

修士学位論文

Individuality and Wholeness through Data Analysis  
of  
Honey Bee Hive

(セイヨウミツバチの巣内データ解析を通してみる個性性と全体性)

東京大学 総合文化研究科  
広域システム科学系

31-136824 土井 樹



## Abstract

Many global patterns and dynamics observed in a social system often reflect and amplify the underlying characteristics of its constituents. Although there are many studies linking global and the local social dynamics and patterns, the relation between the organized global pattern and the behaviors of the individual constituents has not yet been fully understood. In this thesis, I analyzed a set of individualized behavioral records of a honey bee (*Apis mellifera*) hive. I used the data of the positions and orientations of every bee in a hive recorded every second for approximately one week. I then defined and measured the activity level of each individual as well as the entire hive as a collective activity. The hive often exhibited bursting behaviors and that some of the bees became highly active before the bursts. I found that some of these bees cause bursts multiple times, suggesting that the individuality has hardly ignorable influences on the global organization of the whole social collective behavior.

# Contents

1	Introduction	6
1.1	Individuality and Wholeness . . . . .	6
1.2	Motivation . . . . .	7
1.2.1	Motivation from biology point of view . . . . .	7
1.2.2	Motivation from physics point of view . . . . .	8
1.3	Introduction of Honey bee biology . . . . .	8
1.4	Scope of this thesis . . . . .	10
1.5	Structure of this thesis . . . . .	10
2	Methods/Analysis	11
2.1	Experimental setup . . . . .	11
2.2	Data . . . . .	11
2.3	Detection of bursts . . . . .	13
2.4	Cross-correlation analysis . . . . .	13
2.5	Kullback-Leibler divergence . . . . .	14
2.6	Multivariate statistics . . . . .	14
2.6.1	Non-negative matrix factorization (NMF) . . . . .	14
2.6.2	Non-metric multi dimensional scaling . . . . .	15
3	Results	16
3.1	Bursts as collective behavior in a honey bee hive . . . . .	16
3.1.1	Whole image of activities of bees. . . . .	16
3.1.2	Bursts have two types, endogenous and exogenous . . . . .	22
3.2	Classifying the bees' behavior by their activities and activity timings	30
3.2.1	Classifying the bees' behavior by their activity timing . . . . .	30
3.2.2	Classifying the activities of bees into three types . . . . .	33
3.3	Is there any stable 'personality'? . . . . .	37
4	Discussion	40
4.1	Overall discussion . . . . .	40
5	Conclusions and Future works	42
5.1	Conclusions . . . . .	42
5.2	Future work . . . . .	42
6	Acknowledgment	45



# 1 Introduction

## 1.1 Individuality and Wholeness

The question about relations between individuals (parts) and wholeness has been discussed by many scientists and humanities for a long time. When we observe phenomena, we often decompose them into *indivisible entities* and *their collections* even now.

These indivisible entities often have their own features or individualities. Taking a look at our life level, the individuality of a person has hardly ignorable effects on the group or the society. A society consists of individuals, and the collective dynamics must be due ultimately to the behaviors of the constituent individuals. The latter must often be strongly affected by the former. That is, individual activities should collectively determine the collective dynamics and also the latter should often strongly affect individuals.

How has science handled individuality? The priority of individuality differs dependent on the science fields.

Physics has basically ignored the individuality as the property of elements but instead prefers to find the global tendency exhibited in phenomena. Efforts have been made to reduce accidental elements by paying attention to fundamental laws since Newtonian mechanics. Needless to say, science has developed thanks to paying more attention to global patterns but paying less attention to individuality. For example, statistical physics has illusion in explanation of thermodynamics which had been explained in terms of macroscopic phenomenology. Extracting collective features is a staple of statistical physics, but an individuality is almost difficult things of conventional physics.

On the other hand, biology is traditionally (i.e. natural history) the field which have dealt with the individualities. In biology study, indivisible entities are cells or a individuals themselves. Such indivisible things are categorized based on their own features. For example, a cell has many types, neurons, white blood cells, mast cells or something, also, neurons has many types, pyramidal neurons, chattering cells, basket cells etc. In addition, there are many kinds of life on earth. Natural history has categorized life in terms of their own features and has tried to understand the diversity of life. Namely, the significance point of natural history is the describing the detailed features and individuality of the things. If

natural historian have not dealt with the detailed features of the things, classical biologists could not have conceived evolution. Also, ethology has handled the individuality. For example, in the ethological study of primates, the individuality of components which compose the society is a main issue [Azuma and Toyoshima, 1961]. However, the ethological description with individual identification have basically been confined to vertebrates.

## 1.2 Motivation

The motivations of this thesis are two viewpoints: the physics side, and the other from the biological side.

### 1.2.1 Motivation from biology point of view

From biology point of view, attempts to understand social structures and functions with individual identification have been confined to vertebrates: primates [Azuma and Toyoshima, 1961], cetaceans [Whitehead et al., 2000], corvids [Seed et al., 2009], and some fishes [Acuña-Marrero et al., 2014] and no example outside Deuterostomia exists. Needless to say, sociobiology of Prokaryota and unicellular Eukaryota has been extensively studied, but no individualized study exists. There seem to be some universal features behind social activities, so it should be interesting to try to treat the insect society just as we handle primate societies. One of the reasons that no individualized study exists outside Deuterostomia is that the number of individuals in a group is a large scale (at the level of classical biology) and it is difficult to get detailed data of individuals. Also, it is difficult for classical biological methods to handle such big data. However, in these days, individual tracking methods have been developed and we can get an individualized detailed record of the “history” of a society. In addition, using big data analysis methods, we can extract features of observed phenomena even if the data are too big for human to observe them.

In order to propose an example I was asked to analyze the phenomena that are observed in an insect society composed from a large amount of individuals, I chose honey bee (*Apis mellifera*). A honey bee is known as a eusocial insect that is not Deuterostomia but Protostomia. Also, since bees have thymogenic reactions, and since they must be at least partially under the control of genetics [Chandrasekaran et al., 2011], we can expect personality differences among bees.

To sum up, the motivation from biology point of this study is to propose individualize ethological study of species in Protostomia.

### 1.2.2 Motivation from physics point of view

From physics point of view, the social features are collective features, so the problem of individual-society relation looks like devising collective coordinates to describe an ensemble of entities. However, a major difference is the permanent non-uniformity of the “microscopic” (i.e., honey bee itself) entities (if some sort of personality is stable). Since bees exhibit emotional reactions, and since they must be at least partially under the control of genetics, we can expect personality differences among bees. Extracting collective features is a staple of statistical physics, but individuality is almost a nemesis of conventional physics. In other words, we can say that conventional physics has merely observed individuality independent phenomena. How can we expand the scope of statistical physics? What is the major difference between physical and social collective coordinates? I would like to think about individuality dependent phenomenon in order to expand the scope of statistical physics.

Therefore, the purpose of this thesis is to explore the feasibility of individual-social-collective relation study a honey bee society as an example.

## 1.3 Introduction of Honey bee biology

Here, I introduce honey bee biology shortly. Honey bees are known as insects that show the phenomenon of *eusociality*. *Eusociality* is characterized by the following three features:

1. A reproductive division of labor evolves from sterile castes which often have certain propensities or characteristics associated with helping behavior
2. There is an overlapping of generations which allows for the older generations of offspring to help related younger generations.
3. conducting cooperative care of young.

A typical colony consists of a queen—the reproductive member of the colony—along with several thousand female workers and, in the late spring and summer, some male bees called drones and virgin queens.

The workers perform all tasks related to the day-to-day functioning of the colony, and the experiment is designed to probe division of labor among workers on the timescale of several days.

The simplest classification of workers by task is in two types. The first type is “forager”: those workers that leave the hive and forage for pollen, nectar and



water in the external world and the second type is called “hive bees” that work in the hive. Honey bee division of labor is characterized by temporal polyethism. Young worker bees, sometimes called “nurses”, clean the hive and feed the larvae. They progress to other within-colony tasks as they become older, such as receiving nectar from foragers, and guarding the hive. Later still, a worker takes her first orientation flights and finally leaves the hive and typically spends the remainder of her life as a forager.

My collaborators’ experiments used single-cohort colonies, in which the worker bees are all of the same age (one day old at the start of the experiment) [Robinson et al., 1989]. Single-cohort colonies are initially composed of a few thousand young bees, some bees begin foraging when they are as young as 3-4 days old while others show normal behavioral development and act as nurse bees.

This kind of colony commonly is used in experiments that deal with division of labor in order to control the effect of age, and instead focus on the behavioral development of worker bees as a function of their genetics and social interactions. At the age of three or four days, most worker bees perform orientation flights, which serve the purpose of teaching the bees how to forage in the surrounding landscape. In a wild colony, a bee can spend several days following orientation as a hive bee, before eventually assuming foraging duties. However, in a single-cohort colony experiment, because there are no foragers at the beginning, some of the young worker bees accelerate their development because of some hormone and become precocious foragers, effectively skipping the hive bee stage. Thus, in single-cohort experiments, we can observe a transition from homogeneous to heterogeneous of the characters of bees. A fundamental question in division of labor study is how this behavioral development arises as a result of social interactions among bees. It has been proposed that the development of a honey bee is regulated by a substance known as juvenile hormone [Riddiford, 1994]: foragers are likely to have higher levels of this hormone. The social inhibition hypothesis claims that the presence of foragers inhibits the synthesis of the hormone in the other bees and the colony is able to maintain the number of bees that become foragers [Robinson, 1987].

Direct interactions among bees in a colony take place in many ways. They can emit pheromones that diffuse through the colony and affect their physiology. Bees often exchange food and this can also serve a communicational function. This “mouth-to-mouth” contact communication has been called “trophallaxis”. And they can make movements that are sensed by surrounding bees via antennae; the famous honey bee dance language used in forager recruitment falls into this category. In addition, stigmergy is also argued in eusocial insect study including honey bee. The term “stigmergy” was introduced by French biologist Pierre-Paul Grassé in 1959 to refer to termite behavior. He defined it as: “Stimulation of workers by the performance they have achieved.” Namely, stigmergy means

indirect communication mediated by modifications of the environment [Camazine, 2003].

## 1.4 Scope of this thesis

In order to explore the said feasibility we must choose a well-defined small target. The activity peaks are selected as our target, because that is easily noticeable from the observation of a hive or the time course of a certain hive activity measure, e.g., the kinetic energy and the sum is over all the bees in the hive. The (major) peaks will be called “bursts”. A burst is a hive-wise commotion in which many bees increase their activity. The questions we wish to ask are:

- (i) What causes a burst? Or, how does a burst develop?
- (ii) What are the individual contributions to the burst?

In (i) the ‘what’ question is a hard problem that could ask about the intrinsic fluctuation level and physiological states of bees. First, I have to elucidate the ‘how’ question through detailed observations of each burst.

Instead, I will study (ii). The relation between the activities of individual bees and the overall burst is dissected to explore whether some sort of stable “personality” is relevant. I will refer to the definition of “personality” in results section.

## 1.5 Structure of this thesis

This thesis is composed of 6 sections. In following Section 2, I will refer about experimental setup, the composition of data, the data cleaning and analyzing methods. In Section 3, I will give the results with unsuccessful results. In Section 4, I discuss the results. Finally, Section 5 provides the conclusion of this thesis and describes a future plan.

## 2 Methods/Analysis

### 2.1 Experimental setup

All activity-tracking experiments were conducted at the University of Illinois Bee Research Facility in Urbana, Illinois, over the period of a week beginning July 4, 2012. Our collaborator Tim Gernat set up an experiment in which individual bees in a single-cohort colony were labeled with matrix codes, placed inside a special glass-walled hive, and tracked using a high-resolution camera taking a picture per second. The matrix codes were designed to give position and orientation information about each bee, and so we could map the positions and orientations for each individual in this hive over the course of the whole experiment. Since the glass wall was often polluted by the honey bees, the glass wall was cleaned by experimenter (I will call this “glass cleaning”).

Initial help of Mr. Nobutaka Kurobe of DENSO was useful. In addition, the help of Mr. Takashi Iwahori of NITTO was crucial in order to print miniature matrix codes. The hive had a small entrance, which was closed until time July 6, 2012. The number of honey bees gradually decreased once the entrance was opened, due to returning bees losing the location of the hive or being preyed on by other species.

### 2.2 Data

Tim Gernat generated the basic data to this research. The general format of the original data is shown in Table 1. This data includes all coordinates and locations of honey bees as a text file, with time indicated using UNIX time. The range of  $x$  is from 0 to 6576 and that of  $y$  is from 0 to 4384. The hive was composed of an assembly of hexagonal structures; the hexagons measured 100 between sets of parallel sides. As shown in the previous section, some bees disappeared from the hive, so I had to make a list of “survived” bees. I removed bees that were detectable for less than 100 seconds during the evening of the experiment’s final day (July 12, 2012) and, as a result, the number of survived bees was 589, including one queen bee. In addition, honey bees could not be detected when they were sleeping

and data were deficient, so deficient data were supplemented with the data of the preceding period because the sleeping bees were not moving.

	Time	x	y	nx	ny	bee
1	1.341356e+12	5157	2668	-0.16439901	-0.98639400	707
2	1.341356e+12	4507	979	0.26658610	-0.96381116	1520
3	1.341356e+12	3897	3303	0.24783325	0.96880270	1433
4	1.341356e+12	2470	1472	0.18807228	-0.98215526	677
5	1.341356e+12	6262	1282	-0.36765890	-0.92996070	1276
6	1.341356e+12	2175	3023	-0.04163054	-0.99913310	1000
7	1.341356e+12	1272	3457	0.66561490	-0.74629545	148
8	1.341356e+12	2815	2654	0.47885212	-0.87789553	54
9	1.341356e+12	1095	1131	0.82219220	-0.56921005	1161
10	1.341356e+12	1560	1375	0.72758940	-0.68601286	744
11	1.341356e+12	5014	401	-0.88583153	0.46400700	476
12	1.341356e+12	5664	3210	0.10578603	-0.99438894	1200
13	1.341356e+12	5534	1740	0.04163054	-0.99913310	286
14	1.341356e+12	3568	1921	0.00000000	-1.00000000	1722
15	1.341356e+12	3345	2520	0.02040394	-0.99979186	610
16	1.341356e+12	408	1757	0.42288548	-0.90618310	1590
17	1.341356e+12	2406	3115	-0.49613900	0.86824316	288
18	1.341356e+12	5066	2309	0.97368810	0.22788447	1530
19	1.341356e+12	2119	3343	-0.80000000	-0.60000000	667
20	1.341356e+12	2472	839	-0.98354715	-0.18065150	85

Table 1: General format of the original dataset

In order to manage every dataset, we used MySQL, which is the most widely used open-source relational database management system (<http://www.mysql.com/>). Since MySQL can apply an “index” to every datum, we could use it to access the dataset of each bee, each time or each coordinate directly and rapidly. With a view to exploring the feasibility of this method, I had to choose a well-defined small target. We selected the activity peaks as our target, as they easily were noticeable from the hive-wise movie or the time course of a certain hive activity measure.

The step size per second is often used as a measure of the activity of an individual [Jordan et al., 2013]. In my thesis, in order to visualize more clearly individual activity, I used the square of the step size. I defined a bee’s kinetic energy  $K$  as:

$$K = \Delta x^2 + \Delta y^2, \quad (1)$$

where  $\Delta x$  and  $\Delta y$  denote the displacement of the  $x$  and  $y$  coordinates of the bees per second, respectively.

Also, the hive activity level  $K_s(t)$  is defined as the “mean kinetic energy”:

$$K_{global}(t) = \frac{1}{n} \sum_b K_{individual}(t). \quad (2)$$

This value is macroscopic value that characterizes the state of the hive. I used  $K_{global}(t)$  as the indicator of the hive activity. Through such data cleaning and data making, finally, I composed three big matrix (645349rows  $\times$  589columns), in which the rows denote time, the columns denote bee ID, and the cell contents were positions  $(x,y)$  or kinetic energies.

## 2.3 Detection of bursts

As shown in the results section, the time series of  $K_{global}(t)$  often indicated a sudden increase. We call such behavior a “burst”, which results from the collective behavior of honey bees. Since the most salient property of the time series is bursting behavior, analyzing bursts may be a first step toward understanding the relationship between individual behavior and collective behavior.

Baseline and burst periods were determined by using the Kleinberg burst detection algorithm [Kleinberg, 2003]. The Kleinberg algorithm assumes the Poisson process for the activity of the hive. This model is a hidden Markov process in which, after each event, the state of the system probabilistically determines how much time will pass until the next event occurs. While the system is in state  $i$ , the gaps between events are assumed to be drawn from an exponential distribution with expected value proportional to  $s^{-i}$  where  $s$  is the base of the exponent used to determine event frequencies in a given state. The value of  $s$  can be modified; higher values increase the strictness of the algorithm’s criterion for how dramatic an increase of activity has to be to be considered a “burst”. I set  $s = 2$ . The cost of a state change is proportional to the increase in state number; this proportion can be modified by setting the parameter gamma. Higher values mean roughly that bursts must be sustained over longer periods of time in order for the algorithm to recognize them. I set  $gamma = 1$ . Although “burst” means chattering active potential in neuroscience study (i.e., one neuron can show a burst), I define “burst” as global burst synchronization in this thesis. This kind of definition is often used in social or computer science.

## 2.4 Cross-correlation analysis

Cross-correlation is a measure of similarity between two waveforms as a function of a time-lag applied to one of them. Using cross-correlation analysis, I measured a relationship between the activity levels of the hive and of each individual bee. In neuroscience, cross-correlation analysis has been used to estimate the functional

binding in the neural network [Pernice et al., 2011].

$$C(\tau) = \lim_{T \rightarrow \infty} \int_{-\frac{T}{2}}^{\frac{T}{2}} K_{global}(t) K_{individual}(t + \tau) dt, \quad (3)$$

where  $K_{global}(t)$  and  $K_{individual}(t)$  are the hive energy and the individual bee energy.  $K_{global}(t)$  denotes a summation of all  $K_{individual}(t)$ .  $T$  is the measuring time and  $\tau$  is the time lag.

## 2.5 Kullback-Leibler divergence

Kullback-Leibler divergence is a non-symmetric measure of the difference between two probability distributions  $P$  and  $Q$ . The Kullback–Leibler divergence of  $Q$  from  $P$ , denoted by  $D_{KL}(P|Q)$ , is a measure of the information lost when  $Q$  is used to approximate  $P$ . [Kullback and Leibler, 1951]

The equation is

$$D_{KL}(P|Q) = - \sum_x p(x) \log q(x) + \sum_x p(x) \log p(x) \quad (4)$$

where  $p$  and  $q$  denote the densities of  $P$  and  $Q$ . This value is always non-negative and asymmetry.

$$D_{KL}(P|Q) \neq D_{KL}(Q|P) \quad (5)$$

Namely,  $D_{KL}$  does not satisfy the axioms of distance. Hence, I used Kullback-Leibler symmetric distance which is the sum of  $D_{KL}(P|Q)$  and  $D_{KL}(Q|P)$  in order to measure the similarity between time series [Kakizawa et al., 1998].

## 2.6 Multivariate statistics

### 2.6.1 Non-negative matrix factorization (NMF)

A burst results from the summation of activities of each bee. To understand when and which bees got active around burst, I used non-negative matrix factorization . Given a non-negative matrix  $\mathbf{X}$ , find non-negative matrix factors  $\mathbf{W}$  and  $\mathbf{H}$  such as:

$$\mathbf{X} \simeq \mathbf{W}\mathbf{H}$$

a  $n \times m$  matrix  $\mathbf{X}$  where  $m$  is the number of individual bees and  $n$  is the time series of kinetic energy of each bee. This matrix is approximately factorized into an  $n \times r$  matrix  $\mathbf{W}$  and an  $r \times m$  matrix  $\mathbf{H}$ .

The significance of the approximation in the above equation can be rewritten column by column as  $\mathbf{x} = \mathbf{W}\mathbf{h}$ , where  $\mathbf{x}$  and  $\mathbf{h}$  are the corresponding columns of  $\mathbf{X}$  and  $\mathbf{H}$ . Therefore,  $\mathbf{W}$  can be regarded as containing a basis that is optimized for the linear approximation of the data in  $\mathbf{X}$ . Since relatively few basis vectors are used to represent many data vectors, good approximation can only be achieved if the basis vectors discover structure that is latent in the data.

To sum up, non-negative matrix factorization is a method which divides a original matrix into a basis matrix and a weight matrix. [Lee and Seung, 2001]. There are two different multiplicative algorithms for implementing NMF. They differ only slightly in the multiplicative factor used in the update rules. One algorithm can be shown to minimize the conventional least squares error and the other minimizes the generalized Kullback-Leibler divergence [Kullback and Leibler, 1951].

A critical parameter in NMF is the factorization rank  $r$ . It defines the number of candidate bee activities used to approximate the target matrix. Given an NMF method and the target matrix, a common way of deciding on  $r$  is to try different values, compute some quality measure of the results, and choose the best value according to this quality criterion. Several approaches have then been proposed to choose the optimal value of  $r$ . For example, Brunet proposed to take the first value of  $r$  for which the cophenetic coefficient starts decreasing [Brunet et al., 2004], Hutchins suggested choosing the first value where the residual sum of squares curve presents an inflection point [Hutchins et al., 2008]. I used the former estimation.

I will use “nmf” R library in this analysis.

## 2.6.2 Non-metric multi dimensional scaling

A non-Metric Multi-Dimensional Scaling (nMDS) method is a dimensional reduction scheme that attempts to represent factors as points in a low dimensional Euclidean space such that the distances between the points in the low dimensional space are consistent with those in the original data. [Sammon, 1969] The nMDS is a non-linear scheme typically surpasses Principal Component Analysis. nMDS will be used as the dimension-reduction scheme in this thesis, because, the embedding produced by nMDS is more informative than the corresponding PCA result. In this thesis, I used “NeatMap” R package. [Rajaram and Oono, 2010]

## 3 Results

### 3.1 Bursts as collective behavior in a honey bee hive

#### 3.1.1 Whole image of activities of bees.

First, I observed the activation patterns of the hive by examining the temporal dynamics of the hive activity over a week, as shown in Figure 1. I observed that the time series of  $K_{global}(t)$  often indicated a sudden increase in the hive activity much more than times per day. In addition, when the entrance was opened, the time series displayed a roughly periodic pattern that corresponds to circadian rhythm.

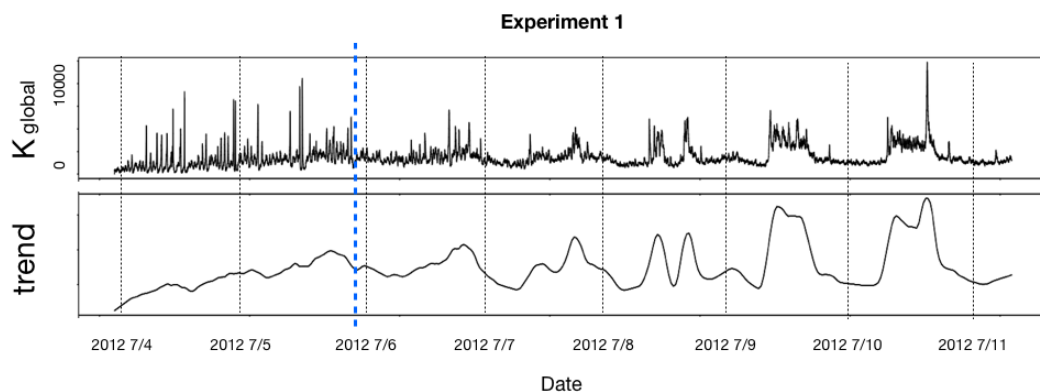


Figure 1: Time series of kinetic energy and its long-term tendency. The period of entrance open are depicted with blue dotted line.



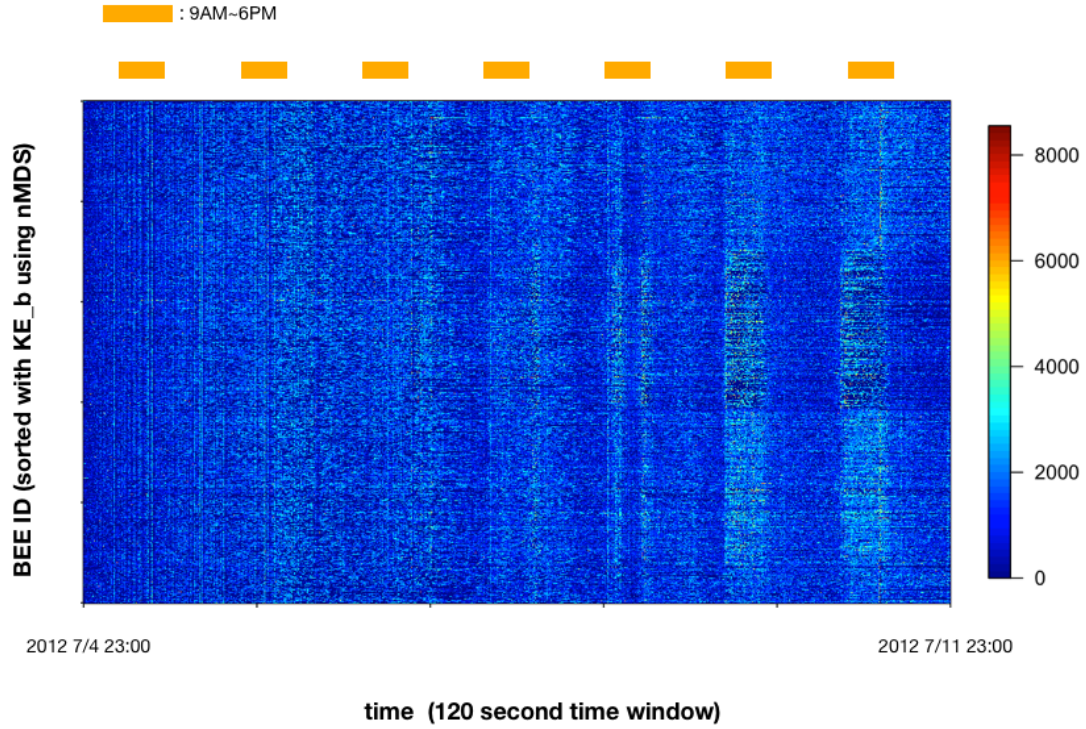


Figure 2: Heat map of kinetic energy of each bee at experiment 1. Each row corresponds to each bee in the hive. The rows were sorted with their similarity about time evolution of kinetic energy. The time length of each column is 120 sec.

The time series of  $K_{individual}$  of each bee was heat mapped over a week, and is shown in Figure 2 throughout week. We can see a global synchronization of high kinetic energy values when  $K_{global}(t)$  indicates a sudden increase. Also,  $K_{individual}$  displayed diurnal cycle when the entrance was opened.

These results suggest we have to think that the term before the entrance opened is different from the term after the entrance opened, because the bees interacted with the external world after the entrance opened and their behavior could have changed. Thus, I divided the overall time series into “before entrance open” and “after entrance open”. In order to make the condition simpler, this research examined only the terms before entrance opening.

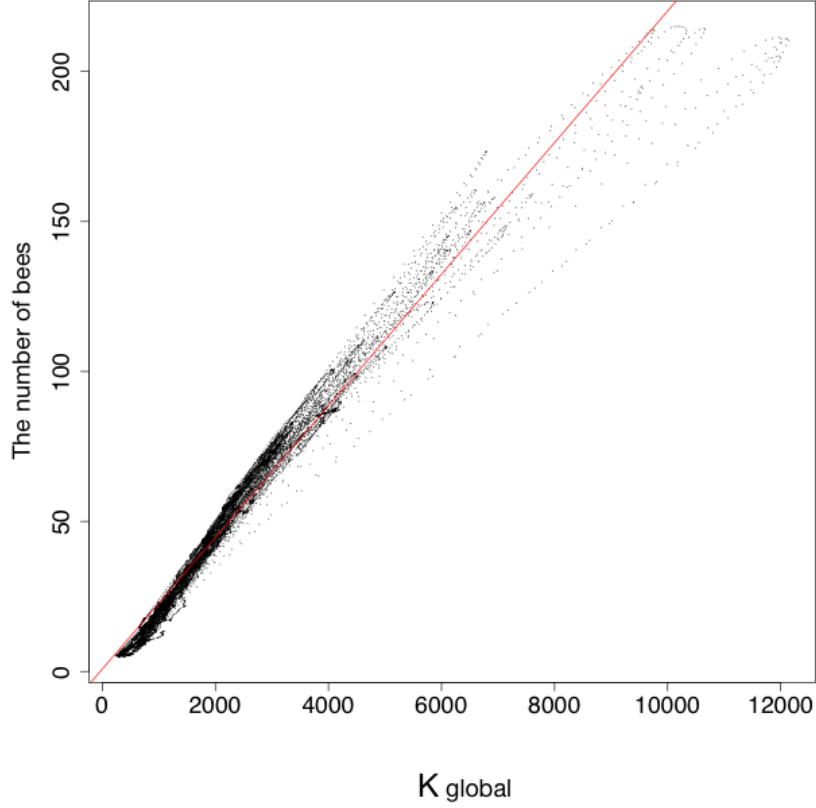


Figure 3: The relation between  $K_{global}$  and the number of bees which kinetic energies indicated higher than 1510 (mean  $K_{global}$ ). The regression coefficient is  $2.19 \times 10^{-2}$  ( $r = 0.97$ ,  $P < 0.001$ ).

Figure 3 shows the number of bees that contributed to high  $K_{global}$ . The relationship between  $K_{global}$  and the number of bees whose kinetic energies indicated more than the average  $K_{global}$  showed positive linear correlation;  $K_{individual}$  for approximately 200 bees was higher than the average  $K_{global}$  when  $K_{global}$  was around 8000. Since this value corresponded to the top of the sudden increases, this result means approximately 200 bees participated in the sudden increases.

A detailed  $K_{individual}$  analysis confirmed that the bees displayed some characteristics in terms of kinetic energy. Figure 4 showed the distribution of each kinetic energy. The distribution of  $K_{individual}$  was well fitted with a straight line whose slope is -0.45 in range below the average  $K_{global}$  (blue dotted line). However, in a range above the average, the distribution of  $K_{individual}$  was curved rather than straight line.

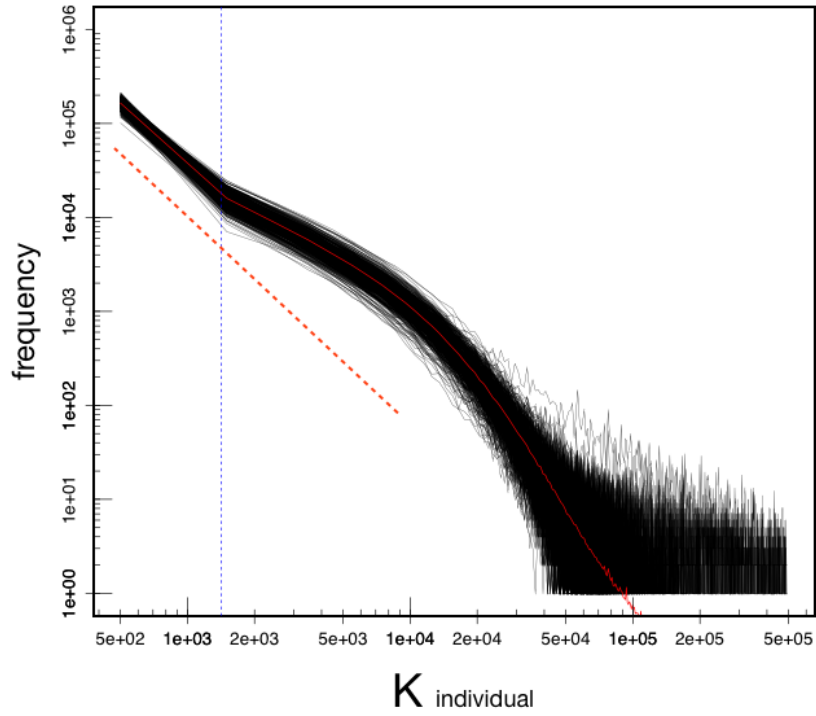


Figure 4: The distributions of  $K_{individual}$  in double logarithm. The mean of distribution curves is depicted with red line. The mean of  $K_{individual}$  is depicted with blue dotted line. The region below the mean of  $K_{individual}$  is well-fitted with red dotted line whose slope is -0.45.

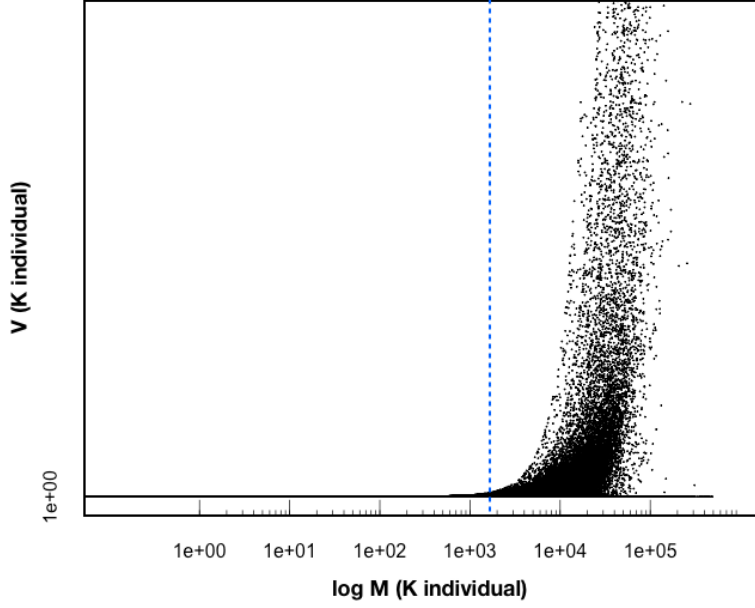


Figure 5: Calculating moving average of the previous 60 sec for the time series of  $K_{individual}$  of each bee and by using the same way, calculating “moving variance” of the previous 60 sec for the time series of  $K_{individual}$  of each bee

I also observed the relationship between the means and variances of  $K_{individual}$ , as shown in Figure 5 and Figure 6. First, I calculated the moving average of the previous 60 seconds for the time series of  $K_{individual}$  of each bee. Next, using the same approach, I calculated “moving variance” of the previous 60 seconds for the time series of  $K_{individual}$  of each bee. In a range below average (blue dotted line), the relationship between the means and variances of  $K_{individual}$  was sideways crawl; however, in the range above average (blue dotted line), variances were suddenly increased. That is, when  $K_{individual}$  was higher than mean  $K_{global}$ , they repeated moving and stopping. I will discuss these results in the discussion section; however, the relationship between the mean and the variance of bees seemed to exhibit two modes: “normal mode” and “burst mode.”

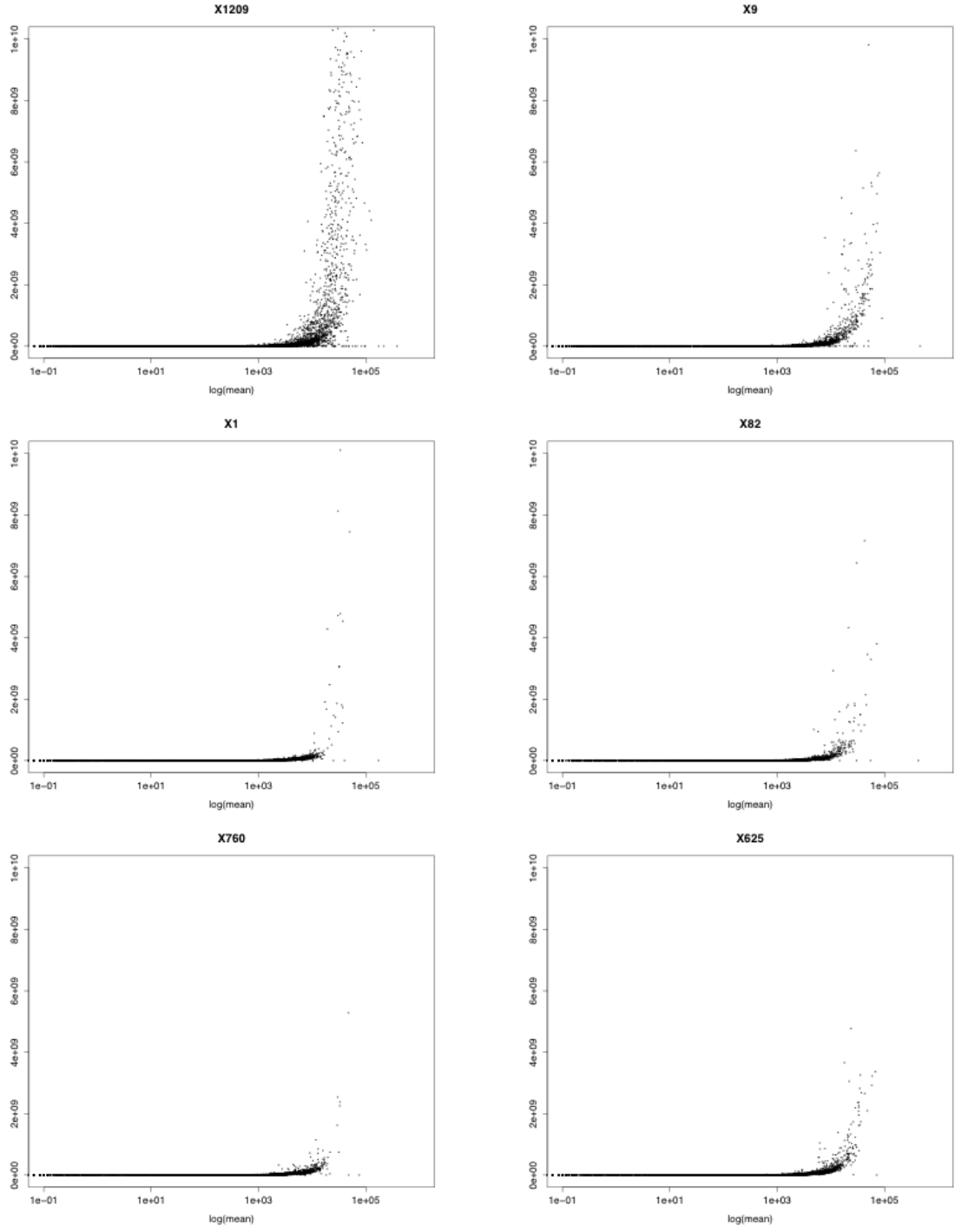


Figure 6: The relation between log mean and variance of representative bees. mean  $K_{individual}$  down from top to bottom.

### 3.1.2 Bursts have two types, endogenous and exogenous

As mentioned in Introduction, the activity peaks of  $K_{global}$  were selected as our initial target. In this section, I describe first the definition of the activity peaks and next I describe the detailed analysis results of the time evolution of the activity peaks in order to understand how they developed.

First, I detected the activity peaks of  $K_{global}$  using the Kleinberg algorithm (Figure 7, top). The number of detected activity peaks were 25. I defined these activity peaks as “bursts”. (In this thesis, I call “Burst X” “BST X” respectively). The periods of some bursts corresponded to the periods in which the glass around the hive was cleaned in order to facilitate filming, suggesting a clear relationship between the two. However, other bursts occurred because of other reasons. The bottom of Figure 7 shows the difference between the two types of bursts.

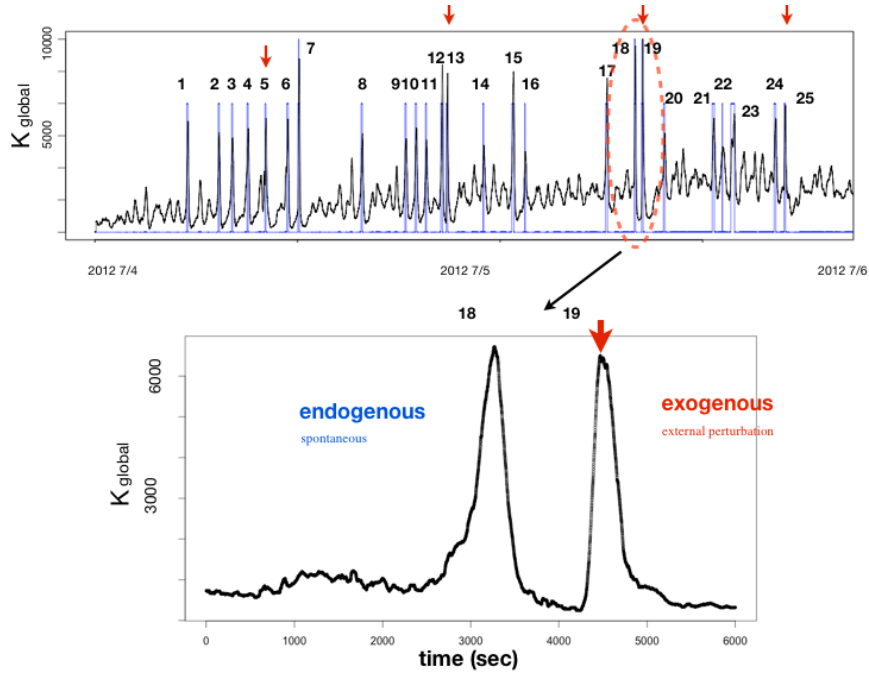


Figure 7: Top: The time series of kinetic energy before the entrance was opened. The original time series are depicted with black line, and the detected bursts are depicted with blue bars with heights indicating the burst level. Red arrows describe the time of glass cleaning. Bottom: the expanded figure of the  $K_{global}$  surrounded by a red dotted circle.

I superimposed the increasing phase of every detected bursts (Figure 8, Figure 9).

The bursts depicted with red were caused by the external stimulus of the glass cleaning. The bursts depicted with blue were not due to external stimuli, suggesting these bursts resulted from intrinsic interactions among honey bees. I call the former “exogenous burst” and the latter “endogenous burst” in this thesis. This kind of name is often used in social network study [Crane and Sornette, 2008].

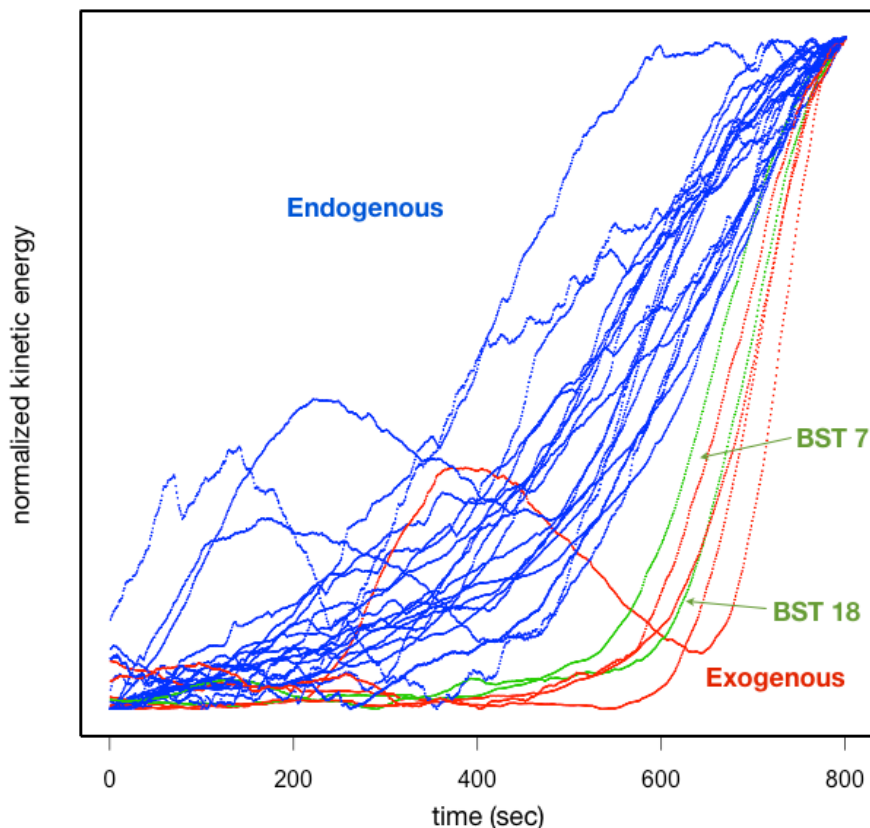


Figure 8: The time evolution of bursts in the increasing phase. Bursts due to an external perturbation are depicted with red line and bursts due to an intrinsic cause are depicted with blue line.

The two types of burst differed in terms of their temporal evolution. The first difference was in the time evolution of the kinetic energy. At the increasing phase of endogenous bursts, kinetic energy increased gradually. In contrast, at that of exogenous bursts, kinetic energy increased suddenly. However, there was no difference between the endogenous bursts and the exogenous bursts at the end. The glass cleaning did not cause BST7 and BST18, but these increases were similar to the other exogenous bursts.

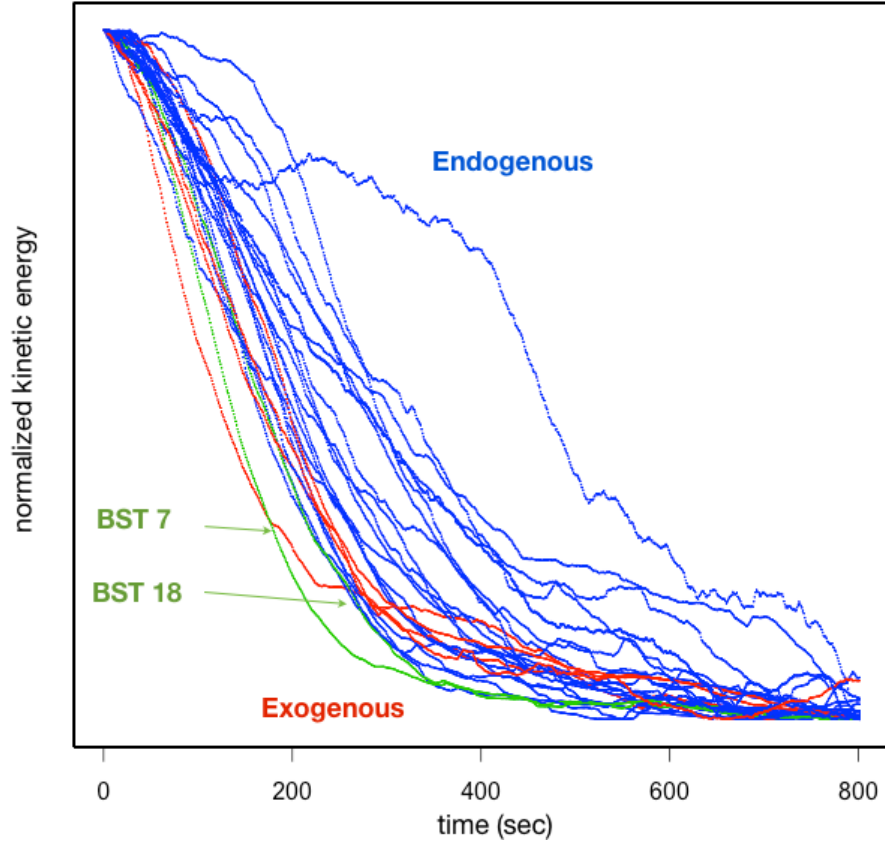


Figure 9: The time evolution of bursts in the decreasing phase. Bursts due to an external perturbation are depicted with red line and bursts due to an intrinsic cause are depicted with blue line.



These curves were fitted with Equation (6).

$$K_{global} = \frac{c}{b + t^a}, \quad (6)$$

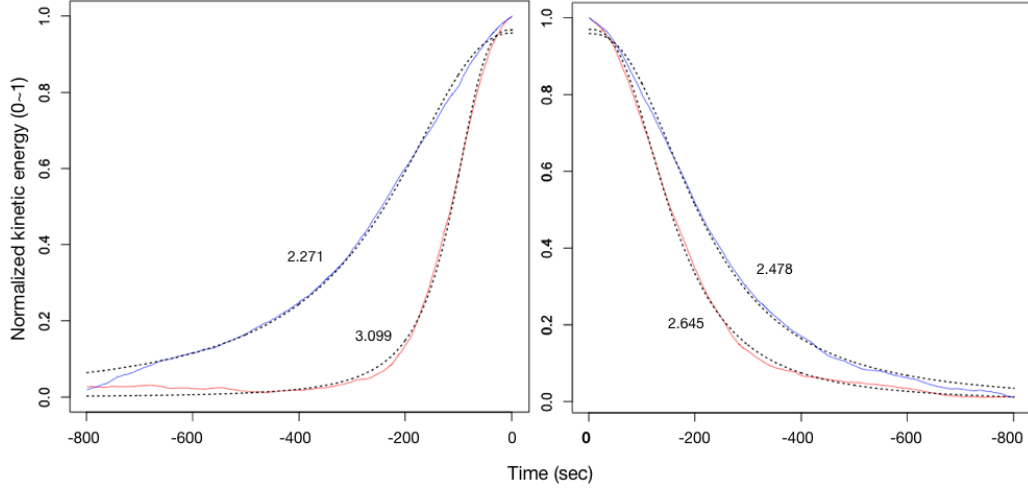


Figure 10: The average curve of the endogenous bursts (blue) and the exogenous bursts (red) and these fitting lines (black dotted curves). The values means  $a$  of each curve. The  $K_{global}$  of all bursts are normalized into range  $0 \sim 1$ . Every residual standard error are less than 0.01. (Left) The average increasing curves. (Right) The average decreasing curves.

In order to measure the difference between the endogenous and exogenous bursts quantitatively, I measured the probability distribution of kinetic energy of endogenous bursts and the exogenous bursts and calculated symmetric Kullback-Leibler divergence ( $D_{KL}(P|Q)$ ) between endogenous and exogenous. Kullback-Leibler divergence evaluates the overlap between two probability distributions ( $P$  and  $Q$ ) and yields 0 for identical distributions. Namely, this value indicates the non-similarity value of each burst. As shown Figure 13, the values of  $D_{KL}(exo|exo)$  or  $D_{KL}(endo|endo)$  were less than 4 and the values of  $D_{KL}(exo|endo)$  were more than 6 at the increasing phase of bursts. On the other hands, at the decreasing phase of bursts, the values of  $D_{KL}(exo|exo)$ ,  $D_{KL}(endo|endo)$  and  $D_{KL}(endo|endo)$  were less than 4 and the  $D_{KL}(exo|endo)$  values of the beginning and ending phases were statistically significant (Wilcoxon rank-sum;  $p < 10^{-15}$ ). Namely, this result shows that, at the increasing phase of bursts, there was difference between the endogenous bursts and exogenous bursts; there was, however, no difference between them, at the decreasing phase, in connection with the distribution of kinetic energy.

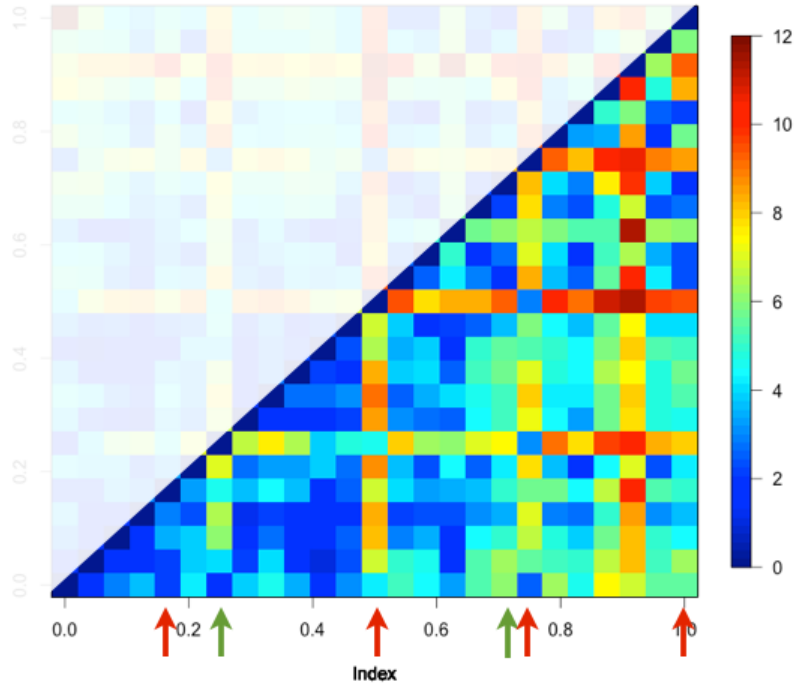


Figure 11: Kullback-Leibler divergence at the increasing phase of bursts. Row and column describe bursts. For example, square (5,3) depicts the summation of  $D_{KL}(BST5|BST3)$  and  $D_{KL}(BST3|BST5)$ . Red arrows depict exogenous bursts and green arrows depict Burst#7 and Burst#18.

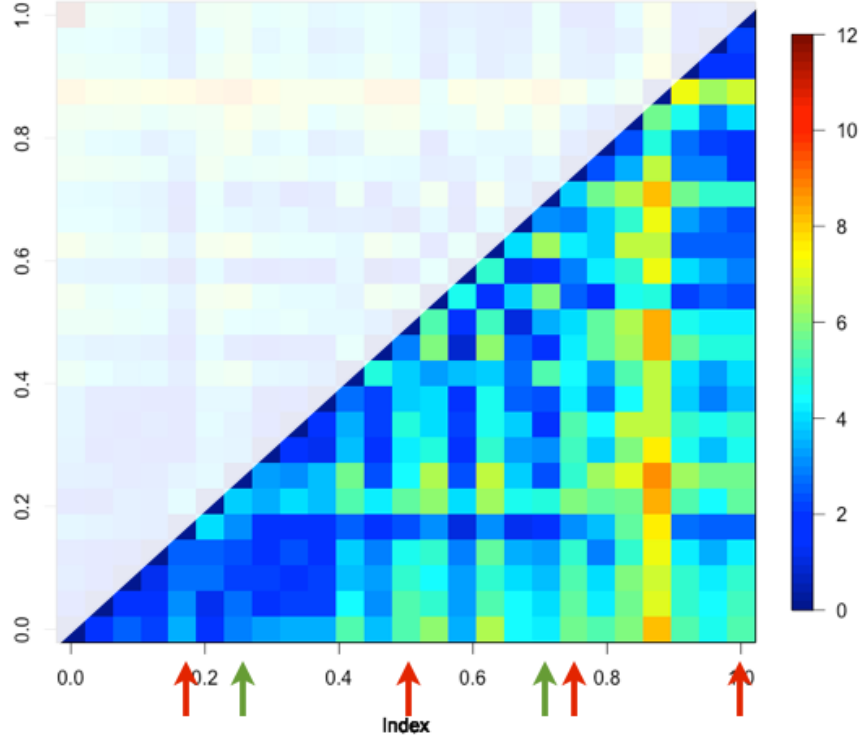


Figure 12: Kullback-Leibler divergence at the decreasing phase of bursts. Row and column describe bursts. For example, square (5,3) depicts the summation of  $D_{KL}(BST5|BST3)$  and  $D_{KL}(BST3|BST5)$ . Red arrows depict exogenous bursts and green arrows depict Burst#7 and Burst#18.

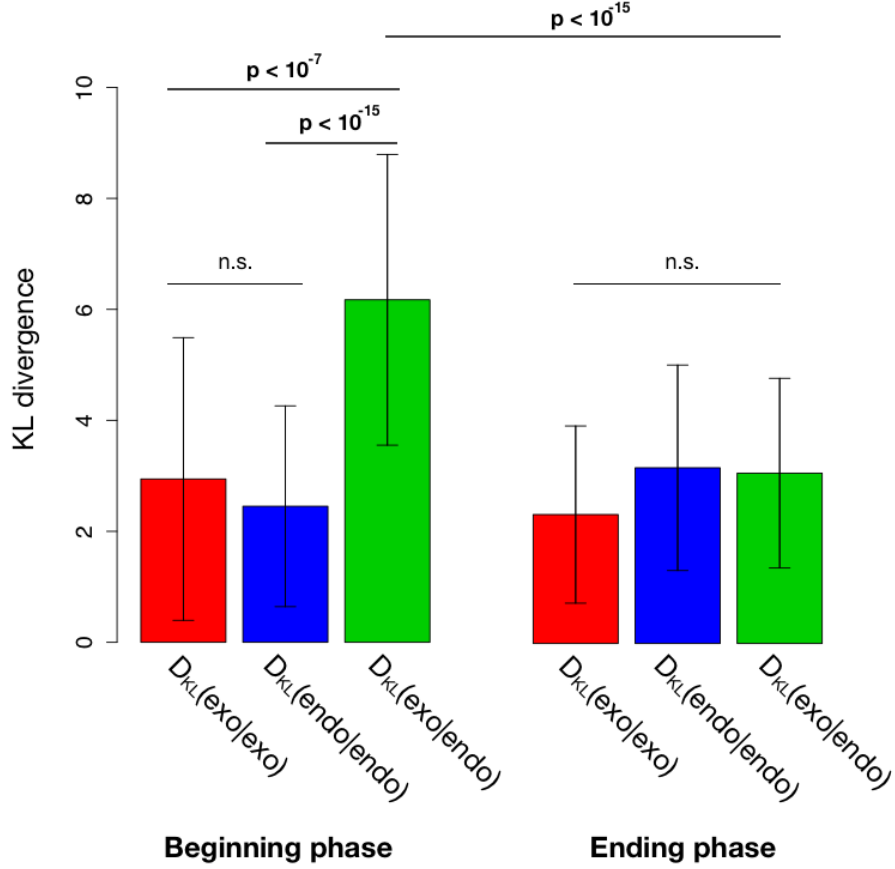


Figure 13: Endogenous bursts and exogenous bursts are different in terms of their distribution of kinetic energy. Red means the average of KL divergence between exo and other exo. Blue mean the average of KL divergence between endo and other endo. Green mean the average of KL divergence between endo and exo. p values for the average differences were obtained with Wilcoxon rank-sum tests

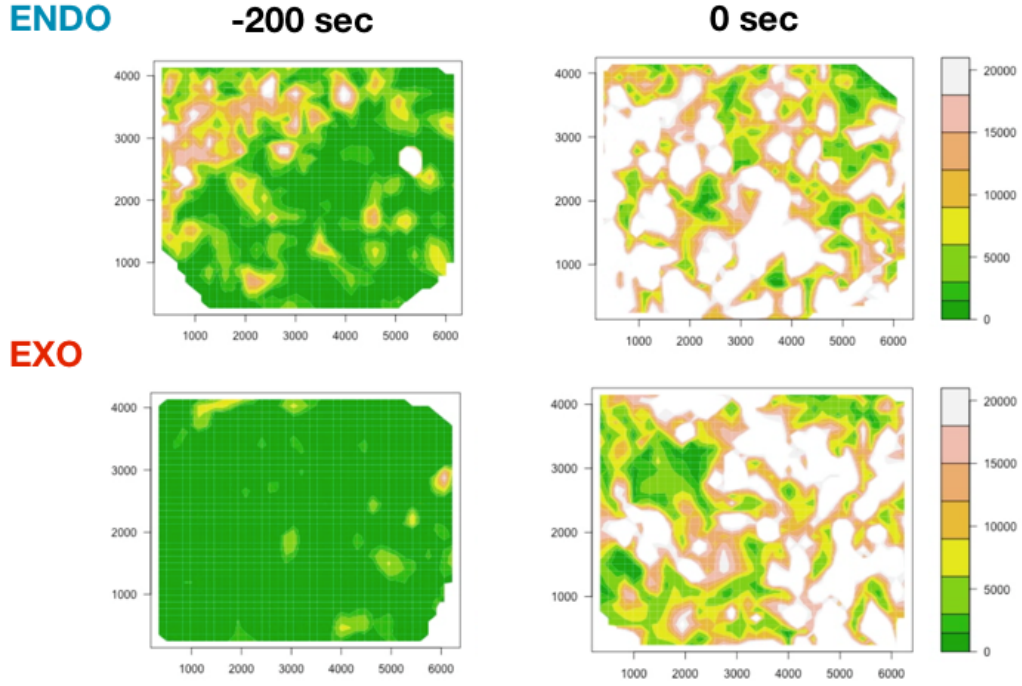


Figure 14: The spatio-temporal evolution of endogenous burst (Burst#18) and exogenous burst (Burst#19).

Also, through spatio-temporal evolutions, I found the difference between the endogenous and exogenous bursts. The right-most figure (0 sec) is the top of each burst. The endogenous burst was different from the exogenous burst in the beginning state. In endogenous bursts, kinetic energy increased gradually. On the contrary, in the beginning state of exogenous bursts, the entire hive became active.

## 3.2 Classifying the bees' behavior by their activities and activity timings

In the previous section, we saw two types of bursts: endogenous and exogenous. Moreover, in terms of their spatio-temporal evolution, the endogenous bursts started from a part of the hive, but the exogenous bursts did not. This leads us to one hypothesis that the endogenous bursts resulted from some bees that produced high kinetic energy before the burst occurred. Extracting these kind of bees are important to understand what are the individual contributions to the burst.

Moreover, if the same bees contributed to every bursts, then it suggests the bees have stable character.

In order to prove it, I first analyzed each endogenous burst in terms of individual activities.

### 3.2.1 Classifying the bees' behavior by their activity timing

First, I tried to rank the bees by their activity timings using the results of cross-correlation analysis. To this end, I had to decide on time windows that included one burst and the foot of a second burst. Considering the results in Figure 10, I set the length of the foot of a burst to  $\pm 1000$  sec from the top of the burst. In addition, observed bursts were detected by the Kleinberg algorithm. Using

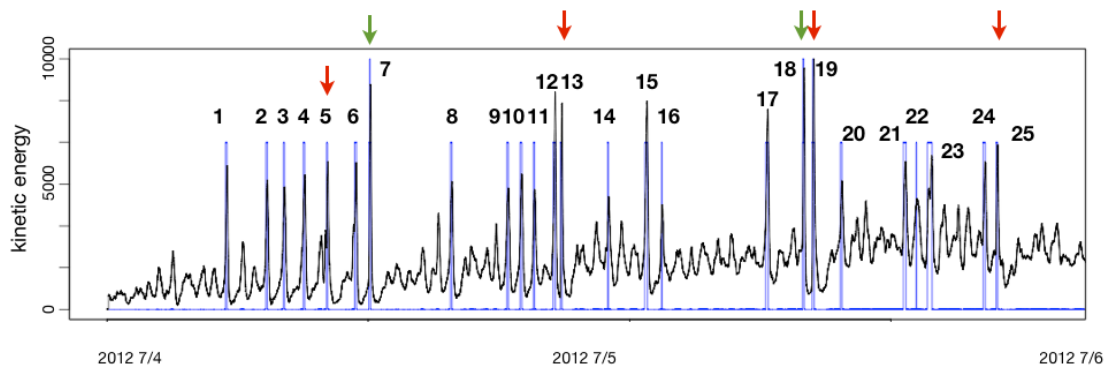


Figure 15: Detected bursts by Kleinberg algorithm. Red arrows describe exogenous bursts. Green arrows means bursts which may be exogenous bursts.

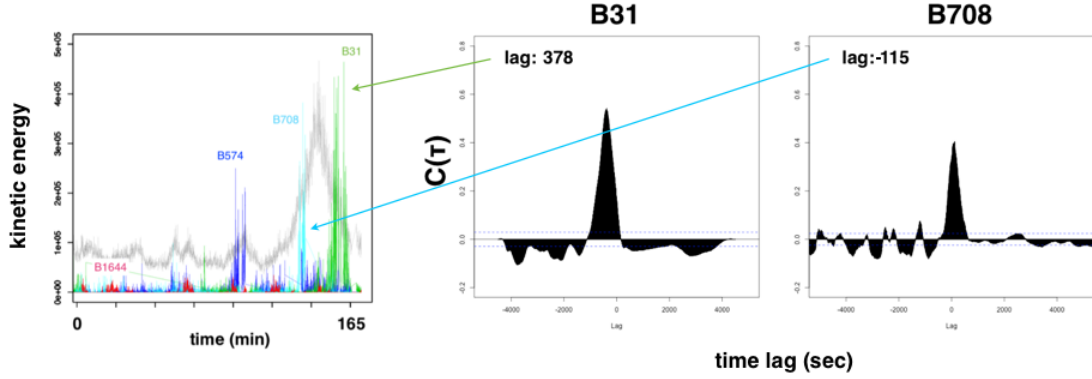


Figure 16: The example results of cross correlation analysis.

cross-correlation analysis, I applied time lag tags to the bees. For example, as shown in Figure15, B31 was tagged 376 and B708 was tagged -115. These tags represented time lags between  $K_{individual}$  and  $K_{global}$  at each burst. I tagged every bee at each burst using this method and made a matrix whose rows represented each bee and columns represented each burst. I applied nMDS to this matrix as shown in Figure17.

However, I could not categorize the bursts in terms of the active timing of each bee. This suggests that it is too detailed to categorize bursts and thus to use the results of cross-correlation analysis. Moreover, this method is only effective when  $K_{individual}$  and that of  $K_{global}$  are almost same. Namely, if a bee became active two times or more in the observed time window, this analysis could not calculate an accurate time lag between  $K_{individual}$  and  $K_{global}$ . For this reason, I tried to achieve cause graining for active timing.

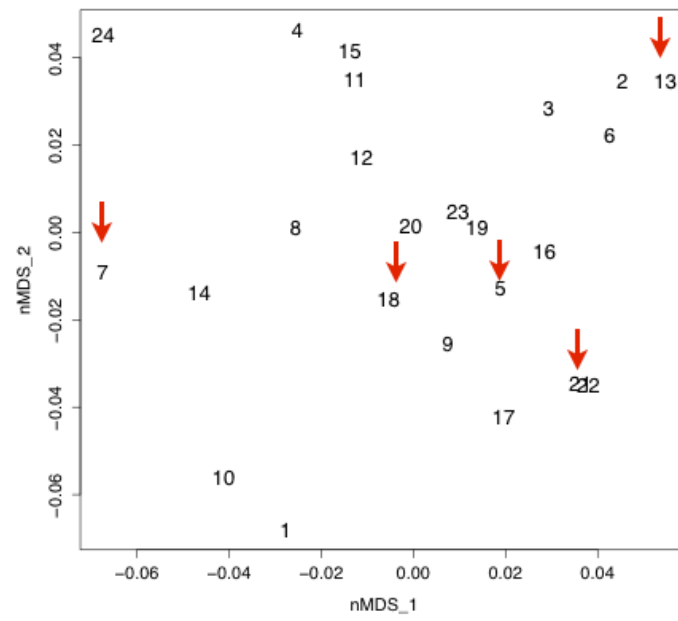


Figure 17: The results of nMDS using cross correlation analysis. Red arrows describe exogenous bursts



### 3.2.2 Classifying the activities of bees into three types

As mentioned earlier, I used non-negative matrix factorization to decompose the original matrix into a basic matrix (i.e., candidate bee’s activity patterns) and a weight matrix. In order to use NMF algorithm, we had to decide on rank  $r$  (i.e., how many bases we use). A critical parameter in NMF is the factorization rank  $r$ . It defines the number of candidate bee activities used to approximate the target matrix. Given an NMF method and the target matrix, a common way of deciding on  $r$  is to try different values, compute some quality measure of the results, and choose the best value according to this quality criterion. Several approaches have then been proposed to choose the optimal value of  $r$ . For example, Brunet proposed to take the first value of  $r$  for which the cophenetic coefficient starts decreasing [Brunet et al., 2004], Hutchins suggested choosing the first value where the residual sum of squares curve presents an inflection point [Hutchins et al., 2008]. I used the former estimation. Figure 18 is the example of NMF and Figure 19 is the relation between  $r$  and its cophenetic correlation coefficients. For example, about this burst, I set  $r$  to 7 according to the estimation.

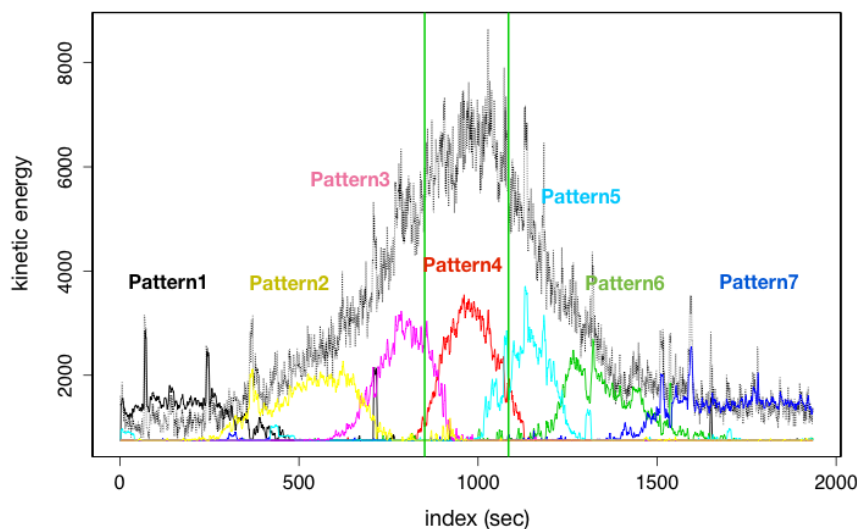


Figure 18: One example of classifying of bees using NMF. “pattern” is basis. The range enclosed with two green perpendicular lines corresponds to the range of detected bursts by Kleinberg algorithm.

Since estimated  $r$  is different depending on bursts (the range of estimated  $r$  is

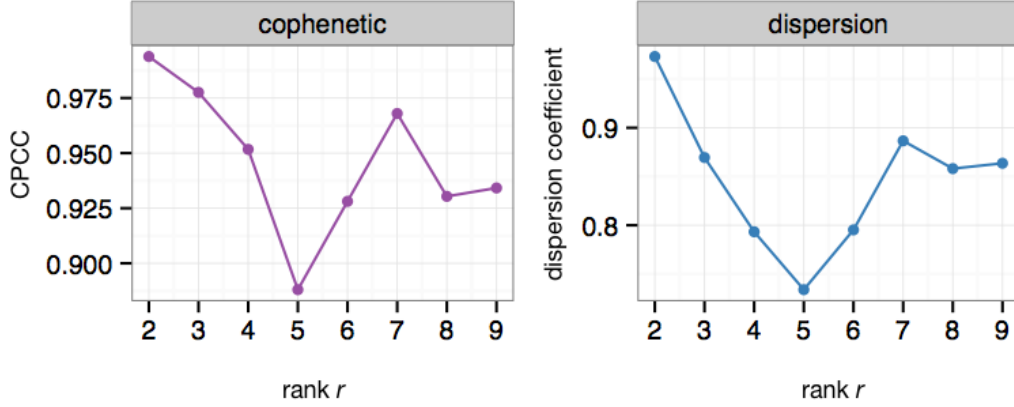


Figure 19: Cophenetic correlation coefficients shows a dip at  $r = 5$ , where reproducibility is poor, and suggests  $r = 7$  as the largest number of classes recognized by NMF for this data set.

from 4 to 7), we could not compare bursts. Consequently, I categorized extracted bases (i.e., candidate patterns of  $K_{individual}$  around each burst) into three types.

Type 1 was when the top of the extracted base was below the range of the detected burst, Type 2 was when the top of the extracted base was in the range of the detected burst, Type 3 was when the top of the extracted base was above the range of the detected burst. Thus, using this categorization, we could categorize when the bees got active and which bees got active at the increasing phase of endogenous bursts. As shown earlier, my hypothesis is that the endogenous bursts result from some bees that displayed high activity before the burst occurred. Therefore, I decided to focus on Type 1 and called the bees in this category “pioneer bees.” I made a binary matrix  $PM_{i,j}$  where the columns represented each burst, the rows represented Bee ID, and the contents were 0 or 1. If a bee  $i$  was categorized Type 1 at Burst  $j$ , then  $content_{i,j} = 1$ . If a bee  $i$  was not categorized Type 1 at Burst  $j$ , then  $content_{i,j} = 0$ .

$$PM_{i,j} = \begin{cases} 1 & (\text{bee } i \text{ was categorized Type 1 at Burst } j) \\ 0 & (\text{otherwise}) \end{cases}$$

Also, I made a matrix where the columns represented each burst, the rows represented Bee ID, and the contents were the number of seconds during which a bee became more active than the mean  $K_{global}$  in each burst. Finally, calculating Hadamard product between these two matrices, I built the matrix of “pioneer bees”. Figure 21 describes the list of “pioneer bees” of each burst. The order depended on the number of seconds during which a bee became more active higher

than mean  $K_{global}$ . Also, Figure 22 describes the number of pioneer bees in each burst. As shown in Figure 21, some bees became active at the increasing phase of bursts five times or more.

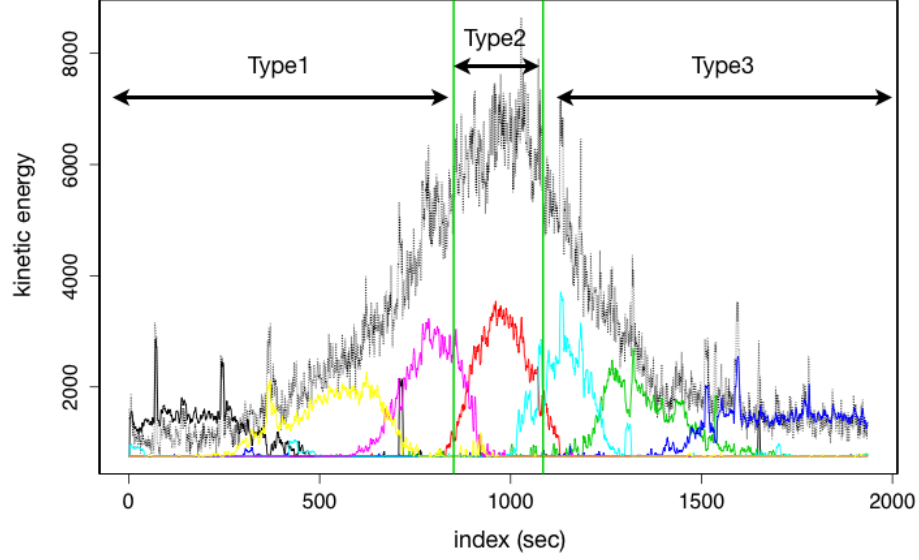


Figure 20: Classifying the bees into 3 types. Colored curves describe extracted bases by NMF. Black dotted curves is  $K_{global}$ . The range between the two green perpendicular lines corresponds to the range of detected bursts by Kleinberg's algorithm.

	BST 1	BST 2	BST 3	BST 4	BST 5	BST 6	BST 7	BST 8	BST 9	BST 10	BST 11	BST 12	BST 13	BST 14	BST 15	BST 16	BST 17	BST 18	BST 19	BST 20	BST 21	BST 22	BST 23	BST 24	BST 25
1	B1718	B1009	B1750	B705	B583	B1137	B1209	B705	B592	B1432	B414	B1433	B418	B706	B188	B1580	B611	B1649	B579	B1209	B119	B1799	B1103	B737	B1156
2	B1420	B1221	B1009	B504	B1487	B165	B119	B1717	B1209	B1050	B213	B649	B175	B1215	B1285	B1433	B14	B1400	B632	B333	B1431	B662	B760	B1649	B1628
3	B570	B1795	B1702	B1161	B94	B1820	B644	B21	B102	B545	B494	B298	B1134	B525	B487	B1645	B1719	B1214	B578	B1009	B11	B1427	B154	B1170	B245
4	B489	B504	B738	B31	B117	B642	B661	B418	B1175	B642	B217	B657	B637	B651	B1139	B1154	B1519	B704	B611	B1644	B1	B1286	B60	B1175	B1119
5	B1009	B583	B53	B1771	B1221	B1355	B39	B205	B173	B579	B455	B438	B1160	B1187	B1580	B489	B713	B1218	B247	B1731	B1621	B1716	B1681	B443	B1725
6	B334	B1702	B1138	B1604	B1702	B218	B413	B545	B205	B410	B685	B1791	B455	B1630	B1621	B1127	B1652	B719	B357	B1610	B533	B410	B39	B1214	B1223
7	B1864	B704	B1313	B216	B1218	B1138	B489	B644	B540	B1275	B1114	B333	B564	B1166	B175	B117	B1453	B786	B1611	B219	B637	B473	B592	B1843	B1163
8	B1237	B349	B1731	B786	B1688	B1403	B571	B661	B1486	B731	B711	B1671	B454	B1246	B1716	B655	B349	B1150	B1736	B607	B1154	B1453	B523	B711	B1433
9	B104	B786	B1717	B737	B70	B1382	B611	B218	B1578	B1009	B312	B442	B1675	B1649	B719	B1286	B617	B206	B489	B349	B1731	B340	B1286	B61	B238
10	B333	B1431	B198	B652	B1191	B655	B1791	B650	B1583	B181	B1668	B1290	B1660	B579	B1578	B1706	B337	B772	B663	B1166	B250	B193	B1368	B462	B499
11	B1200	B1161	B1864	B1261	B1000	B1454	B298	B350	B358	B1621	B1382	B436	B327	B1543	B1543	B1103	B1091	B655	B1115	B217	B736	B312	B175	B796	B1570
12	B175	B1427	B1681	B1355	B1668	B219	B637	B1435	B15	B1136	B369	B14	B1175	B163	B650	B85	B1736	B464	B175	B713	B1121	B579	B1525	B1794	B1197
13	B1261	B1652	B288	B1103	B642	B1322	B1116	B1645	B1210	B349	B1854	B120	B217	B545	B1156	B564	B1660	B1748	B250	B1139	B1864	B1237	B1487	B1272	B219
14	B760	B245	B570	B1769	B1659	B1486	B1117	B1244	B198	B312	B1139	B1050	B1705	B1453	B1355	B649	B1799	B188	B1843	B1621	B1747	B533	B85	B1005	B1106
15	B578	B1681	B1005	B1794	B1517	B1187	B570	B607	B1398	B665	B1285	B1420	B1486	B458	B637	B1702	B1731	B1843	B219	B1287	B599	B760	B1486	B730	B1611
16	B1416	B672	B1032	B163	B20	B349	B1009	B355	B1004	B454	B315	B719	B1602	B1799	B1645	B1259	B247	B1105	B126	B1500	B669	B1345	B1123	B1117	B148
17	B1716	B1039	B744	B625	B1722	B544	B1799	B1748	B485	B1668	B21	B1551	B1261	B1420	B426	B1794	B442	B445	B71	B205	B1187	B1669	B1894	B705	B649
18	B245	B117	B1420	B85	B300	B1037	B1311	B357	B1345	B1427	B564	B665	B1272	B1772	B1725	B206	B53	B1154	B333	B1645	B1386	B546	B183	B1567	B1287
19	B1322	B39	B1854	B228	B760	B10	B1287	B173	B1666	B1155	B1520	B1288	B1520	B1517	B1182	B719	B1433	B1772	B670	B566	B1713	B649	B642	B1716	B1182
20	B413	B705	B154	B505	B1480	B661	B1854	B723	B494	B1681	B669	B1531	B1731	B1431	B1639	B705	B579	B545	B431	B642	B1742	B1119	B1259	B638	B1103

Figure 21: The top 20 largest  $K_{individual}$  “pioneer bees” of each burst. Column number corresponds to the burst number. Colored bees denotes the increasing phase of bursts 5 times or more.

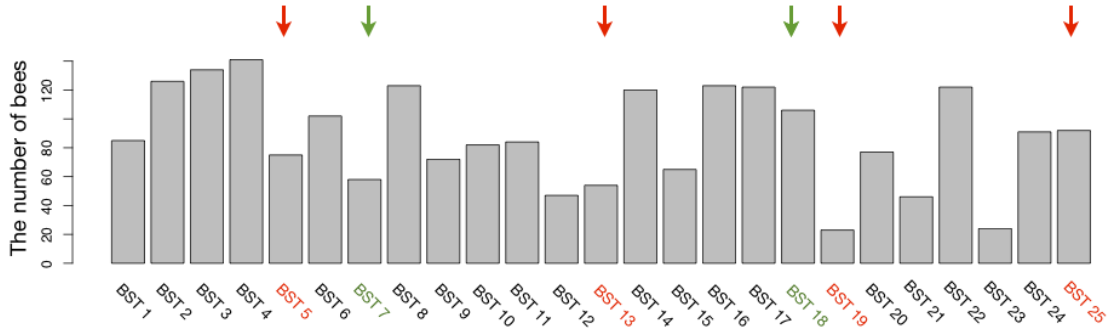


Figure 22: The number of bees in each burst. Red arrows describe exogenous bursts and green arrows describe bursts that may be exogenous.

### 3.3 Is there any stable ‘personality’?

As stated previously, some results suggested that the endogenous bursts resulted from a certain subset of the bees; these bees were termed “pioneer bees.” As I said in Introduction, if the characteristics of “pioneer bees” were stable, we could not consider this system to be a homogeneous system. Therefore, this study was an attempt to think about phenomena that are dependent upon individuality. First, I analyzed bursts according to these pioneer bees using nMDS and the “pioneer bees” matrix. If the same bees were pioneers at different bursts, then these bursts were plotted near one another; otherwise, they were plotted far apart. As Figure 23 shows, the exogenous bursts tended to be plotted far from the previous endogenous bursts. Moreover, we can see at least two clusters: Burst1  $\sim$  Burst6 (Cluster A) and Burst#7  $\sim$  Burst#25 (Cluster B). Next, considering this observed result, I categorized using nMDS and the transposed “pioneer bees” matrix as shown in Figure 24. Bees appearing more frequently in Cluster A than in Cluster B are depicted with red; otherwise, the color is blue.

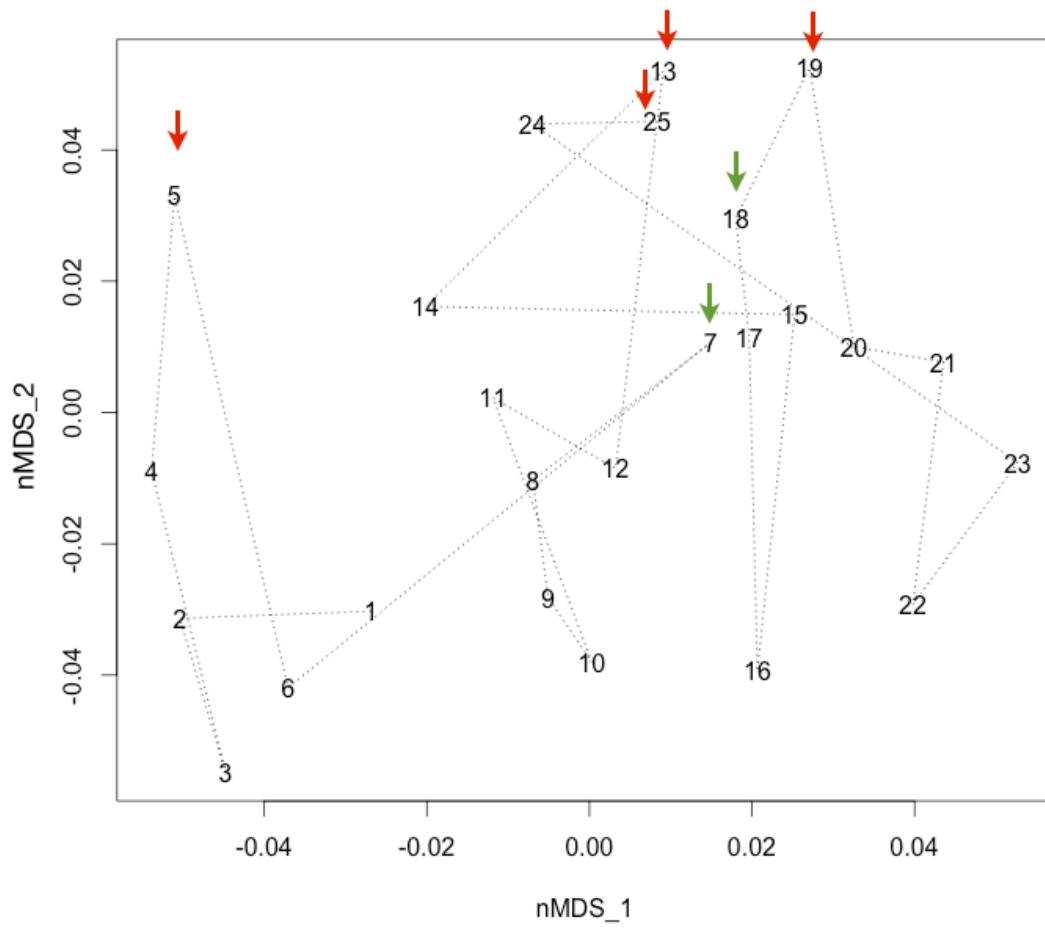


Figure 23: Classifying of bursts according to pioneer bees. Red arrows indicate exogenous bursts. Green arrows describe bursts that may be exogenous.



# 4 Discussion

## 4.1 Overall discussion

This thesis explored the activity levels of the beehive and of the individual bee activity in order to investigate their global/local (or social/individual) relationships. First, I introduced  $K_{global}$  to quantify the collective behavior that demonstrated bursting behavior. Figure 3 shows that approximately 200 bees demonstrated higher  $K_{individual}$  than the average of  $K_{global}$  at the top of the bursts. In addition, as shown in Figure 4, there were some bees whose  $K_{individual}$  was higher than the average  $K_{global}$ , even if the hive was not in the “bursting” state. This suggests that the highly active bees do not always cause the burst. We need some other conditions for causing bursting behavior. The active bees may act as “noise,” but they also may sometimes function as a “signal” to the other bees.

In Figure 6, we can see there are two branches of mean-variance relation for  $K_{individual}$ . This result suggests that the honey bees states are divided into active or inactive states at a minimum. The relationship between these activity states and bursting behavior is very important to understand the social-individual relationship. In addition, we have seen which bees displayed unique characteristics in terms of the distributions of kinetic energy. However, there are no big differences among the distributions of  $K_{individual}$ . These distributions seem to be a feature of all bees rather than an individual characteristic. It is difficult to determine whether this common distribution results from their sociality.

As I mentioned in Introduction, my initial questions were as follows:

- (i) What causes a burst? or How does a burst develop?
- (ii) What is the individual contribution to the burst?

We discussed “How does a burst develop?” in Section 3.1.2. Bursting triggers were classified as either endogenous or exogenous. The features of exogenous bursts were (1) sudden increase of  $K_{global}$  that was (2) observed in the entire hive and which (3) occurred because of the external stimuli. On the other hand, the features of endogenous bursts were (1) the gradual increase of  $K_{global}$  that (2) started from a part of the hive and which (3) may have occurred because of the intrinsic interactions.



At the decreasing phase, there were no differences between endogenous and exogenous bursts (Figure13). In other words, the increasing phase and the decreasing phase were asymmetric. This result suggests that the organization of the social activity is different from its relaxation. There may exist two types of relaxation. One type results from the nature of each bee. Honey bees cannot maintain their active states for long. Once the bees become active, they only remain active for a short time before the total burst pattern relaxes. The other type results from some bees that tell other bees to stop the burst, which is a kind of mutual suppression among bees. Since the curve of the decreasing phase of bursts was fitted with power function, there may be positive feedback behind the burst. In consequence, the disorganization of the social activity may result from some kind of interaction with other bees or their sociality rather than the nature of each bee.

On the other hand, the organization of the endogenous bursts was triggered by some special bees, as discussed in Section 3.2. Figure 21 shows that those special bees contributed to the organization of the social activities many times. We say that the special individuality as “pioneer bees” was displayed by some bees (“What is the individual contribution to the burst?”). Moreover, as shown in Figure 23, we can see two clusters in nMDS space at least, Cluster A and Cluster B. In nMDS space, when the same bees were “pioneer bees” in different bursts, these bursts were plotted near each other; otherwise, the bursts were plotted far apart. Hence, this result suggests that the “pioneer bees” were sometimes replaced with other bees. As shown in Figure 24, the bees that participated the most in Cluster A and the bees that participated the most in Cluster B were plotted on different locations in the nMDS space. It suggests that the two clusters in Figure23 result from these bees. In addition, the exogenous bursts tended to be plotted far from the preceding endogenous bursts in nMDS space. This result suggests that the “pioneer bees” forming the exogenous bursts were different from those of the endogenous bursts. A detailed study of “pioneer bees” is required to investigate this further.

Moreover, bursts were detected by the Kleinberg algorithm in this study; however, the method automatically ignored some potential bursting peaks. These bursts may not have been global bursts but, rather, spatially local bursts. If these spatially local bursts were the cause of the global bursts, it is important to investigate the spatially local bursts. With respect to this argument, a temporal relationship between the preceding baseline fluctuation and the successive burst may be indicated. Oka et al. (2014) investigated bursting behaviors in Twitter time series, showing that the endogenous and exogenous bursts can be separated by a critical baseline fluctuation [Oka et al., 2014].

# 5 Conclusions and Future works

## 5.1 Conclusions

In this thesis, it is demonstrated that there are bees who have the tendency to lead to endogenous bursts. Since we obtained results suggesting that activity in other aspects and this “leading behavior” are correlated, the “leading behavior” may be recognized as a personal syndrome. Bursts as a sort of the “social atmosphere” which must be a collective feature of the bees social activity levels were classified into the endogenous and the exogenous categories. Burst was different in terms of spatio-temporal evolution at the increasing phase of bursts, on the contrary, at the decreasing phase of bursts, each bursts were not different. I showed that some bees lead to the social activity burst and the bees’ features (i.e., personality) as “pioneer bees” were basically stable. This result may suggest that the individuality has hardly ignorable effects on the global organization of the whole social collective behavior.

## 5.2 Future work

Throughout the works of this thesis, I observed indirect communication. In order to observe more detailed indirect communication, measuring mutual information or transfer entropy is helpful [Schreiber, 2000] [Wang et al., 2012]. This kind of methods usually use many scientific fields. When using such methods, coarse graining is needed to characterize the state of each bee, for example, burst state and rest state. Fortunately, as we have seen, we can divide the state of bees into two states, burst state and rest state, in terms of the variance and mean of each kinetic energy. Using the results of transfer entropy, we can investigate indirect information flows in the hive. The “pioneer bees” can contribute to be “information source” in the hive, that is, we can divide the bees into “source bee” and “sink bee” in terms of information flow [Oka and Ikegami, 2013]. Seeley’s studies about collective decision making of honey bees suggested that “search bee” had played on important role when the bees searched and moved to a new hive. Moreover, it is known that “search bee” had visited near a queen bee for long time. Hence, it is important to calculate the distance between the queen and each bee and to

reveal “search bees”. They may have role as “source bee”. I also have interest in the robustness of the hive. If the half of bees are removed from the hive, does the endogenous burst occur? Specifically, if the pioneer bees or source bees are removed from the hive, does the endogenous burst occur?

In order to resolve such questions, I have to make an agent based model which can make a burst and experiment in many conditions and this is challenging for the future.



## 6 Acknowledgment

First and foremost, I have to thank my research supervisors, Dr. Takashi Ikegami. Without your assistance and dedicated involvement in every step throughout the process, this paper would have never been accomplished. I would like to thank you very much for your support. I discussed early versions of this thesis with Dr. Mizuki Oka. She raised many precious points in our discussion and I hope that I have managed to address several of them here. I also feel grateful to the colleagues of the laboratory, and the classmates of the college for many discussions and kindnesses, especially, Yhoichi Mototake, he taught me many kind of analysis methods and discussed with me for long time. Thank you very much.

# References

- [Acuña-Marrero et al., 2014] Acuña-Marrero, D., Jiménez, J., Smith, F., Doherty Jr, P. F., Hearn, A., Green, J. R., Paredes-Jarrín, J., and Salinas-de León, P. (2014). Whale shark (rhincodon typus) seasonal presence, residence time and habitat use at darwin island, galapagos marine reserve. *PloS one*, 9(12):e115946.
- [Azuma and Toyoshima, 1961] Azuma, S. and Toyoshima, A. (1961). Progress report of the survey of chimpanzees in their natural habitat, kabogo point area, tanganyika. *Primates*, 3(2):61–70.
- [Brunet et al., 2004] Brunet, J.-P., Tamayo, P., Golub, T. R., and Mesirov, J. P. (2004). Metagenes and molecular pattern discovery using matrix factorization. *Proceedings of the national academy of sciences*, 101(12):4164–4169.
- [Camazine, 2003] Camazine, S. (2003). *Self-organization in biological systems*. Princeton University Press.
- [Chandrasekaran et al., 2011] Chandrasekaran, S., Ament, S. A., Eddy, J. A., Rodriguez-Zas, S. L., Schatz, B. R., Price, N. D., and Robinson, G. E. (2011). Behavior-specific changes in transcriptional modules lead to distinct and predictable neurogenomic states. *Proceedings of the National Academy of Sciences*, 108(44):18020–18025.
- [Crane and Sornette, 2008] Crane, R. and Sornette, D. (2008). Robust dynamic classes revealed by measuring the response function of a social system. *Proceedings of the National Academy of Sciences*, 105(41):15649–15653.
- [Hutchins et al., 2008] Hutchins, L. N., Murphy, S. M., Singh, P., and Graber, J. H. (2008). Position-dependent motif characterization using non-negative matrix factorization. *Bioinformatics*, 24(23):2684–2690.
- [Jordan et al., 2013] Jordan, D., Kuehn, S., Katifori, E., and Leibler, S. (2013). Behavioral diversity in microbes and low-dimensional phenotypic spaces. *Proceedings of the National Academy of Sciences*, 110(34):14018–14023.
- [Kakizawa et al., 1998] Kakizawa, Y., Shumway, R. H., and Taniguchi, M. (1998). Discrimination and clustering for multivariate time series. *Journal of the American Statistical Association*, 93(441):328–340.

- [Kleinberg, 2003] Kleinberg, J. (2003). Bursty and hierarchical structure in streams. *Data Mining and Knowledge Discovery*, 7(4):373–397.
- [Kullback and Leibler, 1951] Kullback, S. and Leibler, R. A. (1951). On information and sufficiency. *The Annals of Mathematical Statistics*, pages 79–86.
- [Lee and Seung, 2001] Lee, D. D. and Seung, H. S. (2001). Algorithms for non-negative matrix factorization. In *Advances in neural information processing systems*, pages 556–562.
- [Oka et al., 2014] Oka, M., Hashimoto, Y., and Ikegami, T. (2014). Self-organization on social media: endo-exo bursts and baseline fluctuations. *PloS one*, 9(10):e109293.
- [Oka and Ikegami, 2013] Oka, M. and Ikegami, T. (2013). Exploring default mode and information flow on the web. *PloS one*, 8(4):e60398.
- [Pernice et al., 2011] Pernice, V., Staude, B., Cardanobile, S., and Rotter, S. (2011). How structure determines correlations in neuronal networks. *PLoS computational biology*, 7(5):e1002059.
- [Rajaram and Oono, 2010] Rajaram, S. and Oono, Y. (2010). Neatmap-non-clustering heat map alternatives in r. *BMC bioinformatics*, 11(1):45.
- [Riddiford, 1994] Riddiford, L. M. (1994). Cellular and molecular actions of juvenile hormone i. general considerations and premetamorphic actions. *Advances in insect physiology*, 24:213–274.
- [Robinson, 1987] Robinson, G. E. (1987). Regulation of honey bee age polyethism by juvenile hormone. *Behavioral Ecology and Sociobiology*, 20(5):329–338.
- [Robinson et al., 1989] Robinson, G. E., Page, R. E., Strambi, C., and Strambi, A. (1989). Hormonal and genetic control of behavioral integration in honey bee colonies. *Science*, 246(4926):109–112.
- [Sammon, 1969] Sammon, J. W. (1969). A nonlinear mapping for data structure analysis. *IEEE Transactions on computers*, 18(5):401–409.
- [Schreiber, 2000] Schreiber, T. (2000). Measuring information transfer. *Physical review letters*, 85(2):461.
- [Seed et al., 2009] Seed, A., Emery, N., and Clayton, N. (2009). Intelligence in corvids and apes: a case of convergent evolution? *Ethology*, 115(5):401–420.

- [Surowiecki, 2005] Surowiecki, J. (2005). *The wisdom of crowds*. Random House LLC.
- [Wang et al., 2012] Wang, X. R., Miller, J. M., Lizier, J. T., Prokopenko, M., and Rossi, L. F. (2012). Quantifying and tracing information cascades in swarms. *PloS one*, 7(7):e40084.
- [Whitehead et al., 2000] Whitehead, H., Christal, J., and Tyack, P. L. (2000). Studying cetacean social structure in space and time. *Cetacean societies: field studies of dolphins and whales*, pages 65–86.