtář, 2013).

Again, this leads to the discussion between efficiency and flexibility in task allocation. Particularly, in contrast to traditional studies (Oster and Wilson, 1978; Charbonneau and Dornhaus, 2015a), our game-theoretical model with social learning suggests that specialisation may not necessarily promote efficiency but favours flexibility by making a colony adapt to environmental changes within a shorter period. Colonies based on the model with social learning tend to behave with weak specialisation in static environments with high-quality food resources (when b is large, see Figure 5.7). When the quality of food resources become worse (when b is small) or tend to fluctuate, these colonies are more likely to behave with strong specialisation, which is less efficient but more flexible (see Figure 5.7 and Figure 5.12(b)).

5.4 Conclusion

In this chapter, we focused on efficiency analysis for colonies based on our models of task allocation introduced earlier in this thesis. For individual behaviour, it is generally assumed that the efficiency can be measured by how well the demand of the focal task is satisfied. Apart from this, we suggest that the efficiency of task allocation can depend on how much workforce is available to other tasks, indicating one advantage of task specialisation, by extended simulations of the time-resolved model. When the environment tends to fluctuate, our simulations suggest that how well task allocation can adapt to environmental changes may be influenced by the focal timescale and the balance between the
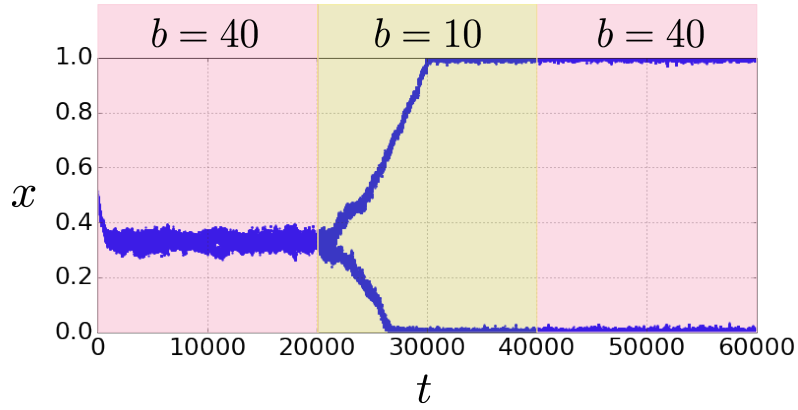
(a) Strategies of all workers
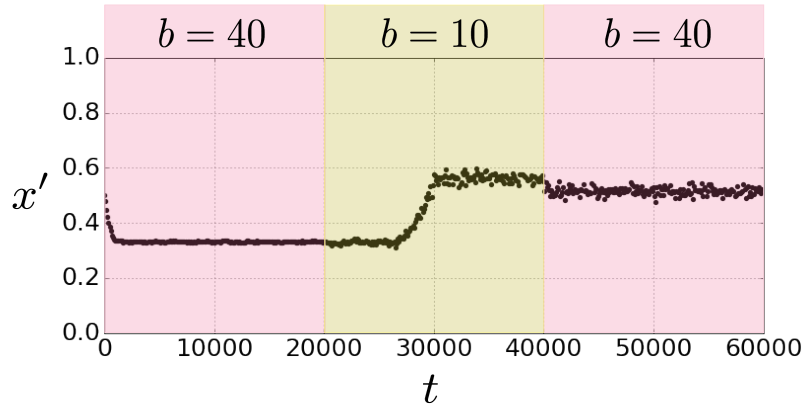
(b) Mean strategy of workers
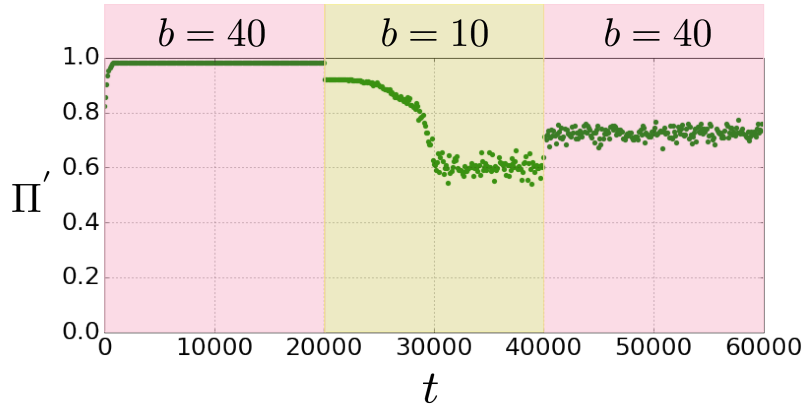
(c) Colony efficiency

Figure 5.12: An example of the model with social learning in dynamic environments ($N = 2000$, $t_{end} = 60000$, $n = 10$, $r = 0.7$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$). The above figures show the dynamics of workers' strategies (x), mean strategy ($x^{'}$) and efficiency ($\Pi^{'}$) in a colony over time (t) under environmental fluctuations (b). The environment is set up as three stages: (1) $b = 40$ for $t \in [0, 20000]$; (2) b is switched to 10 at $t = 20000$ and keeps still until $t = 40000$; (3) b is switched back to 40 and keeps still until the end of simulation.

rates of individual learning and the characteristics of environmental dynamics. For social behaviour, we find that the efficiency achieved by colonies based on our game-theoretical models can be influenced by environmental conditions and mechanisms that determine how workers' strategies develop over time. Particularly, workers in a colony tend to adjust their strategies in favour of the less-costly task even though this can reduce the level of colony efficiency, demonstrating the principle "Tragedy of the Commune" in cooperative games (Doebeli et al., 2004). Surprisingly, we find that in dynamic environments, task allocation can exhibit an effect of hysteresis, as the behavioural patterns depend on the previous history of environmental conditions. This provides new insights into our understanding of how task allocation can adapt to dynamic environments as colonies are normally assumed to be highly responsive to the current environmental conditions (see Section 2.3).

Chapter 6

Conclusion

6.1 Thesis Summary

In this thesis, we explored the mechanistic processes of task allocation in social insects on worker-life timescales from different novel perspectives. Particularly, the viewpoints that we focused on are not well-studied in the literature (reviewed in Chapter 2). Following a bottom-up approach based on timescales, we built theoretical models to explain and simulate the interplay between insect colonies and their environments. Based on these models, we analysed and discussed the colony-level efficiency as well as the flexibility in dynamic environments. Here we divided the factors that can influence task allocation into two categories: within-worker causes and between-worker interactions and approached each of them separately.

We investigated the effect of within-worker factors by taking account of the influence of time, which tends to be ignored by most studies (see Chapter 3). Accordingly, we performed survival analysis for the data from experiments on the fanning task in bumblebees. Particularly, these experiments adopt a novel set-up which makes it possible that the environmental condition is measured and controlled precisely. Surprisingly, our results suggest that neither stimulus intensity nor individual experience strongly influence workers' task engagement. This is in contrast with most established empirical studies (O'Donnell and Foster, 2001; Weidenmüller et al., 2002; Weidenmüller, 2004; Westhus et al., 2013) and theoretical models (Bonabeau et al., 1996; Theraulaz et al., 1998; Gautrais et al., 2002; Lichocki et al., 2012; Duarte, Pen, Keller and Weissing, 2012), which do not account for the temporal influence. Moreover, our survival analysis suggests that workers tend to be less active after receiving rewards of fanning, which cannot be identified by traditional analysis. This contrasts with the general expectation that workers' perception of rewards should encourage them to engage in the task at a higher level.

We find that the processes of workers' fanning in bumblebees are not homogeneous Poisson but close to power laws, indicating the timing-patterns of workers' activities indeed cannot be omitted at short timescales. Consequently, we built a time-resolved model of task allocation, which can be verified with the empirical data and also used to explain the

data. Based on this model, we illustrated that the colony-level efficiency cannot only be measured by how well the task-related demand is satisfied but also by how much work-force is available to other tasks (see Chapter 5). When the environment tends to fluctuate, how well a colony can adapt to environmental changes seems to depend on both the focal timescale and the balance between the rates of individual learning and the characteristics of environmental dynamics.

We applied game theory as a basic framework to explore the influence of social interaction on task allocation (see Chapter 4). Game theory provides a mathematical foundation and a modelling perspective to study social interactions, which can guide empirical work as the interactions between workers in a colony involve complex processes and are difficult to measure and control in biological experiments. Based on our game-theoretical models, we find that specialisation can emerge from the interaction dynamics between workers and their environments alone. This offers a new way of understanding the question – What are the primary sources that can cause variation in workers' task preference, which is one of the core interests in the study of task allocation (Gordon, 2016). Most studies regard inherent inter-individual differentiation as the main cause (Jeanson and Weidenmüller, 2014), while it is also shown that task specialisation can result from a colony of identical workers with experience-based reinforcement (Theraulaz et al., 1998) or spatial variation of localised task demands (Tofts and Franks, 1992; Johnson, 2010). Our results suggest that an alternative source of variation in task preference can be social interactions between workers.

We find that variation of environmental conditions and mechanisms that determine the dynamics of workers' strategies over time can cause different behavioural patterns and efficiency achievements of task allocation. Our game-theoretical models can be used to explore the dynamics of cooperative games and illustrated the principle "Tragedy of the Commune" (Doebeli et al., 2004). For dynamic environments, our simulations suggest that surprisingly, the processes of task allocation may exhibit an effect of hysteresis as the behavioural patterns depend on the previous history of environmental conditions (see Chapter 5). This provides new insights into our understanding of how the processes of task allocation can adapt to environmental fluctuations, in addition to the traditional assumption that colonies are highly responsive to the current environmental conditions.

6.2   Further Research

6.2.1   Empirical Studies

Our time-resolved model of task allocation conceptually captures multiple tasks in an insect colony (see Figure 3.16). It was reduced to only two tasks for comparison and verification with the data from the experiments in which, as a first step, only one controlled task was set, due to practical difficulties. Further empirical studies could test our time-resolved model by setting up experiments with an additional controlled task, such

as foraging. The reason behind the negative influence of individual efficiency on workers' fanning engagement is likely to be that fanning is a homeostatic task, the stimulus of which needs to be maintained within a certain range rather than reduced at the lowest possible level (see Section 3.5). In addition, by the experiments with a controlled task of foraging, we can verify if the general expectation that the perception of rewards of performing a task tends to encourage workers to engage in the task more strongly holds for a maximising task.

The results of our survival analysis suggest that individual experience does not strongly influence workers' task engagement on the moment-to-moment timescale. It would be interesting to empirically explore the influence of individual experience on task engagement at an extended timescale, for example, over a few days (Anja Weidenmüller, personal communication). Apart from individual experience, future work can investigate the influence of social experience on workers' task engagement by extending the experimental set-up (see Section 3.2) to multiple workers and brood dummies within one test arena (Linda Garrison and Anja Weidenmüller, experiments ongoing). The experiments in which multiple workers and brood dummies are set in a single test arena may also be used to test the hypotheses about the influence of social interaction on task allocation, for instance, the predictions from our game-theoretical models (see Chapter 4).

6.2.2 Theoretical Approaches

Our task-allocation game (introduced in Section 4.2) can be integrated with a variety of learning mechanisms that determine the dynamics of workers' strategies over time. Particularly, the model with task recruitment (see Section 4.5), potentially has much richer ecological details to further explore. The outcomes of our game-theoretical models are based on a game of allocation between a homeostatic task and a maximising task. Future research may investigate how the results can vary if a different type of task is introduced into this task-allocation game. One potential option could be inactivity, which is widely observed to take a large proportion of task repertoire in social insects (Charbonneau and Dornhaus, 2015a). The results may contribute to our understanding of the functional roles of the presence of inactive workers in a colony.

The question of how colonies can adapt to dynamic environments needs to be further studied. For the influence of within-worker factors, future work may explore whether environment-dependent rates of workers' reinforcement by individual experience can lead to a trade-off between efficiency and flexibility; For the influence of interactions between workers, further research could systematically investigate how fast colonies with different behavioural patterns can adapt to environmental fluctuations.

Overall, the outcomes of this research contribute to the knowledge of how the colony-level patterns of task allocation can emerge from individual task choice in social insects. Our methodology demonstrates a set of approaches for modelling in an interdisciplinary study. For the influence of within-worker factors, we regard task allocation as time-dependent

stochastic processes and explore temporal dynamics, facilitating a fine-grained analysis of
the empirical data and consequently improves our understanding of the underlying mecha-
nisms. How workers interact with others and their environments is one of the key questions
in the study of task allocation (Gordon, 2016). The modelling framework based on game
theory opens numerous opportunities to explore the dynamics of social interaction between
workers in a variety of ecological contexts. The game-theoretical models provide a new
self-organisational perspective for how task allocation can vary with environmental con-
ditions, as an alternative to the response-threshold models which are widely regarded as
the main paradigm in the literature (reviewed in Section 2.3.1). Our models can be used
to explain and predict the behavioural patterns of task allocation and to guide further
biological experiments. Our results may ultimately benefit the bio-inspired applications
such as swarm robotic systems (Krieger et al., 2000; Zhang et al., 2007) and multi-task
scheduling in factories (Bonabeau, Sobkowski, Theraulaz and Deneubourg, 1997; Campos
et al., 2000; Cicirello and Smith, 2004).

Appendix A

The Game-Theoretical Models

In this appendix, we give the supplementary material used to support the analysis and results for our game-theoretical models of task allocation. For each model, we present the additional results of our simulations including the mean payoff (evaluated as the average of mean payoffs of the colony over five time-periods at the steady state), the standard deviation and the Shannon entropy over a range of parameter values. In order to highlight the variation within a model under different environmental conditions, each figure presented in this section has a unique colour scheme.

A.1   Social Learning

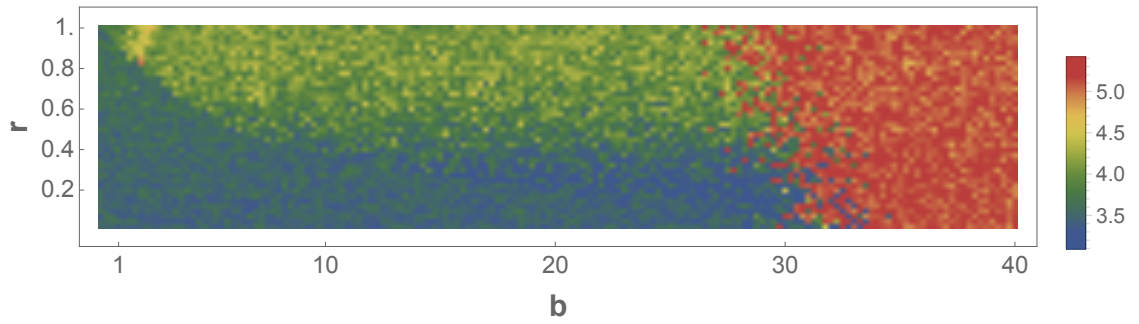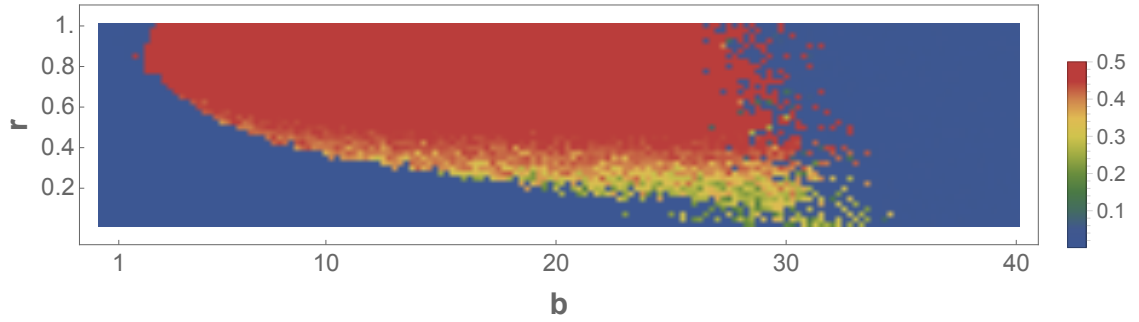(a) Mean Payoff

(b) Standard Deviation

(c) Shannon Entropy

Figure A.1: Results of the model with social learning for constant n at the steady state ($N = 2000$, $t_{end} = 120000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$).

(a) Mean Payoff

(b) Standard Deviation
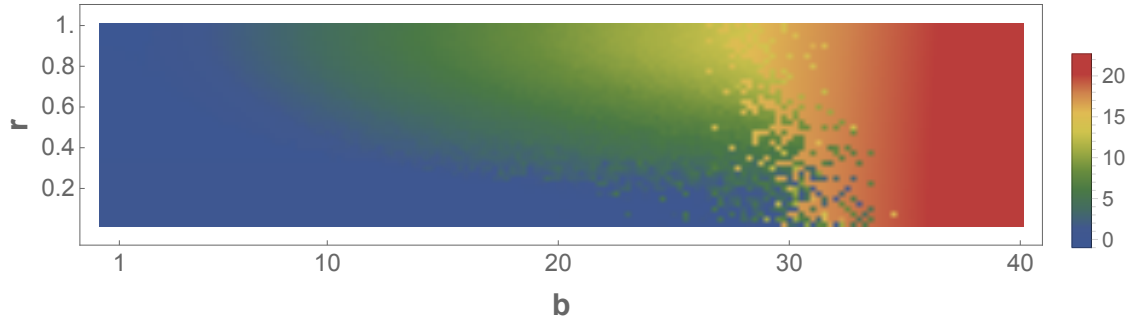

(c) Shannon Entropy

Figure A.2: Results of the model with social learning for constant b at the steady state ($N = 2000$, $t_{end} = 120000$, $b = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$).

A.2   Individual Reinforcement

(a) Mean Payoff
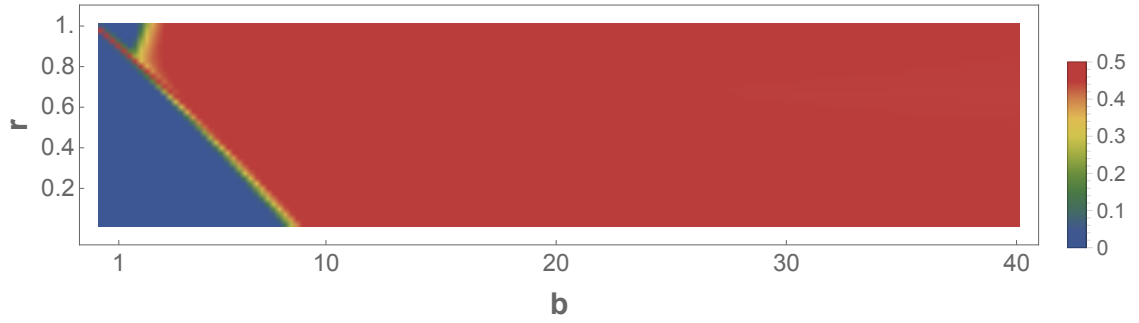
(b) Standard Deviation

(c) Shannon Entropy

Figure A.3: Results of the model with individual reinforcement at the steady state ($N = 2000$, $t_{end} = 120000$, $n = 10$, $\beta = 0.01$, $\gamma = 0.005$).

A.3   Task Recruitment
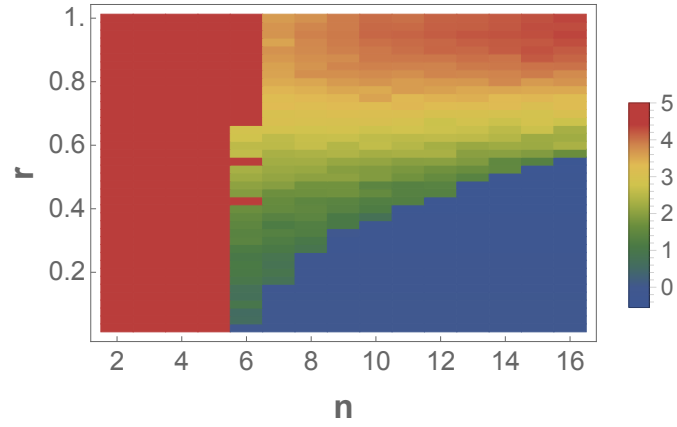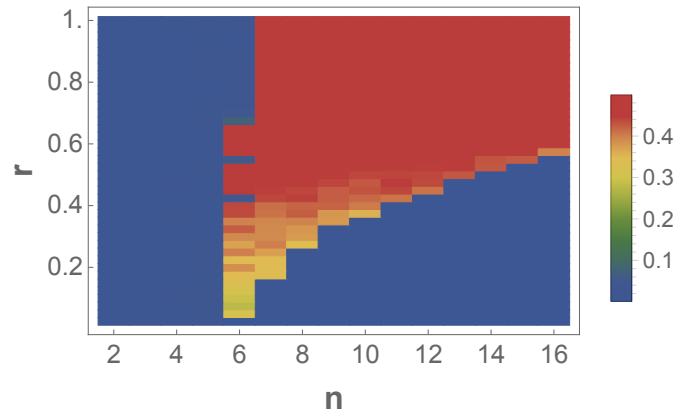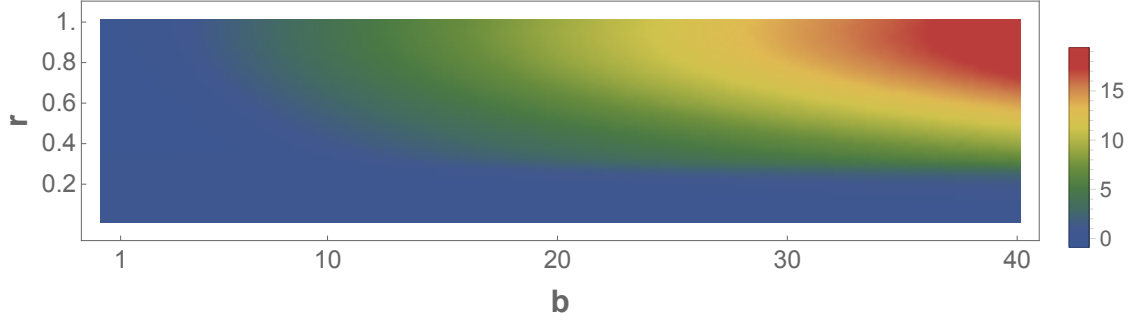

(a) Mean Payoff
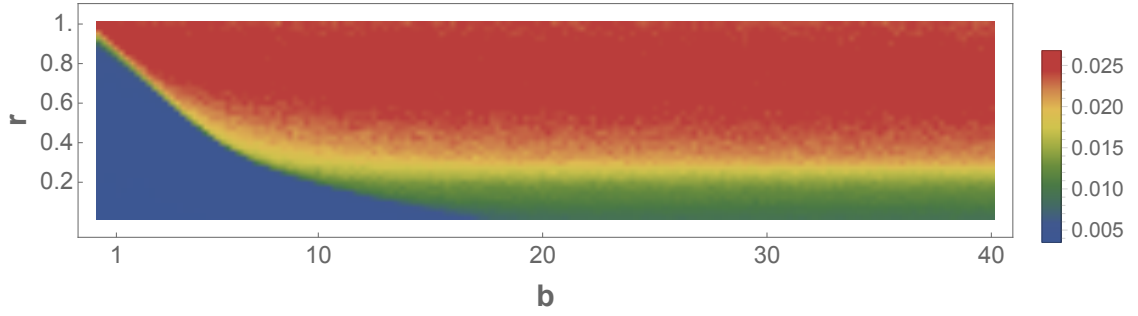
(b) Standard Deviation
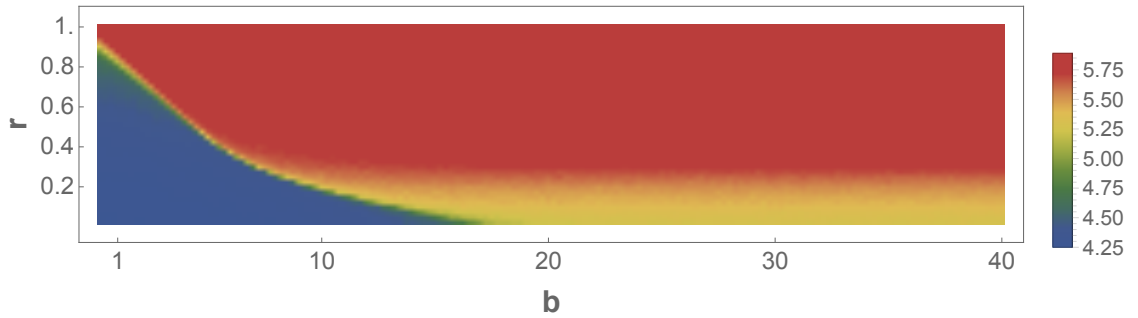
(c) Shannon Entropy
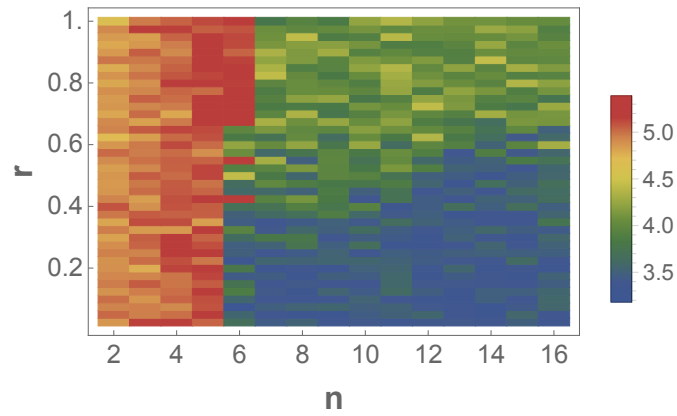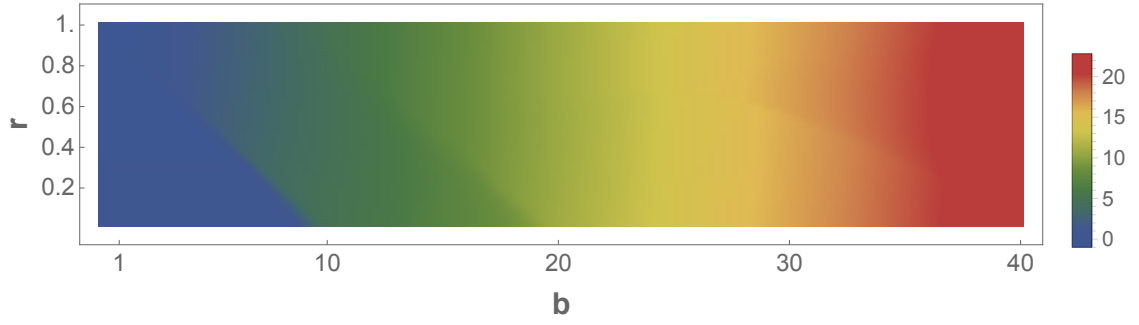
Figure A.4: Results of the model with task recruitment at the steady state ($N = 2000$, $t_{end} = 4000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$, $\rho = 0.005$).

A.3.1   Integration with Experience-based Reinforcement

(a) Mean Payoff

(b) Standard Deviation

(c) Shannon Entropy
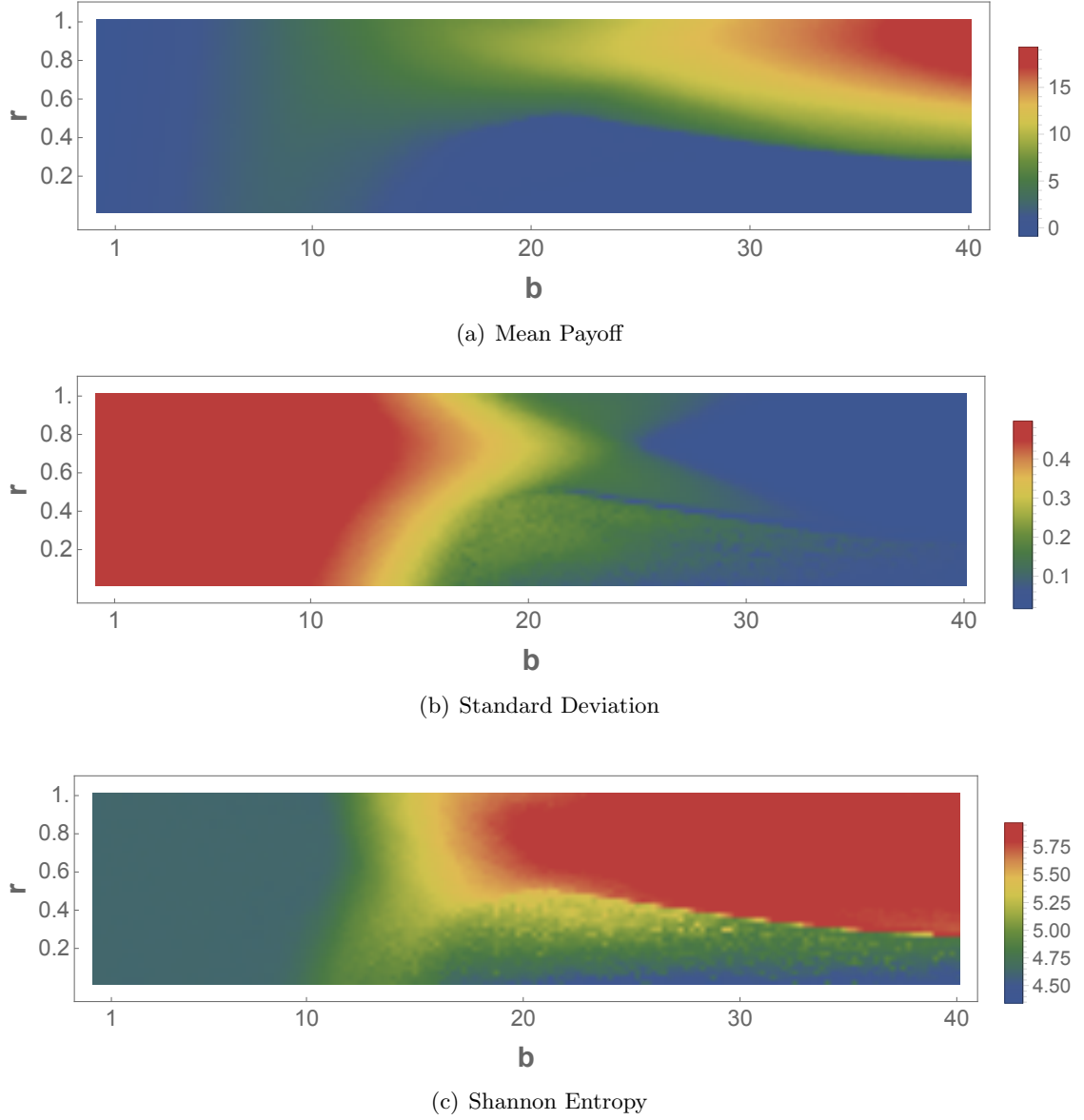
Figure A.5: Results of the model with task recruitment and reinforcement by individual experience at the steady state ($N = 2000$, $t_{end} = 4000$, $n = 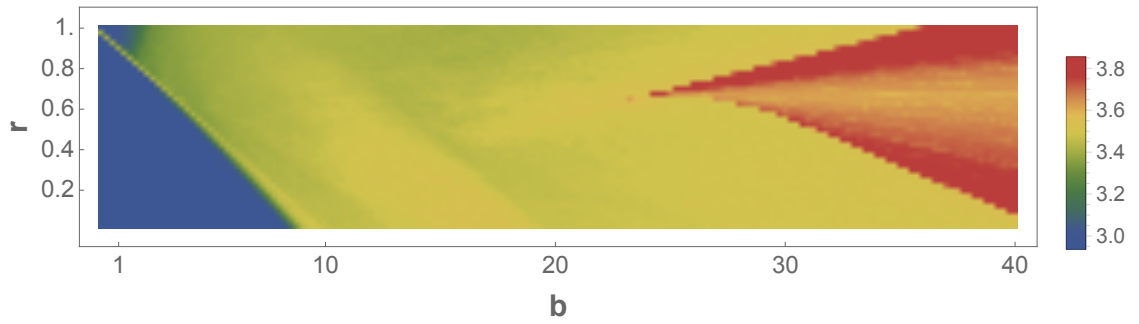10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$, $\rho = 0.005$, $E_0 = 1$, $\xi_{max} = 1.25$, $\varphi = -0.05$).

Algorithm 5 Model with task recruitment and reinforcement by individual experience

---

1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do** (* initialise w_i *)
3:     $x_i \leftarrow 0.5$ (* strategy *)
4:     $E_i^A \leftarrow E_0, E_i^B \leftarrow E_0$ (* individual experience *)
5:     $r \leftarrow random(0, 1)$
6:     $\xi_i^A \leftarrow r\xi_{max}, \xi_i^B \leftarrow \xi_{max} - \xi_i^A$ (* rate of experience reinforcement *)
7: **end for**
8: uniformly select and partition workers in the colony into multiple games of size n
9: **while** $t < t_{end}$ **do**
10:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
11:         $r \leftarrow random(0, 1)$
12:         **if** $r < x_i$ **then**
13:             $x_i^{'} \leftarrow 1$ (* w_i selects Task A *)
14:         **else**
15:             $x_i^{'} \leftarrow 0$ (* w_i selects Task B *)
16:         **end if**
17:     **end for**
18:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
19:         $\Pi_i \leftarrow B(X^{'}) - C(x_i^{'})$ (* w_i evaluates her payoff in the game g of workers with allocated tasks $X^{'} = \{x_j^{'} | w_j \in g\}$ *)
20:     **end for**
21:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
22:         $O \leftarrow merge(\{\Pi_k | k = 1, 2, ..., N\}, \{E_i^A, E_i^B\})$
23:         **if** $x_i^{'} = 1$ **then**
24:             $E_i^A \leftarrow E_i^A + \xi_i^A$
25:         **else**
26:             $E_i^B \leftarrow E_i^B + \xi_i^B$
27:         **end if**
28:         $E_i^A \leftarrow E_i^A e^{\varphi}, E_i^B \leftarrow E_i^B e^{\varphi}$
29:         select k randomly according to probabilities $p_k = e^{\alpha O_k} / \sum_k e^{\alpha O_k}$
30:         (* $k = 1, 2, ..., N + 2$ *)
31:         **if** $k = N + 1$ **then**
32:             $x_i^{'} \leftarrow 1$
33:         **else if** $k = N + 2$ **then**
34:             $x_i^{'} \leftarrow 0$
35:         **else**
36:             $x_i^{'} \leftarrow x_k^{'}$
37:         **end if**
38:         (* w_i follows a task based on her experience or a task others perform *)
39:         **if** $x_i^{'} = 1$ **then**
40:             $x_i \leftarrow \rho + (1 - \rho)x_i$
41:         **else**
42:             $x_i \leftarrow (1 - \rho)x_i$
43:         **end if**
44:     **end for**
45:     $m \sim Binomial(N, \beta)$
46:     select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
47:     **for** worker $w_i \in M$ **do**
48:         $x^{''} \sim Normal(x_i, \gamma)$
49:         $x_i \leftarrow x^{''}$
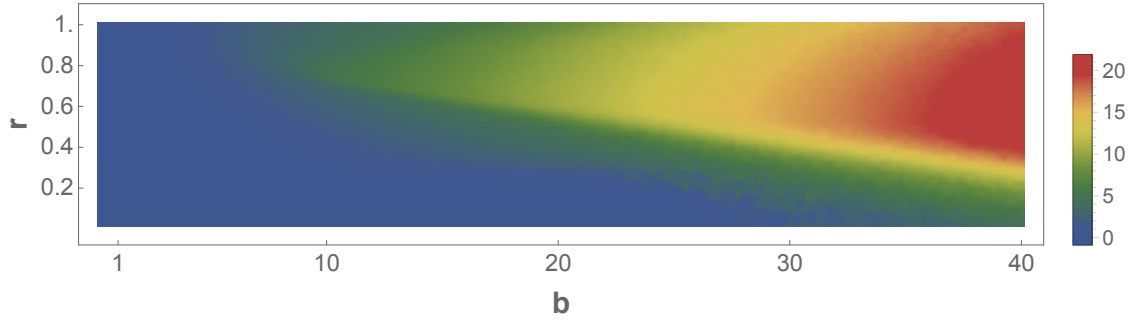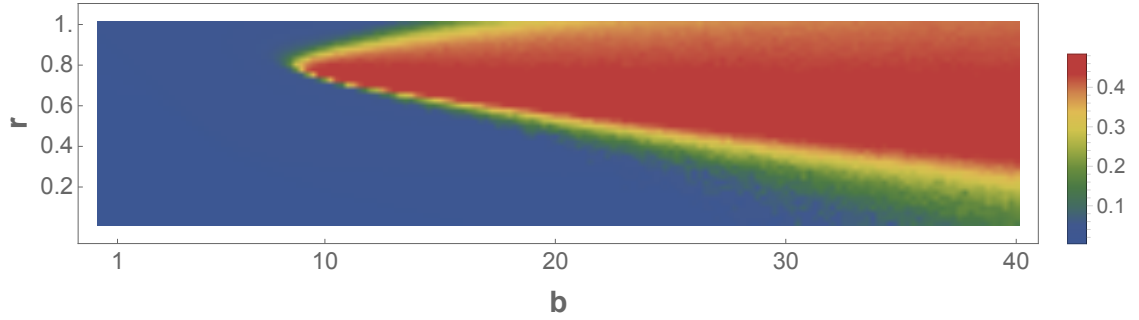50:   (* w_i innovates her strategy *)
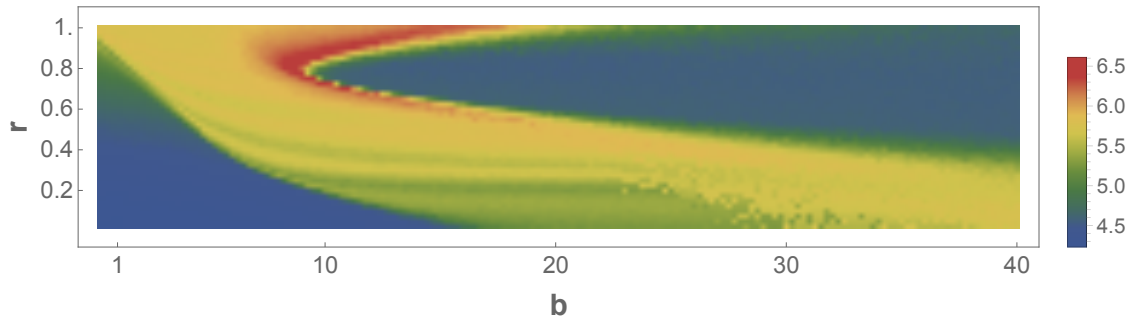51:   **end for**
52: **end while**

(a) Mean Payoff

(b) Standard Deviation

(c) Shannon Entropy

Figure A.6: Results of the model with task recruitment and reinforcement by social expe-
rience at the steady state ($N = 2000$, $t_{end} = 4000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$,
$\rho = 0.005$, $E_0 = 1$, $\varphi = -0.325$).

Algorithm 6 Model with task recruitment and reinforcement by social experience
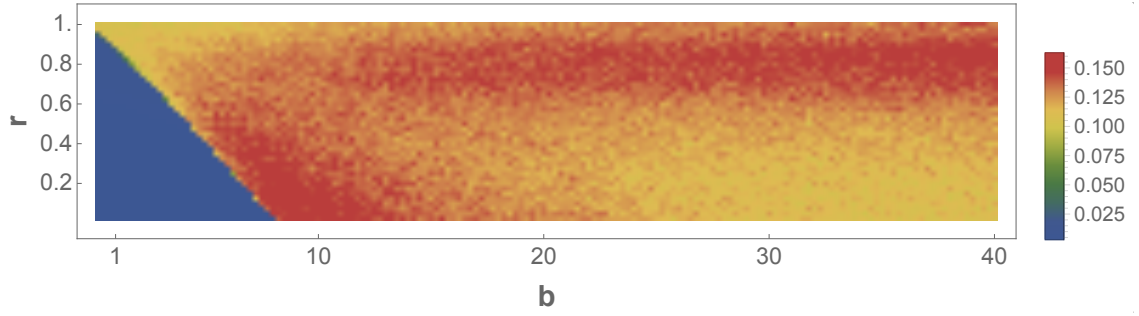

1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do** (* initialise w_i *)
3:      $x_i \leftarrow 0.5$ (* strategy *)
4:      $E_i^A \leftarrow E_0, E_i^B \leftarrow E_0$ (* social experience *)
5: **end for**
6: uniformly select and partition workers in the colony into multiple games of size n
7: **while** $t < t_{end}$ **do**
8:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
9:          $r \leftarrow random(0, 1)$
10:          **if** $r < x_i$ **then**
11:              $x_i' \leftarrow 1$ (* w_i selects Task A *)
12:          **else**
13:              $x_i' \leftarrow 0$ (* w_i selects Task B *)
14:          **end if**
15:      **end for**
16:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
17:          $\Pi_i \leftarrow B(X') - C(x_i')$ (* w_i evaluates her payoff in the game g of workers with allocated tasks $X' = \{x_j' | w_j \in g\}$ *)
18:      **end for**
19:      **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
20:          $O \leftarrow merge(\{\Pi_k | k = 1, 2, ..., N\}, \{E_i^A, E_i^B\})$
21:          **if** $x_i' = 1$ **then**
22:              $E_i^A \leftarrow E_i^A + \Pi_i$
23:          **else**
24:              $E_i^B \leftarrow E_i^B + \Pi_i$
25:          **end if**
26:          $E_i^A \leftarrow E_i^A e^\varphi, E_i^B \leftarrow E_i^B e^\varphi$
27:          select k randomly according to probabilities $p_k = e^{\alpha O_k} / \sum_k e^{\alpha O_k}$
28:          (* $k = 1, 2, ..., N + 2$ *)
29:          **if** $k = N + 1$ **then**
30:              $x_i' \leftarrow 1$
31:          **else if** $k = N + 2$ **then**
32:              $x_i' \leftarrow 0$
33:          **else**
34:              $x_i' \leftarrow x_k'$
35:          **end if**
36:          (* w_i follows a task based on her experience or a task that others perform *)
37:          **if** $x_i' = 1$ **then**
38:              $x_i \leftarrow \rho + (1 - \rho)x_i$
39:          **else**
40:              $x_i \leftarrow (1 - \rho)x_i$
41:          **end if**
42:      **end for**
43:      $m \sim Binomial(N, \beta)$
44:      select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
45:      **for** worker $w_i \in M$ **do**
46:          $x'' \sim Normal(x_i, \gamma)$
47:          $x_i \leftarrow x''$
48:          (* w_i innovates her strategy *)
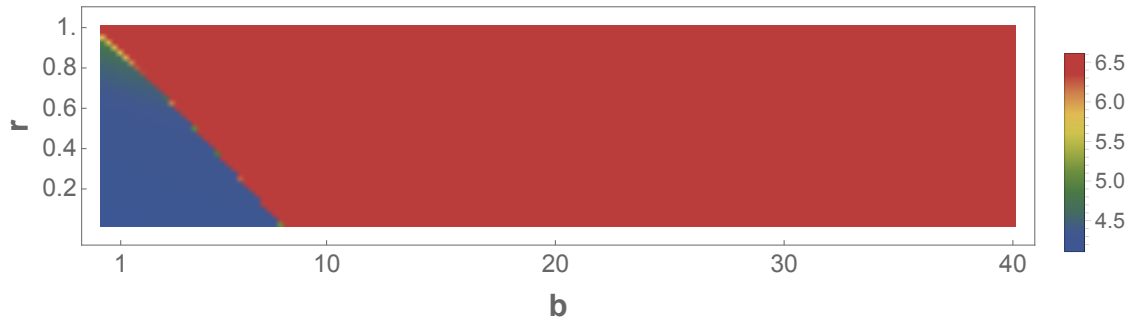49:   **end for**
50: **end while**

A.3.2 Integration with Spatial Fidelity
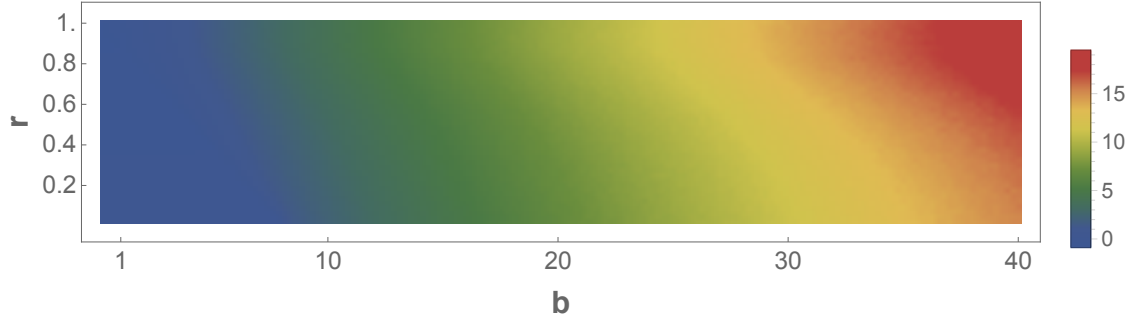
(a) Mean Payoff

(b) Standard Deviation

(c) Shannon Entropy

Figure A.7: Results of the model with task recruitment and spatial fidelity at the steady state ($N = 2000$, $t_{end} = 10000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$, $\rho = 0.005$, $n' = 10$).

Algorithm 7 Model with task recruitment and spatial fidelity

1: $t \leftarrow 0$ (* initialise time *)
2: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
3:     $x_i \leftarrow 0.5$ (* initialise w_i *)
4: **end for**
5: uniformly select and partition workers in the colony into multiple recruiting groups of size n'
6: **while** $t < t_{end}$ **do**
7:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
8:         $r \leftarrow random(0, 1)$
9:         **if** $r < x_i$ **then**
10:             $x'_i \leftarrow 1$ (* w_i selects Task A *)
11:         **else**
12:             $x'_i \leftarrow 0$ (* w_i selects Task B *)
13:         **end if**
14:     **end for**
15:     uniformly select and partition workers in the colony into multiple games of size n
16:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
17:         $\Pi_i \leftarrow B(X') - C(x'_i)$ (* w_i evaluates her payoff in the game g of workers with allocated tasks $X' = \{x'_j | w_j \in g\}$ *)
18:     **end for**
19:     **for** each recruiting group g in the colony **do**
20:         **for** worker $w_i \in g$ **do**
21:             select w_k randomly according to probabilities $p(w_k) = e^{\alpha \Pi_k} / \sum_k e^{\alpha \Pi_k}$
22:             (* $w_k \in \{w_j | w_j \in g\}$ *)
23:             $x'_i \leftarrow x'_k$
24:             (* w_i selects a worker w_k from g and follows her task *)
25:         **end for**
26:     **end for**
27:     **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
28:         **if** $x'_i = 1$ **then**
29:             $x_i \leftarrow \rho + (1 - \rho)x_i$
30:         **else**
31:             $x_i \leftarrow (1 - \rho)x_i$
32:         **end if**
33:     **end for**
34:     $m \sim Binomial(N, \beta)$
35:     select m workers uniformly from $\{w_j | j = 1, 2, ..., N\}$ into M
36:     **for** worker $w_i \in M$ **do**
37:         $x'' \sim Normal(x_i, \gamma)$
38:         $x_i \leftarrow x''$
39:         (* w_i innovates her strategy *)
40:     **end for**
41: **end while**

Appendix B

The Extended Time-Resolved Model

Algorithm 8 Extended time-resolved model of task allocation at short timescales

---

1: $t \leftarrow 0$ (* initialise time *)
2: $T_{in} \leftarrow \theta_A$ (* initialise nest temperature *)
3: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
4:     $state(w_i) \leftarrow B$
5:     $rate(w_i) \leftarrow \lambda_B$
6:     (* initialise w_i *)
7: **end for**
8: **while** $t < t_{end}$ **do**
9:     $H \leftarrow \sum_i rate(w_i)$ (* $i = 1, 2, ..., N$ *)
10:     $\Delta t \sim Exponential(H)$ (* draw next event interval *)
11:     $t \leftarrow t + \Delta t$
12:     select w_i randomly according to probabilities $p(w_i) = rate(w_i)/H$
13:     **if** $state(w_i) = A$ **then**
14:         $state(w_i) \leftarrow R$
15:         $rate(wi) \leftarrow \lambda_A$
16:         (* w_i starts her refractory period after performing Task A *)
17:     **else**
18:         $n \leftarrow random(0, 1)$
19:         **if** $n < p_A(w_i) \wedge T_{in} > \theta_A$ **then**
20:             $state(w_i) \leftarrow A$
21:             $rate(w_i) \leftarrow \mu_A$
22:             (* w_i starts to perform Task A *)
23:         **else**
24:             $state(w_i) \leftarrow B$
25:             $rate(w_i) \leftarrow \lambda_B$
26:             (* w_i starts to be engaged in Task B *)
27:         **end if**
28:     **end if**
29:     $G_A = \{w_i | state(w_i) = A, i = 1, 2, ..., N\}$
30:     $N_A \leftarrow |G_A|$ (* number of workers engaged in Task A *)
31:     $T_{in} \leftarrow T_{in} + \left(T_{out} - T_{in} + \frac{\alpha - \beta N_A}{Kr}\right)(1 - e^{-r\Delta t})$ (* update nest temperature *)
32: **end while**

Algorithm 9 Extended time-resolved model of task allocation at long timescales

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1: $t \leftarrow 0$ (* initialise time *)
2: $T_{in} \leftarrow \theta_A$ (* initialise nest temperature *)
3: $T_{out} \leftarrow 30$ (* initialise ambient temperature *)
4: **for** worker $w_i \in \{w_j | j = 1, 2, ..., N\}$ **do**
5:    $state(w_i) \leftarrow B$
6:    $rate(w_i) \leftarrow \lambda_B$
7:    $E_A^i \leftarrow E_0$ (* experience of Task A *)
8:    $E_B^i \leftarrow E_0$ (* experience of Task B *)
9:    (* initialise w_i *)
10: **end for**
11: **while** $t < t_{end}$ **do**
12:    $H \leftarrow \sum_i rate(w_i)$ (* $i = 1, 2, ..., N$ *)
13:    $\Delta t \sim Exponential(H)$ (* draw next event interval *)
14:    $t \leftarrow t + \Delta t$
15:    select w_i randomly according to probabilities $p(w_i) = rate(w_i)/H$
16:    **if** $state(w_i) = A$ **then**
17:      $E_A^i \leftarrow (1 - \rho)E_A^i + \rho c$
18:      $state(w_i) \leftarrow R$
19:      $rate(wi) \leftarrow \lambda_A$
20:      (* w_i starts her refractory period after performing Task A *)
21:    **else**
22:      **if** $state(w_i) = B$ **then**
23:        $E_B^i \leftarrow (1 - \rho)E_B^i + \rho c$
24:      **end if**
25:      select a task k randomly according to probabilities $p_k = \frac{(E_k^i+m)^\gamma}{\sum_k (E_k^i+m)^\gamma}$
26:      (* $k = A, B$ *)
27:      **if** $k = A \wedge T_{in} > \theta_A$ **then**
28:        $state(w_i) \leftarrow A$
29:        $rate(w_i) \leftarrow \mu_A$
30:        (* w_i starts to perform Task A *)
31:      **else**
32:        $state(w_i) \leftarrow B$
33:        $rate(w_i) \leftarrow \lambda_B$
34:        (* w_i starts to be engaged in Task B *)
35:      **end if**
36:    **end if**
37:    $G_A = \{w_i | state(w_i) = A, i = 1, 2, ..., N\}$
38:    $N_A \leftarrow |G_A|$ (* number of workers engaged in Task A *)
39:    $T_{out} \leftarrow 2\sin(0.01t + \pi) + 30$
40:    $T_{in} \leftarrow T_{in} + \left(T_{out} - T_{in} + \frac{\alpha - \beta N_A}{Kr}\right)(1 - e^{-r\Delta t})$ (* update nest temperature *)
41: **end while**

Vita

Publications arising from this thesis include:

Meyer, B., Weidenmüller, A., Chen, R. and García, J. (2015). Collective homeostasis and time-resolved models of self-organised task allocation, *Proceedings of the 9th EAI International Conference on Bio-inspired I.C.T.*, New York City, NY.

Chen, R., Weidenmüller, A., and Meyer, B. (2017). Moment-to-moment task allocation in bumblebees, in preparation.

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