8-2014

An Agent-Based Model of Ant Colony Energy and Population Dynamics: Effects of Temperature and Food Fluctuation

Guo Xiaohui
East Tennessee State University

Recommended Citation

Xiaohui, Guo, "An Agent-Based Model of Ant Colony Energy and Population Dynamics: Effects of Temperature and Food Fluctuation" (2014). *Electronic Theses and Dissertations.* Paper 2395. https://dc.etsu.edu/etd/2395

An Agent-Based Model of Ant Colony Energy and Population Dynamics: Effects of Temperature and Food Fluctuation

---

A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for the degree

Masters of Science in Biology

---

by

Xiaohui Guo

August 2014

Dr. Istvan Karsai, Chair

Dr. Thomas F. Laughlin

Dr. Christopher D. Wallace,

Keywords: Ant colony, agent-based model, metabolic theory of ecology, energy dynamic, Kruskal-Wallis test

ABSTRACT

An Agent-Based Model of Ant Colony Energy and Population Dynamics: Effects of Temperature and Food Fluctuation

by

Xiaohui Guo

The ant colony, known as a self-organized system, can adapt to the environment by a series of negative and positive feedbacks. There is still a lack of mechanistic understanding of how the factors, such as temperature and food, coordinate the labor of ants. According to the Metabolic Theory of Ecology (MTE), the metabolic rate could control ecological process at all levels. To analyze self-organized process of ant colony, we constructed an agent-based model to simulate the energy and population dynamics of ant colony. After parameterizing the model, we ran 20 parallel simulations for each experiment and parameter sweeps to find patterns and dependencies in the food and energy flow of the colony. Ultimately this model predicted that ant colonies can respond to changes of temperature and food availability and perform differently. We hope this study can improve our understanding on the self-organized process of ant colony.

DEDICATION

I dedicate this thesis to my parents Xing Guo and Hexian Fan who have constantly shown keen interest and invested in my education. I also dedicate this work to my girlfriend, Wenjing Mu, who supported and encouraged me to make this work successful.

ACKNOWLEDGEMENTS

I want to express my sincere gratitude to Dr. Istvan Karsai, Associate Professor, Department of Biological Sciences, East Tennessee State University (ETSU) for his acceptance to work with me. I really appreciate the training and research techniques I learned from him that helped to improve the understanding of every aspect of my research. It is my honor to work with him to study ant colony models.

I also thank Dr. Thomas F. Laughlin, Department of Biological Sciences, ETSU for being part of my thesis committee. I really appreciate the useful suggestions he gave me. I also thank Dr. Christopher D. Wallace, Department of Computer Sciences, ETSU for his immersed contribution as a member of my thesis committee towards this work.

I am also grateful for the School of Graduate Studies of ETSU for awarding me the Thesis Scholarship to support our research.

TABLE OF CONTENTS

Page

Chapter

Chapter Page

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Ant’s Sensitivity to the Ecological Event

Insects make good indicators of ecological condition because they are highly diverse and functionally important, can integrate ecological processes, and are sensitive to environmental change (Brown 1997). As one of the famous terrestrial insect, ants have the critical ecological roles in soil turnover and structure (Humphreys 1981; Lobry de Bruyn and Conacher 1994), nutrient cycling (Levieux 1983; Lal 1988), plant protection, seed dispersal, and seed predation (Ashton 1979; Beattie 1985; Christian 2001). Ants have proven sensitive and rapid responders to environmental variables (Campbell and Tanton 1981; Majer 1983; Andersen 1990). In recent analysis of various insect groups as potential bioindicators, ants scored highest (Brown 1997). They have been used as bioindicators to manage mining site restoration because both their abundance and species richness will decline with increasing dry sulfur deposition from mining emissions (Hoffmann 2003). Forest management agencies in Australia also have incorporated ants in monitoring programs associated with fire and logging practices (Andersen 1997). The rapid replacement of the ecologically complex regrowth forest through wildfire and salvage logging caused a substantial increase in ant’s foraging activity (*P. pallidus*) during the first postfire autumn period, and activity remained high for up to 14 months (Neuman 1992). In the coffee agroecosystem in Central America, it was found that microclimate changes, high-light environment, and lack of leaf litter cover in the unshaded system are the determinants of the differences in ground foraging ant diversity (Perfecto and Vandermeer 1996). Monitoring a single species of ant is also recommended to detect trends among threatened and endangered or keystone species (Underwood and Fisher 2006). Ants are important seed dispersers. Their abundance and diversity can also be used to monitor the ecosystem function performed (Majer 1984; Grimbacher and Hughes 2002). Relying on the ant-seed interactions to bush regeneration, the varied proportion of ant species indicates the differences of zone types significantly (Grimbacher and Hughes 2002). In the environment destroyed by grazing and trampling, ant species diversity can respond to these disturbances. For example, in the remnant *Eucalyptus salubris* woodland disturbed by sheep grazing, lower ant diversity was recorded (Abensperg-Traun 1996), and in grasslands at Mount Piper, Victoria, Australia, the same relationship between grazing and ant species richness was detected as well (Miller 1997). The ant community could respond to the habitat fragmentation by declining population sizes as well. Comparing twig-dwelling ants between two 100 ha forest fragments with 2 continuous areas of forest in the Amazon, Carvalho and Vasconcelos (1999) found species richness and abundance to be higher in continuous forest sites than isolated fragment sites. Recently, researchers focused on the responses of ant communities to climate change. By analyzing several niches models, Argentine ants (*Linepithema humile Mayr*) was predicted to retract its range in tropical regions but to expand at higher latitude areas (Roura-Pascual et al. 2004). Retrospecting the adaptation history of ants on climate, Dunn et al. (2009) suggested that the hemispherical asymmetry of ant species distribution was caused by greater climate change since the Eocene in the northern than in the southern hemisphere that made more extinctions in the northern hemisphere with consequent effects on local ant species richness. Meanwhile, Kaspari (2005) also found the number and mass of workers influenced by *NPP* (net primary productivity, g of carbon per m^2 per year), and temperature will determine the ant colony mass independently under climate change.

Climate Change Effects on Animals

Climate change is a significant and lasting change in the statistical distribution of weather patterns over periods ranging from decades to millions of years. It is caused by factors such as biotic processes, variations in solar radiation received by Earth, plate tectonics, and volcanic eruptions. Certain human activities have also been identified as significant causes of recent climate change, often referred to as "global warming" (National Research Council 2010). Climate change does not only cause changes in the climate system ranging from annual precipitation and solar radiation to global land-ocean temperature increment but also affects the biodiversity in land-based ecosystem and ocean ecosystem. In recent major ice ages, the climate change caused distribution changes of most living organisms. As an example of *Chorthippus parallelus*, the common meadow grasshopper of Europe across all northern Europe, their haplotypes showed little diversity and were similar to those in the Balkans, clearly indicating a postglacial expansion from a Balkan refuge (Hewitt 2000). Although there are still debates about the impacts of current climate change on biodiversity, more and more research strongly suggest that significant impacts of climate changes are already discernible in animal and plant populations (Camille Parmesan 2003). Many observable evidences can prove the impacts of climate change and global warming on natural ecosystem and its biodiversity. For example, 39 butterfly species in the North America and Europe have shifted their northward range up to 200 km over 27 years, which related to increased temperatures (Parmesan 1999). As temperature increased Antarctic invertebrates changed their distribution (Kennedy 1995). Amphibians in UK breed earlier in past 25 years than ever before (Blaustein 2001). Based on the extinction risk assessment, it is predicted that, on the basis of mid-range climate-warming scenarios for 2050, that 15–37% of species in samples of regions and taxa will be ‘committed to extinction’ (Thomas 2004). However, there are no effective observation and analysis to illustrate and predict relationships between warming world and ant biodiversity distribution and changes (Jenkins et al.

2011).

Allometric Equation for Metabolism

Huxley (1924) was the first one to construct a so-called allometric equation and to illuminate the quantitative relationship between rate of relative growth and body size by it. He pointed out that the rate of relative body growth of different organisms (y) was a power function to the size of body (x) and particular parameters (k and b), which is described below:

$$y = b \cdot x^k$$

b and k are constants. b is a normalized constant, and it has no particularly biological significance. However, k is significant one because it implies a constant ratio between rate of growth of organism and absolute body size (Huxley 1932). This equation disclosed potential allometric growth laws that absolute size of body could be teemed as an estimator of other parameters involving growth, such as rate of growth, life span, and so on. In most studies exploring values of k and b, Kleiber (1932) verified the metabolic rate scaled to the 3/4 power of body size, and mass was considered as a better parameter to be treated as index of body size than surface of body, although the surface law with 1/3 power seemed to be reasonable to explain how metabolic rate originated from heat dissipation scaling with body surface area. The 3/4 power relationship is shown below:

$$I = I^0 \cdot M^{3/4} \qquad \text{(equ. 1)}$$

I is the metabolic rate. I_0 is the normalization of constant independent of body size. M is the mass of the animal. West et al. (1997) suggested that quarter-power law be validate by its general model in which the body size was depicted as a series of space-filling fractal networks of branching tubes, and materials were transferred to the part of body through this network system. The branching structure is a prevailed pattern to all of animals and even plant because natural selection tends to maximize metabolic rate by maximizing exchanging surface and minimizing distance of fractal networks (West 1997, 1999). Gillooly et al. (2001) suggested some corrections on the allometric equation to display more details by adding temperature effects. In their opinions, animal metabolic rate depends on three factors: 1, intensity of reactant, 2, fluxes of reactants, and 3, kinetic energy of the system. The first two factors are determined by supply and removal of products. The last factor involves the effect of temperature, which could be quantified by equation, $e^{-Ei/kT}$, being used to describes how temperature affects the rate of reactions by changing molecules' movement with sufficient kinetic energy. E the activation energy is, measured in electron volts (1eV=23.06 kcal/mol=96.49 kJ/mol). The relationship between metabolic rate (B) and temperature (T) is:

$$B = B_0(T) \cdot M^{3/4} = B_0 \cdot M^{3/4} \cdot e^{-E_i/kT} = B_0(T_0) \cdot M^{3/4} \cdot e^{E_i T_c/kTT_0} \quad \text{(equ. 2)} \quad \text{(Gillooly 2001)}$$

B_0 is a basal metabolic rate; B is actual metabolic rate; T_0 is standard temperature for B_0 in k; and T is the absolute air temperature in K; T_c is difference between T and T_0 in K; E is the activation energy; k is Boltzmann's constant.

The temperature and mass dependences are also shown in the allometric population growth model by Savage et al. (2004) in which the population grows under the population logistic growth law and individual metabolic rules. By applying the Euler integration, the way temperature, mass, and time scale play their influences was clarified into the equation:

$$\overline{B}_{pop}(M,T,t) = r[(1+\frac{E_0}{S_0})\frac{B_0}{r_1}+E_0] \quad \text{(equ. 3)} \quad \text{(Savage et al. 2004)}$$

E_0 is a normalization of activation energy; S_0 is a constant of mortality rate; B_0 is a basal metabolic rate; r_1 is a taxon- and environment-dependent normalization constant. All of these variables are temperature and mass independent. The population growth rate was just controlled by population metabolic rate regarding with total mass of population, temperature, and time. Models described above are also extended to predict the allometries of ontogenetic growth trajectories (West 2001) and other life-history attributes (Savage et al. 2004) that display the prevalence of allometric equation to explain biological processes in various hierarchies.

The Significance of Ant Workers in Population and Energy Dynamics of Ant Colony

Like the life cycle of the individual ant, the life cycle of an ant colony can be conveniently divided into three parts: founding stage, ergonomic stage, and reproductive stage (Hölldobler and Wilson 1990, 143 p). In ergonomic stage, over the weeks and months the population of workers grows, the average size of the workers increases, and new physical castes are sometimes added (Hölldobler and Wilson 1990, 143 p). Among the key life history traits of social insects, the nutritional storage of colonies in response to spatial and temporal variation has been of considerable interest (Kondoh 1968; Wilson 1974; Rissing 1984; Hasegawa 1993). In that colonies in the fall season store nutrients in the form of workers' fats that can be used during overwinter periods of food scarcity or seeds collected are stored by workers in the nest (Risch anf Carroll 1986), the size and population of the workers become significant index to estimate ant colony dynamic. In the seasonal dynamic change of colony size and population, there has been some evidence that incipient colonies are monomorphic and consist of small workers only, but as colonies grow, production of larger workers causes the size-frequency distributions to become strongly skewed. Kaspari (2005) found ants altered colony mass by independently changing worker mass and/or worker number. It was found that energetic efficiency in polymorphic colonies (multiple workers cast) was approximately 10% higher than in colonies composed of only small workers (Porter and Tschinkel 1985). And relying on worker's metabolic rate parameters, it is feasible to monitor the colony energy dynamic status. For example, the colony VO_2 (oxygen consumption rate) could be accurately estimated from individual VO_2 (Lighton 1989). In 3 species of *Pogonomyrmex* Harvester Ants, respiration of the workers was estimated to account for 84-92% of energy assimilated by colony nest (MacKay 1985). Specially, the Damuth's Rule shows that for large compilations of population densities, the relationship between the average mass of a species and its average density is generally well fit to a power function, which enforces the significance of worker size in ant colony (White 2007). Therefore, it is meaningful to test ant colony energy and population dynamics based on individual worker's metabolic process influenced by seasonal changes of temperature and food supply.

The aim of the study reported herein was to investigate ant colonies' energy and population dynamics in response to changes of temperature and food. These variables were simulated under different levels of temperature and food to determine ant colonies' response to changes in the environment. Apart from energy and population dynamics, the study also focused on the effects of temperature on workers' size, immature ants' development, and queen's reproduction. This study tested the following hypotheses:

H_0…there is no effects of temperature and food on ant colony's energy and population dynamics.

H_1…temperature elevations will increase the risk of ant colonies for dying out because they need to consume more energy to sustain themselves.

H_2…Changes of food availability will affect energy and population dynamics of ant colonies. Rich food sources can protect ant colonies from decaying even in very high temperature.

CHAPTER 2

MATERIALS AND METHODS

The ant colony energy dynamic ABM model was constructed on the platform of Netlogo 5.0.4.

Purpose

The goal of the model is to simulate the long-term dynamics of an ant colony, especially focusing on foraging and colony growth. The behavior of individual ants is based on simple rules, and their behavior is linked to a simple energy flow from the environment to the colony and metabolism (metabolic equations). The main idea of the model is to apply MTE (Metabolic Theory of Ecology) to the ant colony to quantify the effects of temperature on the dynamics of ant colony and to analyze possible scenarios of temperature fluctuations caused by climate change.

State Variables and Scales

This model is comprised of several parts: individuals, interaction networks, nest, and environment. The first 2 are modeled explicitly and the last 2 are modeled abstractly. Individual agents spend time behaving and interacting in the simulation environment. We assume that the growth of the ant colony is determined by the queen’s fecundity and workers’ efficiency. For simplification, all stages of offsprings are merged into one state of the “immature ant” agent. This model starts with a situation that the colony has been initiated by one queen with a varying number of immature ants, nurses, and foragers. In the model the “immature ants” are produced by queen at random locations in the nest. The immature ones can develop into nurses or foragers. The life spans of immature ants and adult workers are the functions of expected longevity, temperature, mass, and energy. We assume that only 2 castes exist in the ant colony, foragers and nurses. Foragers work in searching for food outside the nest. They find food resources by random walking or following trail pheromone (Hölldobler and Wilson 1990, 228 p). Nurses feed immature ants and the queen inside the nest. There has been quantitative evidences that rate of the trophallaxis (number of workers/hour feeding a larva) varies with the individual larval size and hunger cues (Cassill 1995, 1999). These relationships strongly suggest that nurses orient toward queen's or immature ants' hunger pheromone. Although workers have different size and behavioral preferences, these 2 castes, foragers and nurses, can switch jobs depending on environment (Gordon 2010, 30 p).

The individuals are characterized by state variables: identity number, task assignments, and internal state (velocity, mass, energy, metabolic rate, and longevity) (Table 1). Workers are represented by mobile agents: nurses feed immature ants and queen inside the nest; foragers forage outside the nest. Both of them move at a velocity, *v*. In the model tasks of workers emerge from interactions with others agents and environment. The queen is modeled as a motionless agent who monopolizes some space in the nest. Her tasks are designed to convert the food into energy and consume energy to live and produce immature ants. Immature ant agents are installed as immobile agents in the nest as well. They consume energy to support their growth until they develop into foragers or nurses. Both queen and immature ants release the hunger pheromone to inform nurses when they are hungry and where they are.

In this model environmental variables are recorded on every step, including intensity of pheromones, diffusing/evaporating rate of pheromones, and amount of food, time, and temperature (Table 1). All of these variables are taken into account in workers' decision-making. According to the MTE (metabolic theory of ecology), however, metabolic rate and speed will be a function of temperature (described below).

This agent-based model works in a discrete space consisting of 141 × 61 unit patches, one grid of a patch scales to 4 meters outside nest and 2 meters inside nest. The space, a rectangular area enclosed by reflecting boundaries, is large enough to capture large-scale spatiotemporal dynamics akin to ones in a real system. The area is divided into 2 independent sections by an impassable border: inside the nest and outside the nest. An entry to the nest is installed on this border. Food is brought into the nest by workers through the entrance. In the nest queen monopolized 10×10 grids, and the rest were for rearing immature ants. Each position of the nest, except the borders and chamber of the queen, can be empty or randomly occupied by a single immature ant. Renewable food patches are arranged randomly outside the nest. One time tick is assumed to be consistent with 1 minute. The intention is to model the long term behavior of the colony. Therefore, the simulation lasts for about 12 months (≈600000 steps). The basic speed of worker is 1 grid per minute to simulate the realistic velocity of ants, which is about 2 meters per minute (Hurlbert 2008).

Table 1 (continued on the next page). Scale of variable and process.

Agent and environment	**Variable**	**Unit**	**Process**
Environment	Temperature Chemical diffusing rate Chemical evaporating rate	*°C* *0.04 grid/min* *0.05 drop-size/min*	Update temperature (scenario) Constant Constant
Foragers	Age Energy Metabolic rate Trail pheromone record	*min* $\times 10^{-4} J$ $\times 10^{-4} J/min$ *Drop-size*	Aging Update Update Update

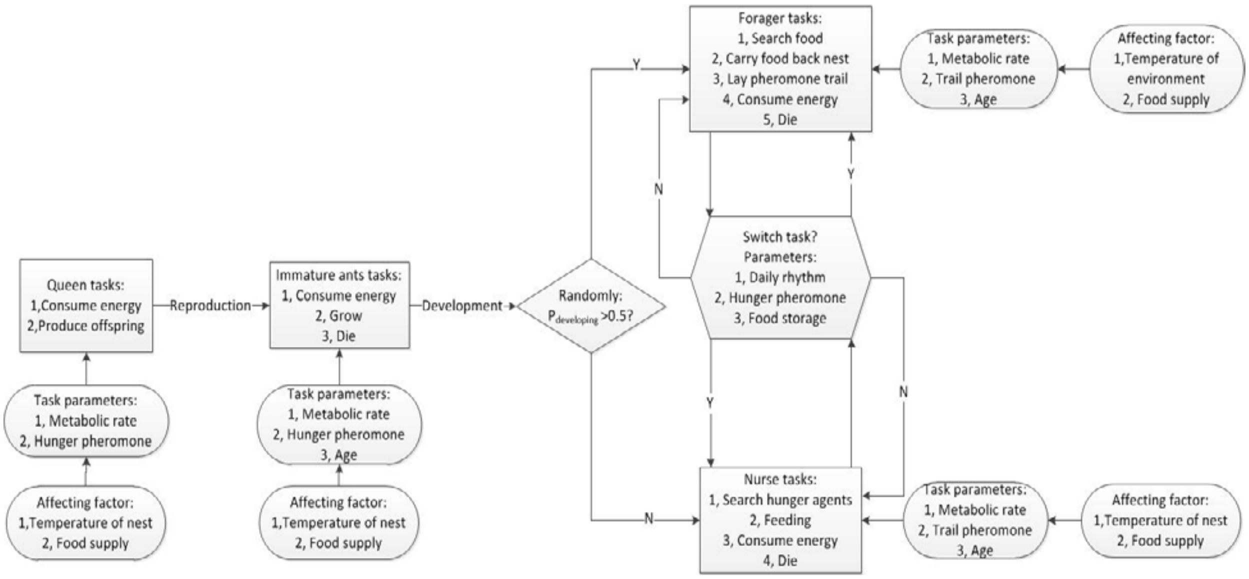
Table 1 (continued). Scale of variable and process.

Agent and environment	Variable	Unit	Process
Nurses	Age	min	Aging
	Energy	$\times 10^{-4} J$	Update
	Metabolic rate	$\times 10^{-4} J/min$	Update
	Trail pheromone record	Drop-size	Update
Queen	Age	min	Aging
	Energy	$\times 10^{-4} J$	Update
	Metabolic rate	$\times 10^{-4} J/min$	Update
	Hunger pheromone record	Drop-size	Update
Larva	Age	min	Aging
	Energy	$\times 10^{-4} J$	Update
	Metabolic rate	$\times 10^{-4} J/min$	Update
	Hunger pheromone record	Drop-size	Update

Process Overview and Scheduling

At each discrete time step, various agents have series of behaviors to perform in a sequential order. Foragers patrol outside the nest, constantly detecting a gradient of trail pheromone; they stop at food sources to carry one mg food (Josens 1998) and return to the nest, depositing a trail pheromone in the way they passed. They put down food in the nest and repeat the process or switch to the role of nurse. Carrying 0.002 mg food (Appendix 4) nurses wander around randomly in the nest. When the nurse locates the hungry queen or immature ant by a gradient of hunger pheromones, it will move to the target grid cell, put down the food, and feed the hungry agent. After finishing, it returns to the food storage. This procedure is also repeated unless it switches to the role of forager. The queen releases the hunger pheromone when her energy is lower than the critical threshold. The immature ants also release hunger pheromone when their energy drops below the energy threshold. They develop into workers when their mass is higher than mass threshold. The behaviors of agents are shown below (Fig.1).

a (colony view):



b (queen):

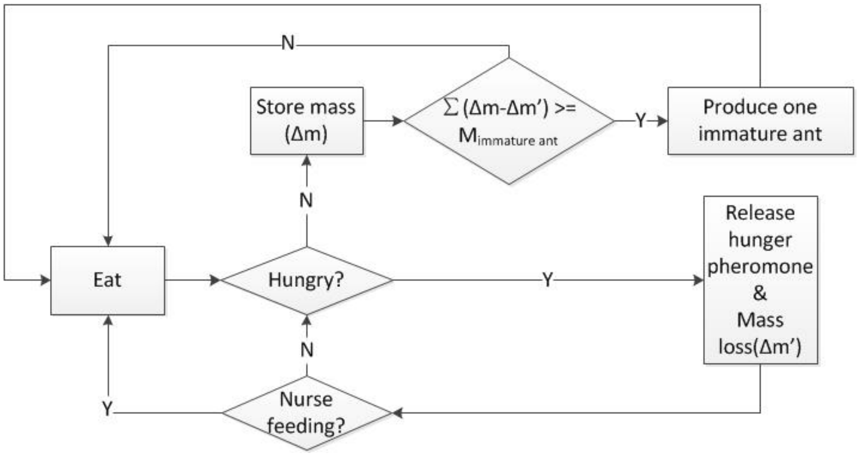
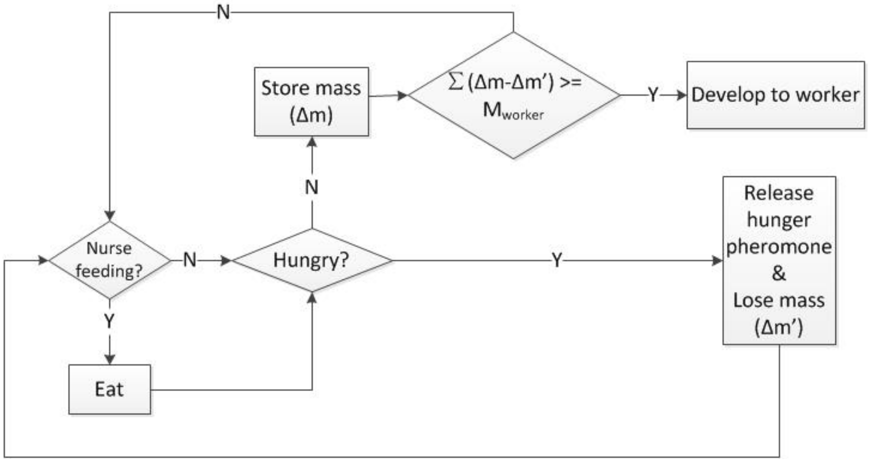


Figure 1 (continued on the next pages). Process of overview of the model. Each task group has a working cycle. a is a colony view, b is a forager.

c (immature ant):



d (forager):

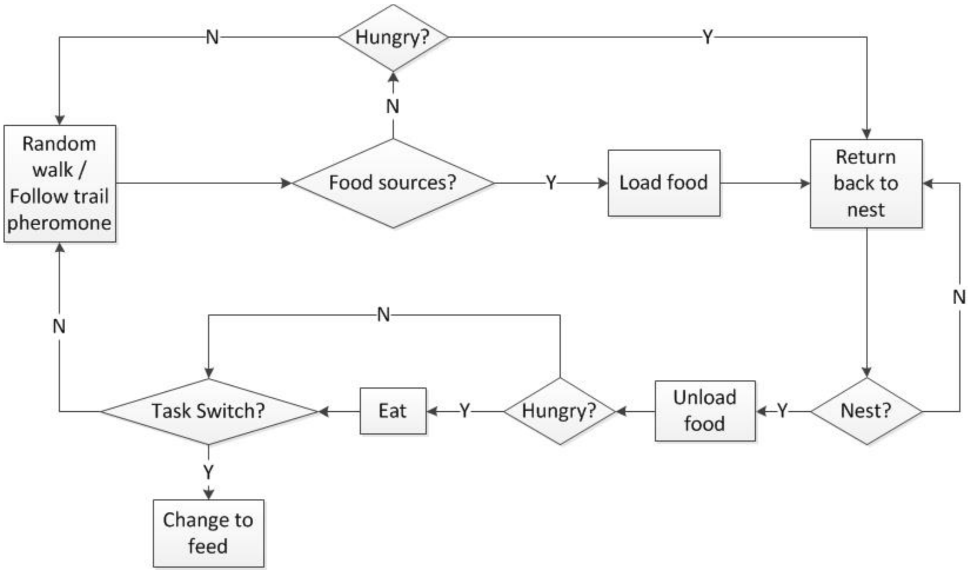


Figure 1 (continued). Process of overview of the model. Each task group has a working cycle. c is a nurse, d is an immature ant.

e (nurse):

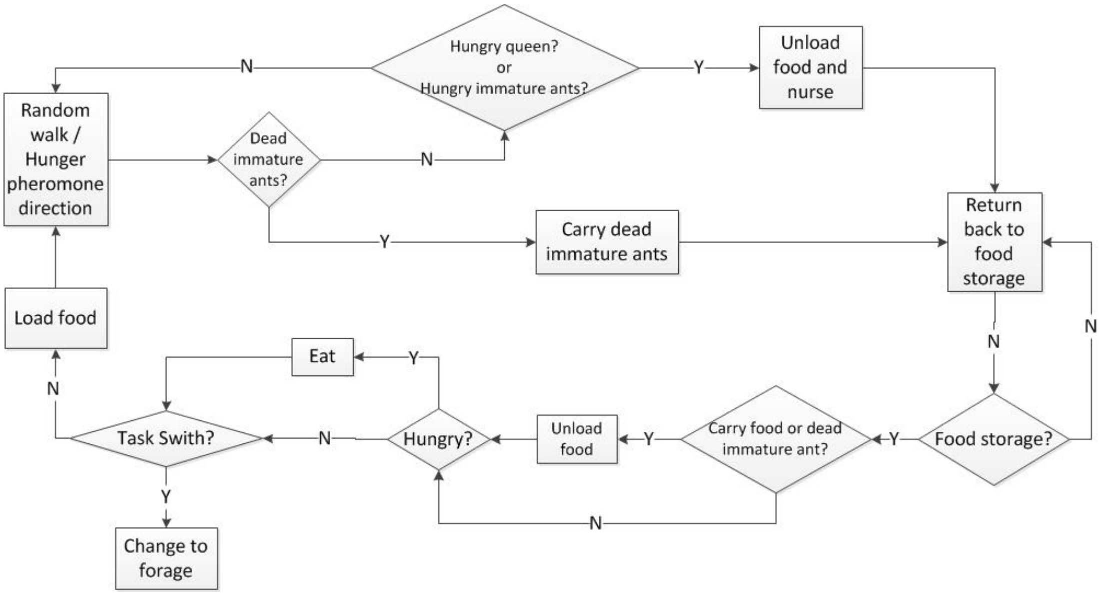


Figure 1 (continued). Process of overview of the model. Each task group has a working cycle. e is a queen.

f (mass & energy networks of agents):

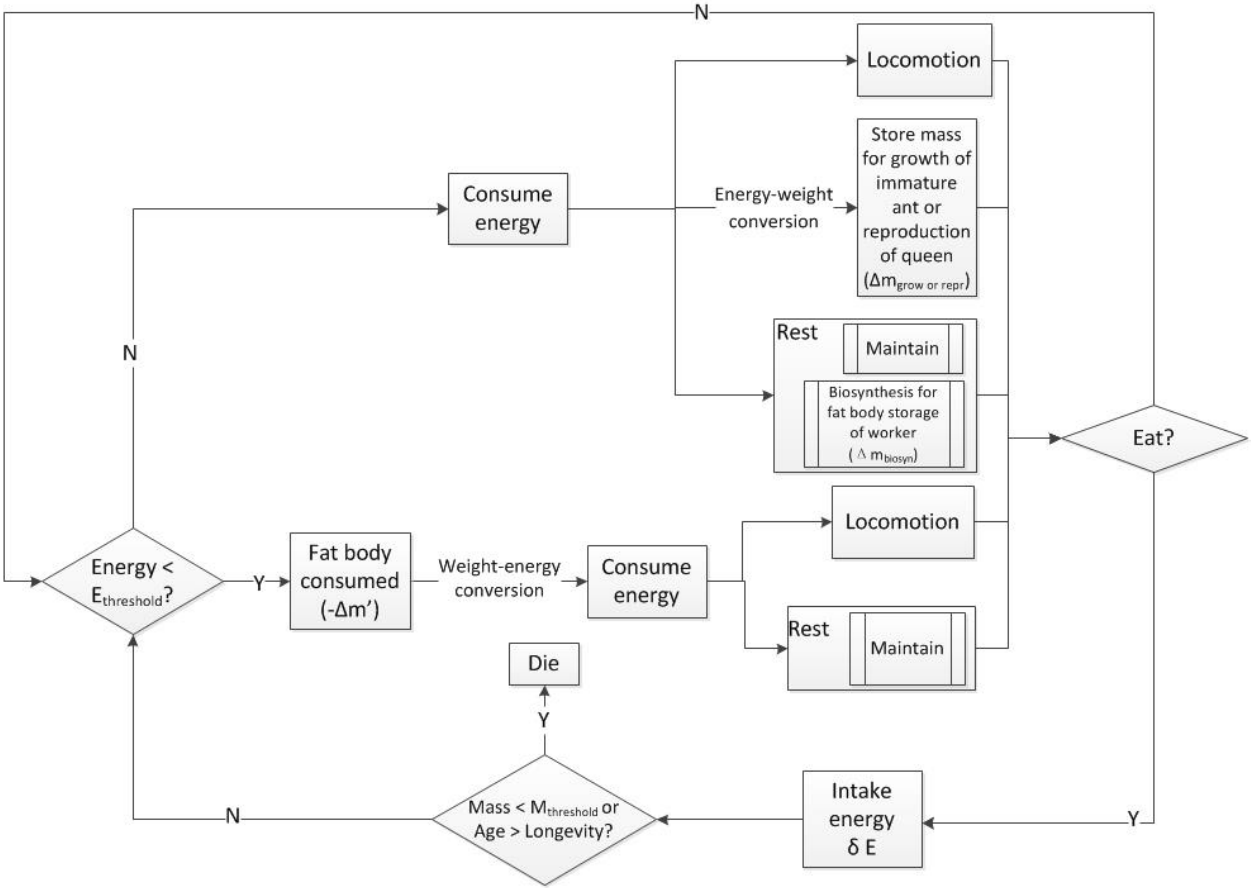


Figure 1 (continued). Process of overview of the model. Each task group has a working cycle. f is energy-mass conversion.

Design Concepts

Emergence

The equilibriums of worker castes, worker's population, energy, and mass dynamics emerge from the individuals' behavior and metabolism, but the behavior and metabolism are entirely described by simple empirical and stochastic rules. The balance between foraging efficiency and feeding efficiency also emerge dynamically from colony needs and prey and food availability. Reproduction and development speed is the function of fulfilling the nutrition need of the queen and immature ants.

Adaptation and Fitness

Adaptation and fitness are not explicitly included in this model. The only exception is in the workers’ decision whether the foraging strategy or feeding strategy will be taken. The decision is based on the amount of food stored in the nest.

Sensing

Individuals are assumed to know their own inner state (energy, mass, age, and assignments) and behave accordingly. Ants’ sensing mainly depends on smelling and tactile sensation. The use of visual signals in ants is very minor, and there is no a single example to be solidly documented (Hölldobler and Wilson 1990, 259 p). Therefore, we assumed ants can sense their neighbors by close antenna touching. Workers have 2 sensing antennas to perceive directional signals (Hölldobler and Wilson 1990, 271 p). We assume they wiggle and orient along varying-concentration odor trail by antennae detection (from right $35^o$to left 35^o). In this model the workers can diagnose the gradients of pheromone diffused in patches. Cassill (1999) suggested the ant queen and immatures may release hunger pheromone to notify workers about their hunger status, akin to the behavior of the brood of honeybees (Fewell 2003). Workers can also recognize the saturation of food storage. (Reyes-López 2002) and distinguish dead larvae from living ones (Robinson et al. 1974).

Interactions

Interactions between different agents are modeled with more details described in the submodel section. Individuals direct interactions happen when workers feed hungry queen or immature ants and when workers move dead immature ants to food storage. The saturations of immature ants and queen could also influence the tasks' switching decisions of workers, but those influences are not represented as explicit interactions between particular individuals. The state variables and behaviors of ant agents are also affected by environmental factors. The temperature is the primary environmental factor to regulate ants' moving velocity and metabolism. Ants tend to move faster and consume more energy in high temperature than ants in low one. Accordingly, workers are designed to have daily rhythm of temperature preference.

In this model workers can't cross the reflecting walls and borders. When they reach the borders and walls, they will redirect randomly. The environment is also changed by ants. The amount of the pheromones deposited in the grid will decay unless ants lay new ones. The food will be reallocated from food sources to food storage by foraging and transporting of workers.

Stochasticity

Random numbers were generated to simulate the realistic process by using the netlogo built in random generator. The following state and environment variables are stochastic: initial location, walking direction, developmental orientation of immature ants, and amount of food per patch. We assume the initial energy of ants, initial number of ants, initial mass of ants, initial age of workers, and initial amount of food in the food sources and storage distributed normally. In the model ants make decisions by possibility that could be quantified in a normal cumulative distribution functions ($\mu = threshold,\ \sigma = 1$).

Collectives

Collectives are represented in the model as task groups of workers, namely adult ants are either nurses or foragers. However, these collectives emerge in nature because in the model workers can switch their tasks freely by interacting with others and environment.

Observation

In this model Netlogo offers a visual platform to monitor the behavior of the system. The monitor is used for inspecting and testing the model step by step. The following parameters are monitored and saved into a file for further analyzes: the population size of the ant colony, number of nurses, number of foragers, number of immature ants, total energy of the ant colony, total mass of the ant colony, amount of food stored, birth rate, growth rate of immature ants, death rate of immature and adult ants, foraging efficiency, feeding efficiency, developing time of immature ants, age structure of the ant colony, temperature of the nest, and temperature of the environment. To test our hypotheses and compare the predictions, Kruskal-Wallis test in SPSS Statistical Package (Version 19) was used.

Initialization

The initial parameters in the model are listed in the Table 2. The simulations were repeated 10 times so as to consider the variability between outputs for the same set of parameters and initial conditions. The variability came from the stochasticity in the processing of the model. The onset of the ant colony imitated the start of a natural colony after the workforce of the colony reached 200. In this stage the queen and $N_{immature\ \mathrm{ant}}$ live in the nest and N_{nurses} work inside the nest to feed the queen and immature ants. $N_{foragers}$ work outside the nest to forage. There is one cluster of food patches arranged randomly outside the nest. And 35 mg food is stored in the nest. Before the model starts running foragers and nurses are positioned in the environment randomly.

Parameters

Table 2 (continued on the next pages). Initial parameters of the model. Each step related parameters one minute was converted into one tick step in the value “used” column.

Description	*Acronym*	*Estimated*	*Used*	*Reference*
Standard metabolic rate of worker	$m_{nurse(forager)}$	$3.13\times(10^{-4} J/min)$	$3\times(10^{-4} J/min)$	*Appendix A*
Metabolic rate of worker for synthesis of fat body	$m_{nurse(forager)\ syn}$	$0.87\times(10^{-4} J/min)$	$1\times(10^{-4} J/min)$	*Appendix C*
Metabolic rate of worker for locomotion	$m_{nurse(forager)\ loc}$	$5.09(10^{-4} J/min)$	$5(10^{-4} J/min)$	*Appendix B*
Standard metabolic rate of immature ant	$m_{immature\ ant}$	$1.51\times(10^{-4} J/min)$	$1.5\times(10^{-4} J/min)$	*Appendix A*
Metabolic rate of larva for growth	$m_{immature\ ant\ grow}$	$3.95\times(10^{-4} J/min)$	$4\times(10^{-4} J/min)$	*Appendix C*
Standard metabolic rate of queen	m_{queen}	$19.77\times(10^{-4} J/min)*$	$20\times(10^{-4} J/min)$	*Appendix A*
Metabolic rate of queen for reproduction	$m_{queen\ rep}$	$960\times(10^{-4} J/min)*$	$960\times(10^{-4} J/min)$	*Appendix C*
Speed of worker	$v_{nurse(forager)}$	*2 cm/s*	*120 cm/min*	*(Schilman and Roces 2005)*
Initial energy of queen	E_{queen}	*380000*	$n(\mu,\sigma^2), (\mu = 380000, \sigma = 1000) \quad (10^{-4} J)$	
Initial energy of worker	$E_{nurse(forager)}$	*38000*	$n(\mu,\sigma^2), (\mu = 38000, \sigma = 1000) \quad (10^{-4} J)$	-
Initial energy of immature ants	$E_{immature\ ants}$	*15200*	$n(\mu,\sigma^2), (\mu = 15200, \sigma = 1000) \quad (10^{-4} J)$	-
Number of nurses	N_{nurse}		*100*	
Number of foragers	$N_{forager}$		*100*	
Number of immature ants	$N_{immature\ ant}$		*20*	
Amount of food in food storage	$F_{storage}$		*20*	

Table 2 (continued). Initial parameters of the model. Each step related parameters one minute was converted into one tick step in the value “used” column.

Description	Acronym	Estimated	Used	Reference
Threshold of food storage saturation	$F_{StoreThreshold}$		$n(\mu,\sigma^2),(\mu = 30,\sigma = 10) \quad (10^{-4}J)$	
Initial mass of worker	$M_{nurse(forager)}$	2 mg	$n(\mu,\sigma^2),(\mu = 2,\sigma = 0.05) \quad (mg)$	(Jensen 1978)
Initial mass of immature ants	$M_{limmature\ ant}$	0.8mg	$n(\mu,\sigma^2),(\mu = 0.8,\sigma = 0.2) \quad (mg)$	(Brian 1973)
Initial mass of queen	M_{queen}	2~80 mg	20 mg	(Tschinkel 1978; Keller 1989)
Initial age of worker	A_{age}		$n(\mu,\sigma^2),(\mu = 10000,\ \sigma = 2000)$	
Expected longevity of nurses (foragers)	$\overline{A_{age}}$	190080	190080	
Diffusing rate of hunger pheromone	$r_{hunger\ diffuse}$		0.046	
Evaporation rate of hunger pheromone	$r_{hunger\ evaporate}$		0.052	
Diffusing rate of trail pheromone	$r_{trail\ diffuse}$		0.04	
Evaporation rate of evaporate pheromone	$r_{trail\ evaporate}$		0.05	
Amount of food at each food patch	F		$n(\mu,\sigma^2),(\mu = 225,\sigma = 50) \quad (food\ unit)$	
Antenna sensing angle	A	70	70	
Catabolism weight-energy conversion factor	c'	19.02J/mg	$190000(10^{-4})J/mg$	(Cummins and Wuycheck 1971; Hou et al. 2008)
Anabolism weight-energy conversion factor	c	>19.02J/mg	$200000(10^{-4})J/mg$	(Perrin 1995;Kaspari 2005)
Energy threshold of queen for hunger	$E_{queen\ threshold}$		$380000\,(10^{-4})J/mg$	(Cummins and Wuycheck 1971)
Energy threshold of worker for hunger	$E_{worker\ threshold}$		$380000\,(10^{-4})J/mg$	

Table 2 (continued). Initial parameters of the model. Each step related parameters one minute was converted into one tick step in the value “used” column.

Description	*Acronym*	*Estimated*	*Used*	*Reference*
Energy threshold of immature ants for hunger	$E_{immature\ ant\ threshold}$		$15200\,(10^{-4})J/mg$	
a (responding factor of hunger pheromone gland toward energy status)	a		5	
Mass lower threshold of worker for dying	$M_{WorkLowerThreshold}$		$1mg$	
Mass upper threshold of worker for dying	$M_{WorkUpperThreshold}$		$5mg$	
Mass threshold of immature ants for dying	$M_{immature\ ant\ threshold}$		$0.5mg$	
Mass of threshold of queen for dying	$M_{queen\ threshold}$		$15mg$	
One bite of ant	B_{ant}	$0.023mg$ $4420(10^{-4})J$	$0.02mg$ $4400(10^{-4})J$	*Appendix D*
Drop size of trail pheromone	$drop_{trail}$	180	180	
Width of food sources	W_{food}		*3 patch wide*	

Input

In the model the environment was parameterized by daily air temperature of Johnson City, TN in 2010. The temperature dataset is from National Ocean and Atmosphere Administration (NOAA) (http://www.ncdc.noaa.gov/cdo-web/). These temperature data was used to construct a smooth distribution with 1-minute steps to conform the resolution of the model. In the “experiment of temperature changes”, new temperature data were created by elevating 2, 4, 6, 8, 10, 12, and 14 centigrade to the current temperature data of Johnson City. Because the advantage of nesting in the soil is the protection provided by the nest against high and low temperature extremes, rain, or wind (Moyano 2013), we assumed the ant colonies nest in the soil. In the model the colonies could not actively thermo-regulate nest temperature (T_{nest}) because of the small size population of colonies. The nest temperature equated to soil temperature in the 10cm depth that correlated well with air temperature because both are determined by the energy balance at the ground surface (Zheng et al. 1993). The soil temperature was regressed to air temperature ($\mathrm{T_{air}}$) in equation 4:

$$T_{nest} = T_{soil} = 0.89 \cdot T_{air} + 2.31 \qquad \textit{euq.4} \text{ (Zheng et al. 1993)}$$

We implemented different levels of food with 1, 2, and 3 patch wide per food source patch in the model to simulate different richness of food sources.

Submodels

The Tasks of Agents

In this model the stationary queen produces all the offsprings labeled “immature ants”. Immature ants are immobile agents as well, and they finally develop into the forager or nurse ants. The events of reproduction and development are controlled by mass and energy (in Reproducing and developing). Foragers leave nest to collect and carry food back to the nest (in Foraging). Nurses enter into the nest to feed hungry queen or immature ants under directions of hunger pheromone (in Feeding).

Reproducing and Developing: The mass of queen and immature ants change dynamically (in Energy and Mass). The event of reproduction or development occurs when queen or immature ants are heavier than their mass thresholds. The queen lays an egg in a random nonoccupied position of the nest and this immature ant stays there until it becomes an adult. When the immature ant becomes a mature one, it will emerge and start work next to the food storage as the nurse ant or will emerge and start to work next the nest entrance as the forager.

Initial decision on the first task is a random process.

Foraging: The foraging task could be viewed as 2 alternating status: start from the nest and reach the food source, and start from the food source laden with food and reach the nest (Panait, 2004). In the first status foragers depart nest in search of food by walking forward with random sniffing angle between left 35° and right 35° or following gradient of trail pheromone they encountered. Their moving velocity v:

$$v = v_0 \cdot M^{1/4} \cdot e^{-Ek/T_{air}} \text{ (equ. 4)} \qquad \text{(Hurlbert 2008)}$$

v_0 is standard velocity of foragers at 20 ℃; T_{air} is environment temperature; M is the mass of agent; E is the activation energy; k is Boltzmann's constant. In the second status we assume that foragers are able to navigate to the nest by using the shortest distance after finding the food. Therefore, the pheromone trail between the food item and the nest is also formed on the shortest distance between the 2 positions. Foragers bring 1 mg food back to nest directly. When they come back, food will be stored in the food storage of the nest.

Feeding: Each turn, the nurse keeps motionless and stays very close to queen or immature ants mouthparts to sweep antenna until larva terminates the feeding and worker move away as Cassill (1995) described it in fire ant, *Solenopsis invicta*. In the model feeding is also viewed as 2 alternating status: start from the food storage laden with food and reach the hungry queen or immature ants, and start from the queen or immature ants and reach the food storage. At the first status nurses carrying 0.002 mg food (Appendix 4) look for hungry agents in the nest by the same random walking as forager until they encounter and follow the gradient of hunger pheromone. Feeding events only happen in hungry agents nurses encounter (Cassill 1995). The nurses move at velocity v' described by equation 4 with exposed nest temperature, T_{nest}. When they reach patches of hungry agents, 0.002 mg food is fed at 1 time-step. At the second status assumedly, nurses can go back to food storage directly.

Dying: Deaths of workers are age-controlled. The age of each individual is monitored. The expected longevity of worker is about 4.4 months (≈ 190080 steps) (Calabi and Porter 1989), but it is influenced by temperature and mass as follows:

$$L = \frac{L_{expected}}{M^{-1/4} \cdot e^{-E/kT}} \qquad \text{(equ. 5)} \qquad \text{(Savage et al. 2004)}$$

Where L is real longevity; $L_{expected}$is expected or average longevity; M is the mass of agent; E is the activation energy; k is Boltzmann's constant. We assume their death is the cumulative function of worker's longevity probability distribution at 24℃, $N(\mu=190080, \sigma=20000)$(min) (Calabi and Porter 1989). When workers are older than L, their death probability will increase considerably by death accumulative probability function:

$$F_{death}(x) = \int f_{longevity}(x)dx,\ \ (\mu = 190080, \sigma = 20000) \qquad \text{(equ. 6)}$$

In another way, when agents starve for a long time, substances such as adipose, protein, and glycogen will be consumed and converted to the energy for basic energy demands. Therefore, the mass of agent can stimulate death event when it drops below mass threshold of agent (Table 2). When death event occurs, agent will be removed from the colony except the dead immature ant that will be transported into the food storage by workers and part of the dead immature ant (50%) is reused as food.

Interactions

In terms of hunger pheromone and trail pheromone, pheromone communication is the primary way to connect ants having no direct interactions. Pheromone chemicals share part of patch-pheromone concentration ($r_{diffuse}$) to its 8 neighboring patches. The patch-pheromone chemicals will decay at an evaporating rate, $r_{evaporate}$. In the model foragers deposit trail pheromone ($drop_{trail}$) per patch at the patches they passed through after they discover food and get ready to return to nest. Hungry queen and immature ants release hunger pheromone based on their energy status:

$$D_{hunger\ phromone} = a \cdot (E - E_{threshold}) \quad \text{(equ. 7)}$$

$D_{hunger\ phromone}$ is the concentration of hunger pheromone of queen or immature ant; E is the energy of queen or immature ant; $E_{threshold}$ is the energy threshold of queen or immature ant; a is responding factor of hunger pheromone gland of queen or immature ant toward energy status. Outgoing foragers detect the trail pheromone at their neighboring patches within 1 grid distance, and nurses sense hunger pheromone within 0.5 grid distance ($\text{grid}_{\text{outside nest}} : \text{grid}_{\text{inside nest}} = 2:1$). Both of workers can recognize the concentration of pheromone and move along the gradient to area of high concentration. Workers will change moving directions when they meet the borders of the environment and nest. The dead immature ants can be recognized and transported to food storage by workers.

Changing of Tasks

Workers have behavioral flexibility. There are 2 worker tasks in this model, foraging and nursing. Their tasks allocation depends on the environment and their inner states. Workers can't change tasks unless they complete the previous one. In this model forager and nurses need to decide whether nursing or foraging at every time they finish previous task. Ant workers tend to change task when more ants are required for particular tasks (Gordon 1989). The harvester ant, *Messor barbarus*, was documented to recognize saturation of food storage and modified foraging strategy based on it (Reyes-López 2002). Therefore, we assume their decisions are based on the amount of the food stored in the nest. The nursing and foraging tendency are quantified as below:

$$P_{nursing}(v; \mu, \sigma) = \int f(v)dv\,, (\mu = 20, \sigma = 5)$$

$$P_{foraging} = 1 - P_{nursing} \quad \text{(equ. 8)}$$

$P_{nursing}$ is the probability to nurse; $P_{foraging}$ is the probability to forage; v is the amount of the food stored in the nest.

Energy and Mass

Energy, food, and mass are 3 most important variables to regulate agents' behaviors. These 3 variables can be quantified and their relationships are described below (Fig.2). Metabolism includes the catabolic and anabolic processes:

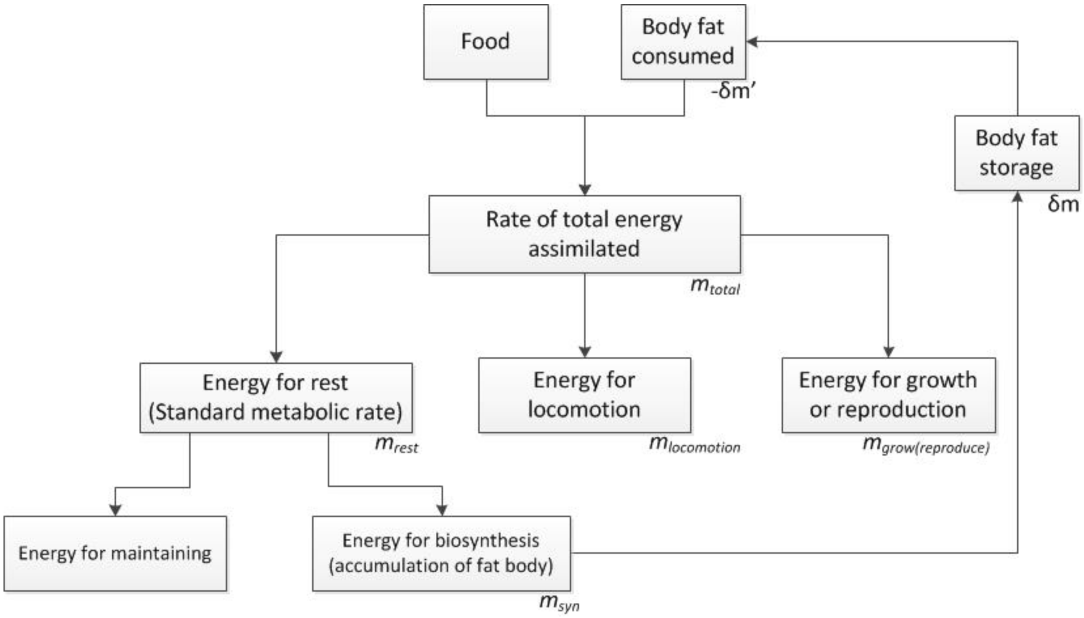


Figure 2. Partitioning of energy assimilated from food.

Agents assimilate energy from food for energy storing (somatic growth and reproduction), restive maintaining, biosynthesis accumulation for fat body, and locomotion (Hou et al. 2008). When agents starve, the storage of fat will be consumed to maintain agents' living (Griffiths 1991). In this model we hypothesized the temperature has no impact on food size selections of ant, and the constant size of food could be eaten as feeding and eating events occur (Cummins 1971). The constant energy converted from food will be allocated to 2 or 3 partitions for immature ants, worker, and queen (Fig. 2, 3). Metabolic rate influenced by temperature and mass controls the process of energy-mass conversion. Energy allocation equations are shown below (equ. 9, 10, 11, 12):

$$m_{nurse\ total} = (m_{nurse\ locomotion} + m_{nurse\ rest}) \cdot M^{3/4} \cdot e^{E_iT_c/kT_0} \quad \text{(equ. 9)}$$

$$m_{forager\ total} = (m_{forager\ locomotion} + m_{forager\ rest}) \cdot M^{3/4} \cdot e^{E_iT_c/kT_0} \quad \text{(equ. 10)}$$

$$m_{immaature\ ant\ total} = (m_{immaature\ ant\ rest} + m_{immaature\ ant\ grow}) \cdot M^{3/4} \cdot e^{E_iT_c/kT_0} \quad \text{(equ. 11)}$$

$$m_{queen\ total} = (m_{queen\ rest} + m_{queen\ reproduction}) \cdot M^{3/4} \cdot e^{E_iT_c/kT_0} \quad \text{(equ. 12)}$$

Known as anabolism, energy is preserved for somatic growth per step by equation 13, 14 (Gillooly et al. 2001; Hou et al. 2008):

$$S = E_c \cdot \frac{dm}{dt} \quad \text{(equ. 13)}$$

From these we derived:

$$\Delta m = \frac{dm}{dt} = \frac{S}{E_c} = \frac{m_{syn}}{c \cdot M^{3/4} \cdot e^{ET/kT_0}} \quad \text{(equ. 14)}$$

Where Δm is a fact body accumulation rate; S is rate of energy stored; E_c is the energy content of biomass; $m_{storing}$ is the energy for storing fat body per step; c is anabolism factor; M is the mass of agent; E is the activation energy; k is Boltzmann's constant; T_0 is standard temperature 20℃.

When the agents starve, catabolism became larger and it elicits energy loss (Perrin 1995). The fat body will be consumed to maintain basic energy requirement (equ. 15), which causes weight loss:

$$\Delta m' = \frac{dm\prime}{dt} = \frac{m_{rest} + m_{locomotion}}{c\prime \cdot M^{3/4} \cdot e^{E_iT_c/kT_0}} \quad \text{(equ. 15)}$$

$\Delta m'$ is a mass loss rate, c' is catabolism factor.

Monitored Values

The number of agents belonging to different groups, age structure, total energy, and mass of ant colony are followed and calculated. When forager or nurses finish their previous tasks, the working efficiency is calculated every step as follow (equ. 16):

$$r_{foraging} = \frac{\sum_0^i Fg_i}{n_{forager}+n_{nurse}},\ r_{nursing} = \frac{\sum_0^i Fd_i}{n_{forager}+n_{nurse}}$$

$$Fg = \begin{cases} 0 & (foraging\ incomplete\ per\ step) \\ 1 & (foraging\ complete\ per\ step) \end{cases}$$

$$Fd = \begin{cases} 0 & (nursing\ incomplete\ per\ step) \\ 1 & (nursing\ complete\ per\ step) \end{cases} \qquad \text{(equ.16)}$$

i is index of workers. During each run the birth rate, death rate, and growth rate of population are calculated by equ. 17, 18, 9, 20:

$$r_{growth} = \frac{\sum_0^t n_{t(new\ workers)}}{t} \qquad \text{(equ. 17)}$$

$$r_{birth} = \frac{\sum_0^t n_{t(new\ immature\ ants)}}{t} \qquad \text{(equ. 18)}$$

$$r_{worker\ death} = \frac{\sum_0^t n_{t(dead\ workers)}}{t} \qquad \text{(equ. 19)}$$

$$r_{immature\ death} = \frac{\sum_0^t n_{t(dead\ immature\ ant)}}{t} \qquad \text{(equ. 20)}$$

t is the number of steps, $\mathrm{n}_{\mathrm{t}(\mathrm{new}\ workers)}$is the number of new workers at the *t*-th step, $\mathrm{n}_{\mathrm{t}(new\ immature\ ants)}$is the number of new immature ants at the *t*-th step, $\mathrm{n}_{\mathrm{t(new\ forager)}}$is the number of forager at the *t*-th step, $\mathrm{n}_{\mathrm{t}(dead\ workers)}$is the number of dead workers at the *t*-th step, $n_{t(dead\ immature\ ant)}$ is the number of dead immature ants a the *t*-th step. The average developmental time of immature ants is recorded based on every individual that has developed. The average developmental time of immature ants is calculated by equ. 21:

$$\bar{t}_{development} = \frac{\sum_0^i t_i}{n_{developed}} \qquad \text{(equ. 21)}$$

i is index of new adult worker. $\bar{t}_{development}$ is an average developmental time of the new adult worker, t_i is the developmental time of new adult worker i, $n_{developed}$ is the number of new adult workers. In order to compare the energy consumption, the hungry rate was monitored by equ. 22:

$$R_{hunger} = \frac{\sum_0^t n_{t(hungry\ events)}/T}{\overline{\sum_0^t n_{t(worker)}}} \qquad \text{(equ. 22)}$$

Where t is the number of steps, T is the time of simulation, $\mathrm{n}_{\mathrm{t(hungry\ events)}}$ is the total number of hungry events in workers at the t-th step, $\overline{\sum_0^t n_{t(worker)}}$ is the average number of workers per step.

Experiment

We did 3 experiments to test temperature and food’s impacts on ant colonies.

Experiment of Temperature Changes

Constant Temperature vs. Dynamic Temperature: In the constant temperature treatment, the model started with the mean temperature in Johnson City 2010, 13.5°C, and the nest temperature was estimated to be 14.3°C (equ. 4). In the dynamic temperature treatment, the daily temperature of Johnson City, TN, in 2010 was parameterized into the model to manipulate dynamic air temperature (maximum 29.15°C, minimum -9.5°C, mean 13°C). Every simulation ran for 516 781 steps (≈ 359 days). In every treatment, 20 parallel simulations were run to estimate statistically.

Different Elevated Temperature Regimes: Based on daily air temperature record in Johnson City TN in 2010, we set up 8 treatments to manipulate elevated temperature regimes: +0°C, +2°C, +4°C, +6°C, +8°C, +10°C, +12°C, and +14°C. Each simulation starts with parameters in Table 2 and ran for 516 781 steps (≈ 359 days). In every treatment, 20 parallel simulations were run to estimate statistically.

Experiment of Food Availability Changes

In this experiment we estimated the food availability based on the width of food patches. Three levels of food richness were implemented into the model: 2 patch wide food sources, 3 patch wide food sources, and 5 patch wide food sources. Each simulation started with temperature of Johnson City in 2010, and ran for 516 781 steps (≈ 359 days). In every treatment 20 parallel simulations were run to estimate statistically.

Experiment of Climate Changes

In order to simulate climate changes in terms of high temperature and food richness, we inserted high food availability and temperature into the model together. The model started with temperature elevated 14^{o}C regime (maximum: 37^{o}C; minimum: 15^{o}C; mean: 27^{o}C). Two levels of food availability were manipulated: 3-patch wide food sources as the control and 5-patch wide food as the treatment. Every simulation ran for 516 781 steps (≈ 359 days). In this treatment 20 parallel simulations were run to estimate statistically.

CHAPTER 3

RESULTS

Effects of Seasonal Temperature Change on Population and Energy Dynamic of Ant Colony

The colonies started with the daily temperature in Johnson City TN in 2010 as the dynamic temperature simulation ($T_{JohnsonCity}$: maximum 23^{o}C, minimum 1^{o}C, mean 13^{o}C) or with 13^{o}C as constant temperature simulation. In single simulation with dynamic temperature, the population size endured 4 stages during the whole year: it shrunk significantly during spring, increased in summer, stabilized in autumn, and declined again in winter (Fig. 3a). Comparing population size distribution to annual temperature (Fig. 3a), we can conclude that temperature-dependent population size keeps growing during the summer until the size of colony arrives at a maximum in the middle of the autumn. Afterwards, the population of colony declines till middle of the spring. In addition, the colony size increases above about 12.5^{o}C and decreases below about 12.5^{o}C. The $r_{foraging}$ (number of times becoming hungry per worker per minute, equ. 22), the average foraging efficiency of worker (Times of a resource-laden ant returning to the nest per worker per min, equ. 16) and average mass of workers varies seasonally as well (Fig. 3c, d). Differently, the colonies simulated with the constant temperature (13^{o}C) have no apparent declining stages, and its size grows in logistic manner (Fig.3b).

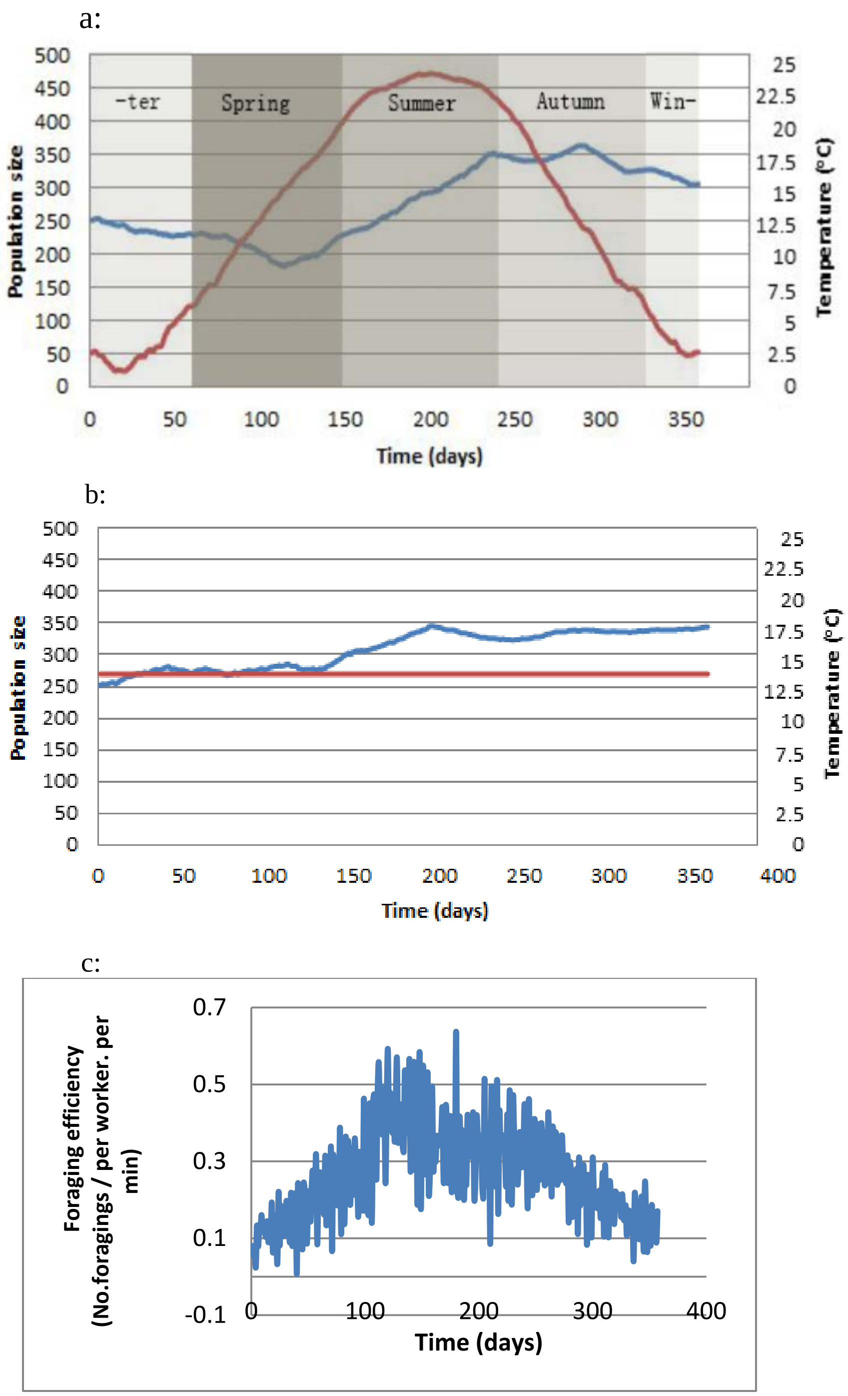


Figure 3 (continued on the next page). Population dynamics in single simulations: (a) Daily temperature in Johnson City TN 2010 (red line); modeled population size of colonies (blue line); (b) Constant temperature (red line); population size of colonies (blue line); (c) Foraging efficiency of workers in dynamic T.

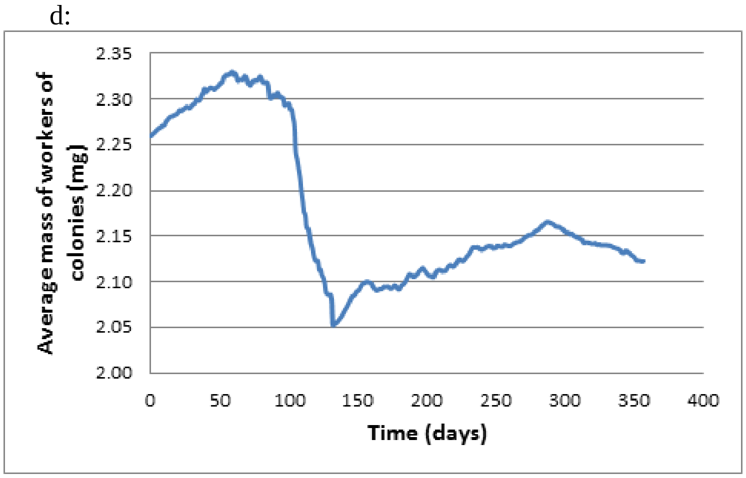


Figure 3 (continued). Population dynamics in single simulations: (d) Average mass of workers in dynamic temperature.

We find the dynamic temperature tends to make more fluctuations in energy, population size of colonies, and foraging efficiency of workers than what constant temperature does (Fig. 4a, b, d). The food storage consumed more extensively in the dynamic temperature than in constant temperature during the summer (Fig.4c).

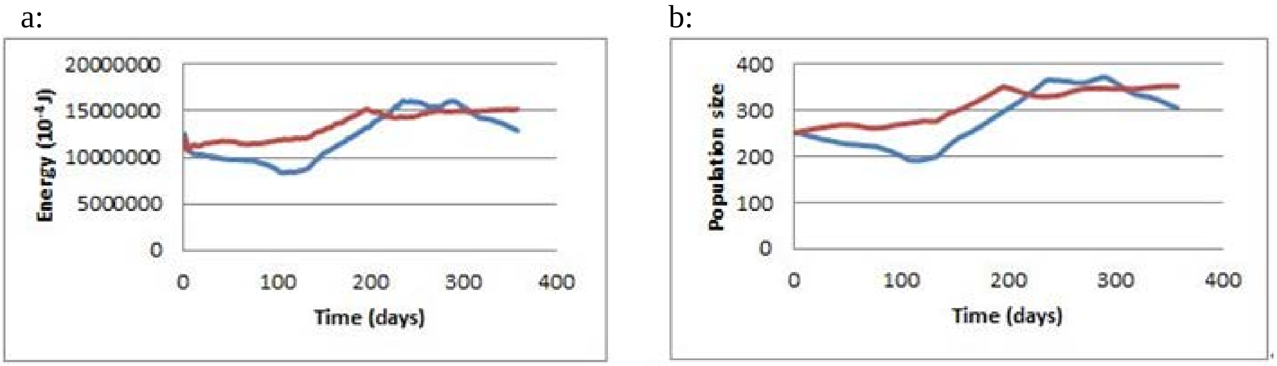


Figure 4 (continued on the next page). Average value of 20 parallel simulations with constant temperature (red line) and dynamic temperature (blue line): (a) energy of ant colony; (b) population size of ant colony.

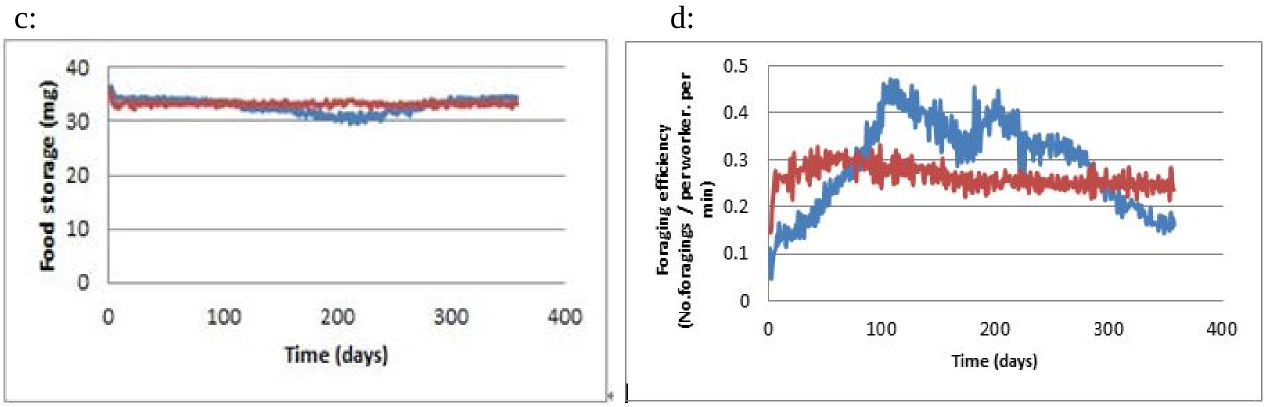


Figure 4 (continued). Average value of 20 parallel simulations with constant temperature (red line) and dynamic temperature (blue line): (c) food storage in the nest; and (d) foraging efficiency of workers.

Effects of Temperature Elevations on Population and Energy Dynamic of the Ant Colony

The resistance of the colonies to elevated temperature regimes is fairly robust. Only 12.5% colonies died out at the end of year. The rest of the experimental modeled colonies could stabilize their colony's size and energy levels (Fig.5a-b). We used 270th day as a time point for comparison, given that this time is the transition of summer to autumn. On the 270th day, the differences of energy and population among 8 temperature elevation regimes were tested in pairwise test if the Kruskal-Wallis test showed that the groups in fact have not the same median (N=159, d.f. = 7). We detected the significant differences in the energy level of the colony between 0°C and 4 °C ($p < 0.05$), 4 °C and 8 °C ($p < 0.001$) and 8 °C and 12 °C ($p < 0.05$) to indicate that the energy of colonies tend to increase as temperature has small elevations (≤4°C), and decline in the higher elevated temperature regimes (≥6°C) (Fig. 5c-d). The dynamic of colonies' size has the same pattern as we described for the energy. There are significant differences between 0°C and 4 °C ($p < 0.05$), 4 °C and 8 °C ($p < 0.001$), and 8 °C and 14 °C ($p < 0.001$).

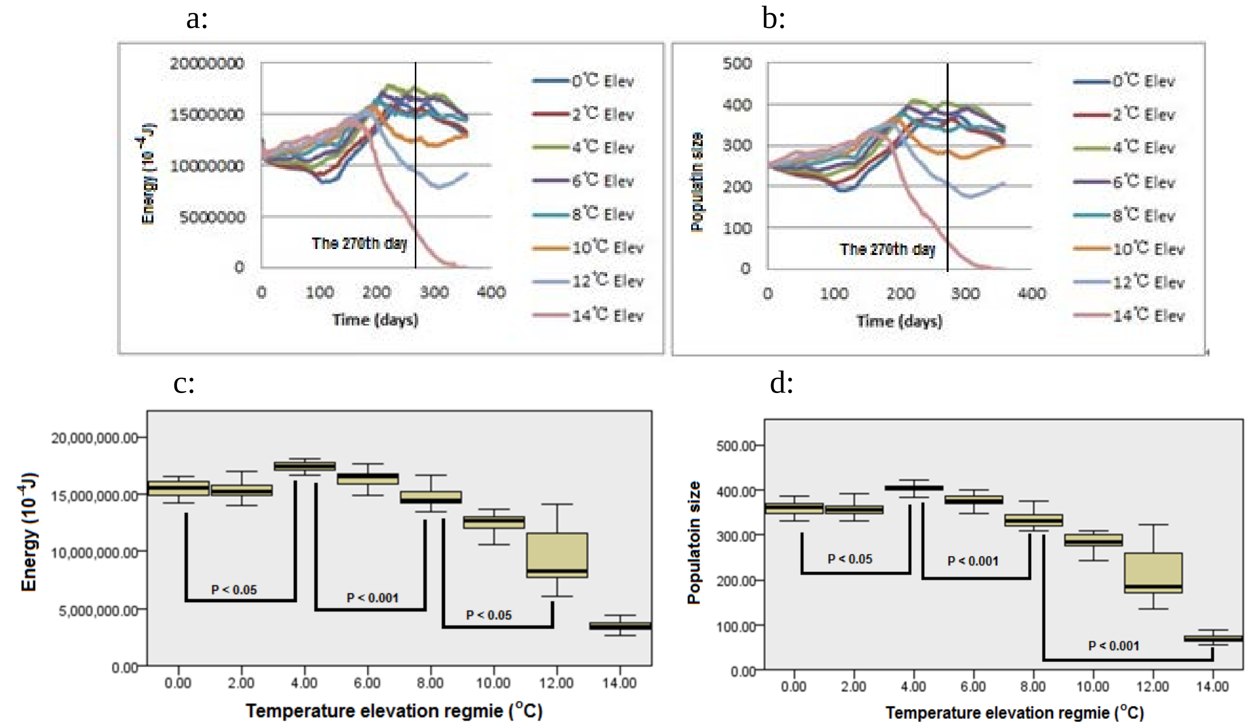


Figure 5. Effects of temperature elevation regime on (a) energy of colonies, (b) population size of colonies, (c) energy of colonies on the 270th day, and (d) average population of colonies on the 270th day. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=159, d.f.=7*).

In the cases of extreme high temperatures, the colonies died out because of food shortage or/and low birth rate of immature ants (Figs.6, 7). The average birth rate of immature ants in 6^{o}C elevations is significantly higher than in 0^{o}C (*Kruskal-Wallis pairwise test, $p < 0.001$, N=160, d.f.=7*), and the rate in 12^{o}C elevation is significantly lower than in 6^{o}C elevation *(Kruskal-Wallis pairwise test, $p < 0.001$, N=160, d.f.=7*). Furthermore, there are no significant differences of birth rate among 4^{o}C, 6^{o}C, 8^{o}C, and 10^{o}C elevations. Those results reveal that the birth rates of workers respond to temperature in the manner of a single-peak (Fig.7).

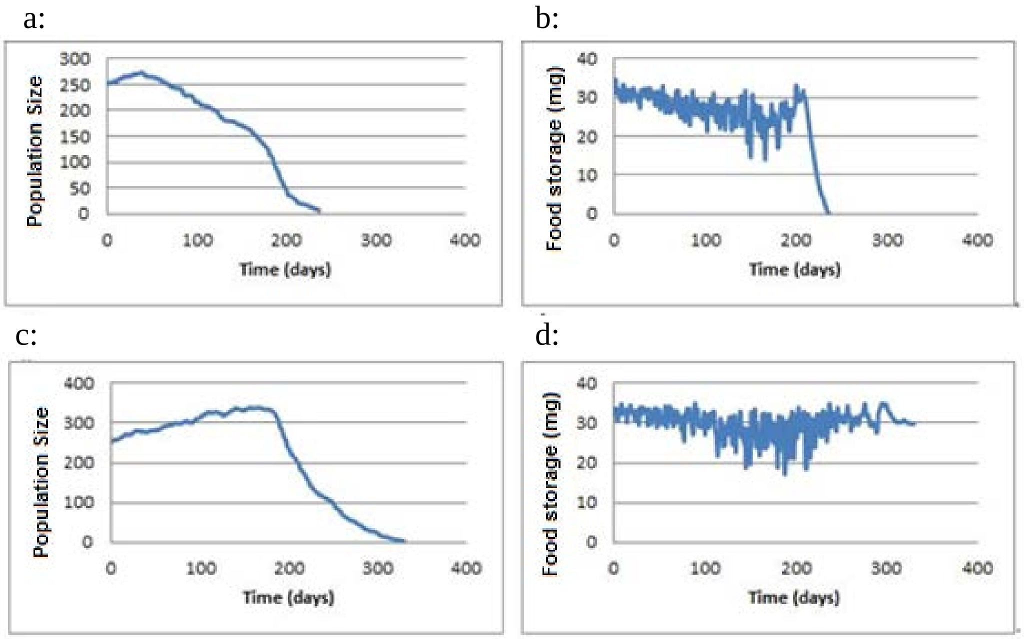


Figure 6. Two cases of colony extinction at the 14^{o}C elevated temperature regime: (a) and (c) energy of colony; (b) and (d) food storage in nest.

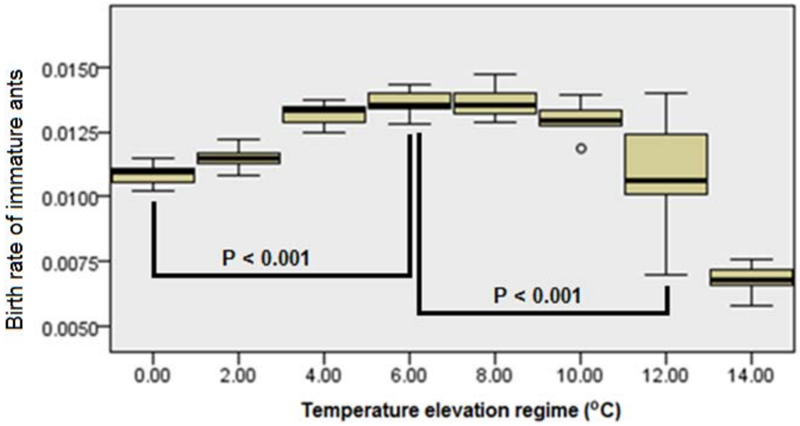


Figure 7. Effects of temperature elevated regime on birth rate of immature ants. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=60, d.f.=7*).

As the temperature increases, the duration of immature ants' stage decreases from 57 days in 0^{o}C elevation to 32 days in 14^{o}C elevation. There are significant differences of developmental time between 0^{o}C and 6^{o}C elevation, and between 6^{o}C and 12^{o}C elevations (*Kruskal-Wallis pairwise test*, $p < 0.001$, *N=160, d.f.=7*) (Fig. 8). However, there are no significant differences among 10^{o}C, 12^{o}C, and 14^{o}C elevations. Therefore, the developmental time could be described by temperature elevations in the exponential decaying pattern ($y = 80469e^{-0.041x}$, $R^2 = 0.9743$, $p < 0.0001$).

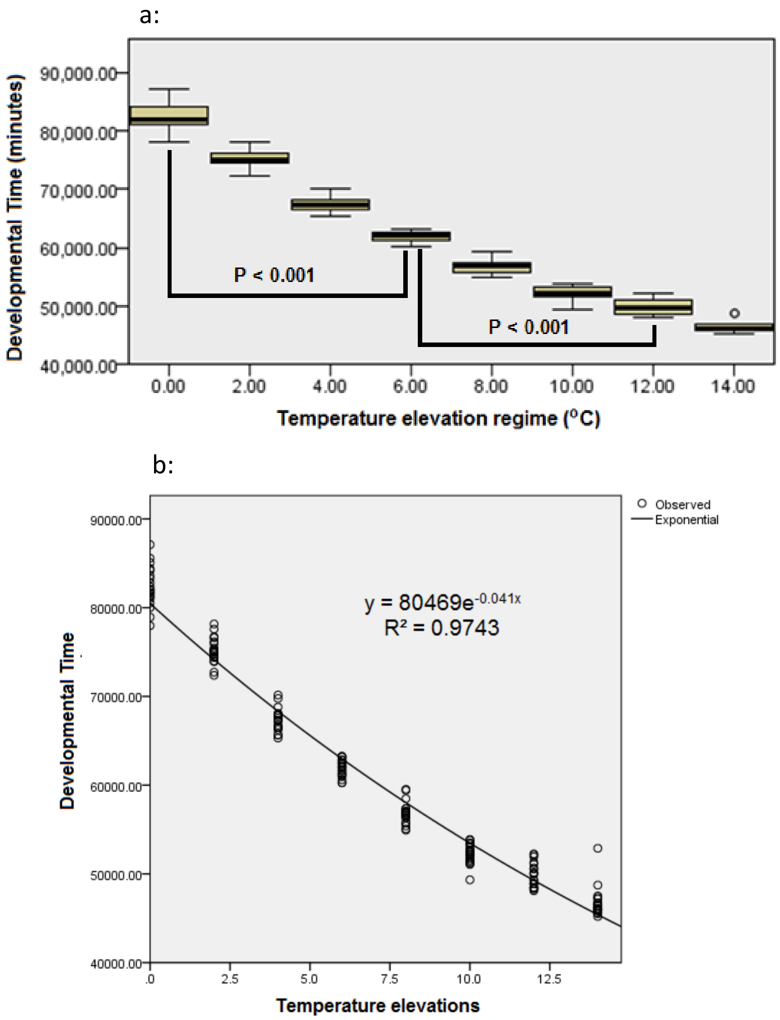


Figure 8. Effects of temperature elevated regime on developmental time of immature ants: (a) significant differences among elevated temperature regimes, *p*-value based on pairwise test using the Kruskal-Wallis test (*N=160, d.f.=7*); (b) regression of developmental time on temperature elevations, $p < 0.001$.

Under the high temperature, workers are more likely to become hungry. The R_{hunger}(hunger rate of workers) in 14°C elevation is the highest, and there are significantly differences between 0°C and 6°C elevations (*Kruskal-Wallis pairwise test*, $p < 0.005$, *N=160, d.f.=7*), and between 6°C and 12°C elevation group (*Kruskal-Wallis pairwise test*, $p < 0.05$, *N=160, d.f.=7)*. Under the exponential relationship between hunger rate and temperature elevation ($y = 0.0005e^{0.0425x}$, $R^2 = 0.442, p < 0.001$), a worker became hungry from 5.5E-04 times to 11.3E-04 times per step as temperature increases. As results, we can say R_{hunger} (hunger rate of workers) is highly temperature dependent (Fig.9).

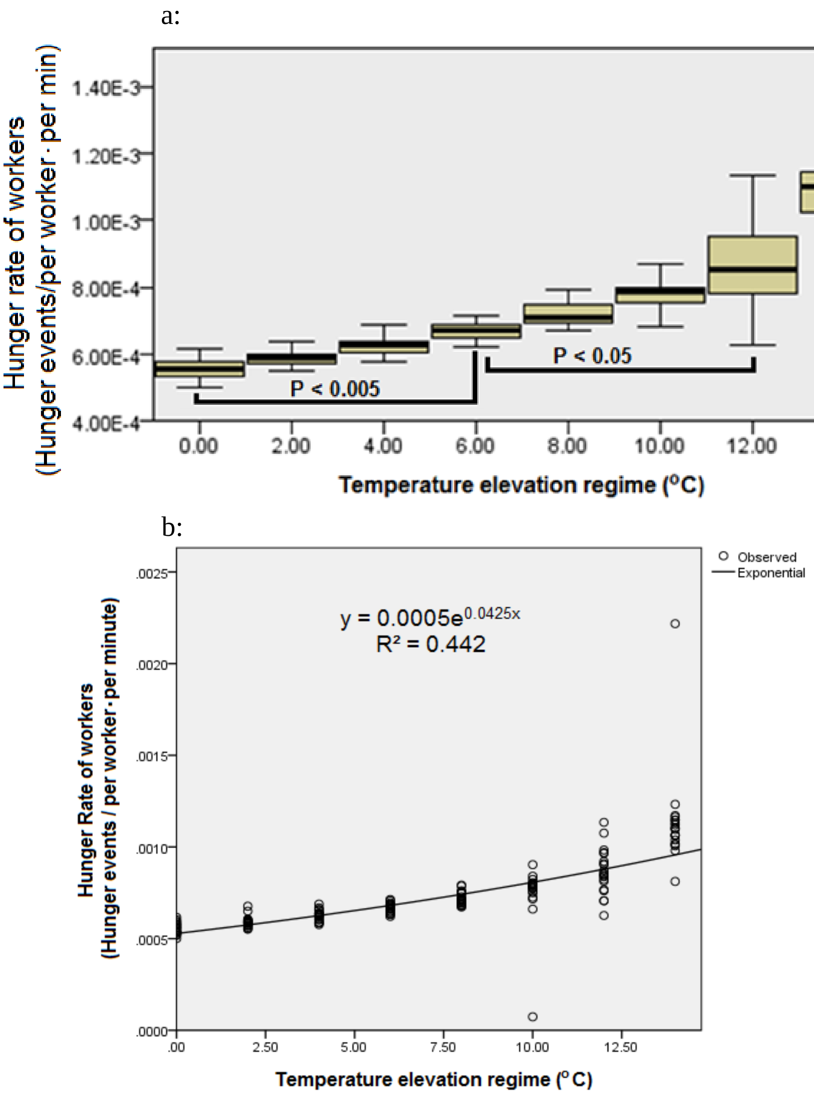


Figure 9. Effects of temperature elevated regimes on hunger rate of workers. (a) Significant differences among elevated temperature regimes. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=160, d.f.=7*). (b) Regression of developmental time on temperature elevations, $p < 0.001$.

To some extent the workers could increase their foraging efficiency significantly (equ.16) to relieve hunger of colonies (*Kruskal-Wallis pairwise test,* $p_{0\,°C\ vs\ 6\,°C} < 0.001$, $p_{6\,°C\ vs\ 10\,°C} < 0.05$, *N=160, d.f.=7*) while temperature is elevated unless the high temperature is too extreme (>12°C elevation regime) to maintain the food and energy balance (Fig.10). The 200th day, the hottest day during the year, might be the best time to test the relationship between temperature and mass of workers. On the 200th day the average mass of workers have no significant differences among 0 °C, 2 °C, 4 °C, and 6 °C elevations (*Kruskal-Wallis pairwise test,* $p > 0.05$, *N=160, d.f.=7*) (Fig 11b). However, while temperature is elevated by 6 °C or higher, the workers' masses drop steadily and significantly different between 0 °C and 8°C elevation and between 8°C and 14 °C elevation because more mass was converted to energy. The nursing efficiency (equ. 16) in the 14°C elevation is significantly lower than in other groups except 0°C elevation (*Kruskal-Wallis pairwise test,* $p < 0.001$, *N=160, d.f.=7*), which might be the byproduct of low birth rate of immature ants (Fig.12).

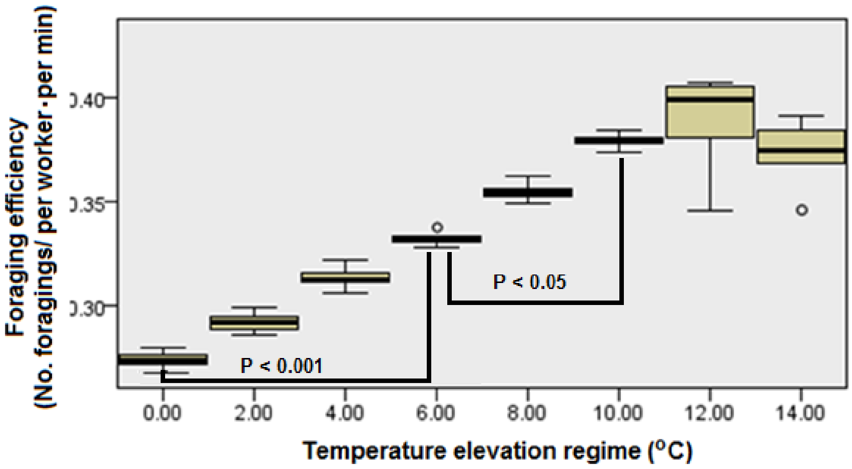


Figure 10. Effects of temperature elevated regime on foraging efficiency. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=160, d.f.=7*).

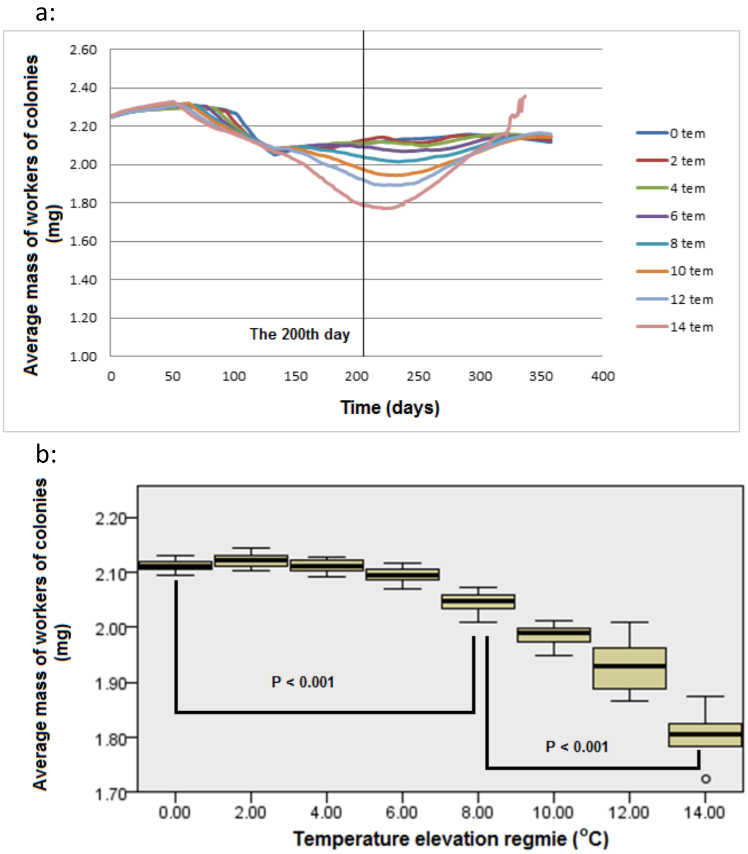


Figure 11. Effects of temperature elevation regime on (a) average mass of workers, (b) the average mass of workers on the 200 th day. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=160, d.f.=7*).

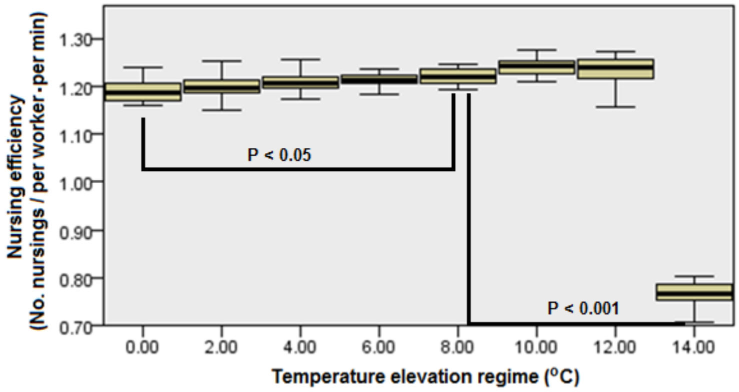


Figure 12. Effects of temperature elevated regime on nursing efficiency. *p*-value based on pairwise test using the Kruskal-Wallis test (N=*160, d.f.=7*).

Effects of Food Availabilities on Population and Energy Dynamic of Ant Colony

The diameter of food sources is used to quantify food availability. If the food source is bigger, it could be richer and found more easily by ant workers. Comparing the energy and population size of colonies under different food availability, we find there are no differences of energy and population at the beginning of simulations. After about 50 days colonies with different food availabilities branch into 3 levels respectively (Fig. 13a-b). On the 270th day the energy and population size of colonies in 3 food levels are significantly different from each other (*Kruskal-Wallis pairwise test*, $p_{energy} < 0.001$, $p_{population} < 0.001$, $N=60$, $d.f.=2$).

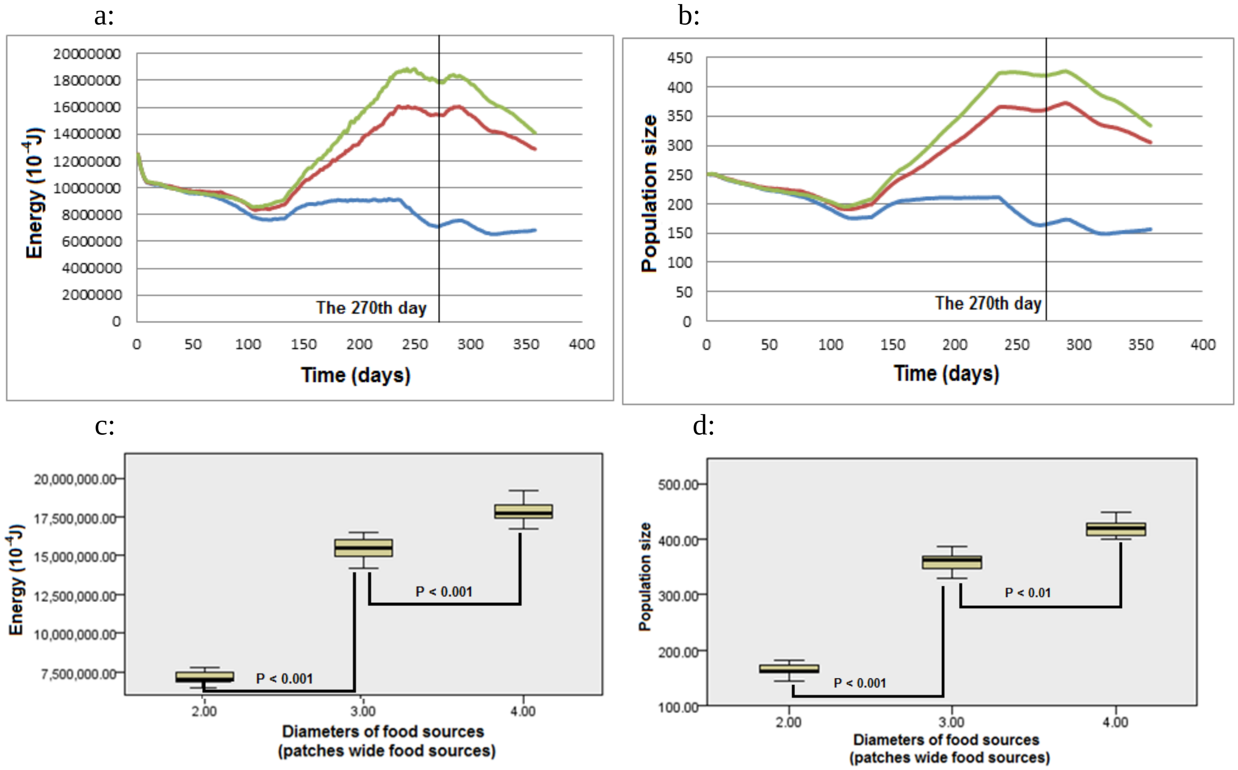


Figure 13. Effects of food availability on (a) energy of colonies, (b) population size of colonies, (c) energy of colonies on the 270th day, and (d) population of colonies on the 270th day. (blue line: 2 patch wide food source; red line: 3 patch wide food source; green line: 4 patch wide food source). *p*-value based on pairwise test using the Kruskal-Wallis test ($N=60$, $d.f.=2$).

As the food availability increases, the nursing and foraging efficiency increase as well (Fig. 15), and the food storage in the nest tends to stabilize during the whole year, especially in the summer (Fig. 14). In the 4-patch wide food sources, the nursing and foraging efficiencies are significantly higher than in other food sources (*Kruskal-Wallis pairwise test*, $p_{foraging} < 0.05$,

$p_{nursing} < 0.001, N=60, d.f.=2$).

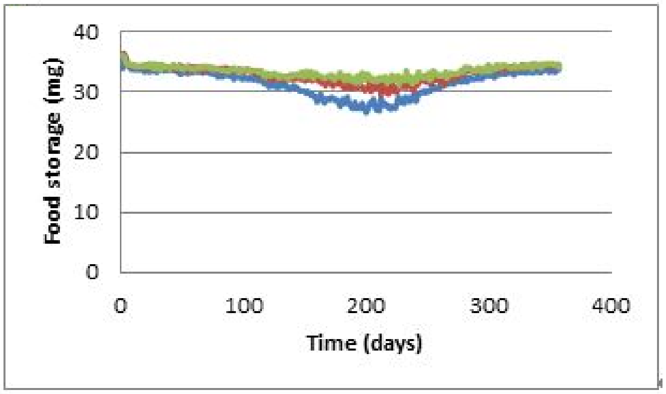


Figure 14. Effects of food availability on food storage (blue line: 2 patch wide food source; red line: 3 patch wide food source; green line: 4 patch wide food source).

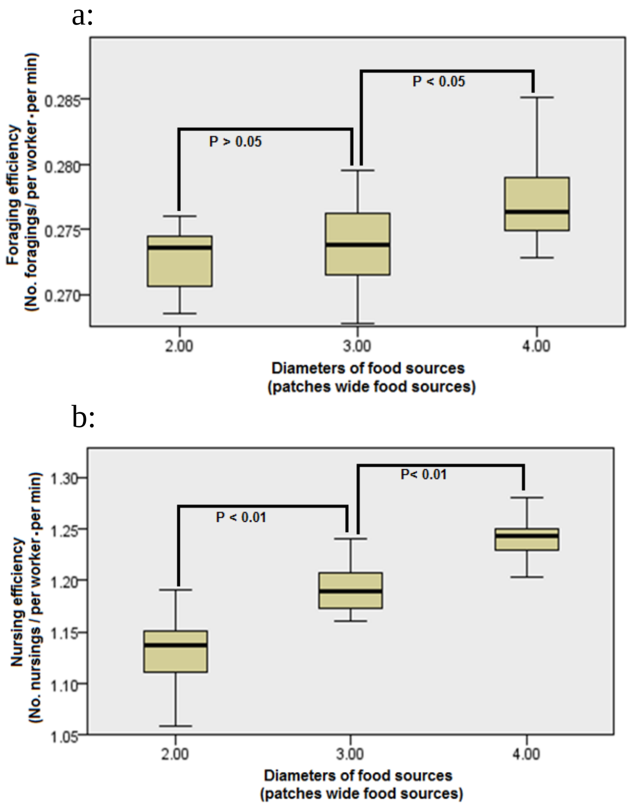


Figure 15. Effects of food availability on (a) foraging efficiency and (b) nursing efficiency. *p*-value based on pairwise test using the Kruskal-Wallis test ($N=60, d.f.=2$).

The birth rates of new workers in 3 food levels are significantly different from each other

(*Kruskal-Wallis pairwise test, $p < 0.001$, N=60, d.f.=2*) and tend to increase with rich food sources (Fig. 16).

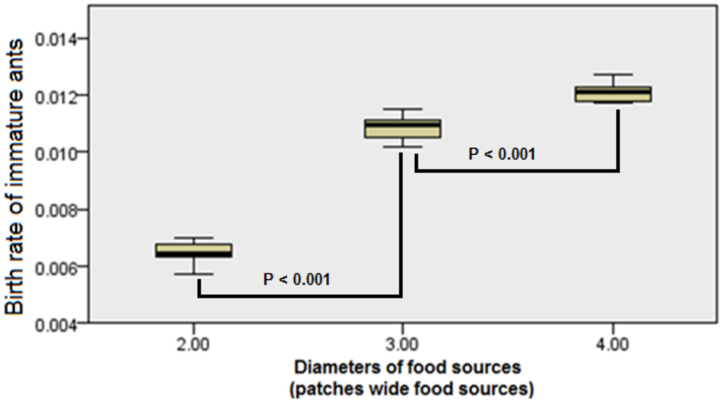


Figure 16. Effects of food availability on birth rate of immature ants. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=60, d.f.=2*).

Effects of High Food Richness and Temperature on Population and Energy Dynamic of Ant Colony

In the environment with high temperature (maximum: 37°C; minimum: 15°C; mean: 27°C), the dynamic energy and population size of colonies could change based on their different food richness. In the 3-patch wide food source group, the population and energy of colonies decline to zero at the end of year. However, in 5-patch wide food sources group, colony size peaks at 512 and energy of colonies is accumulated to 2.15 KJ ultimately (Fig. 17a-b). On the 270th day, the energy and population of colonies are significantly different from each other (*Kruskal-Wallis pairwise test, $p < 0.001$, N=39, d.f.=1*) (Fig. 17c-d).

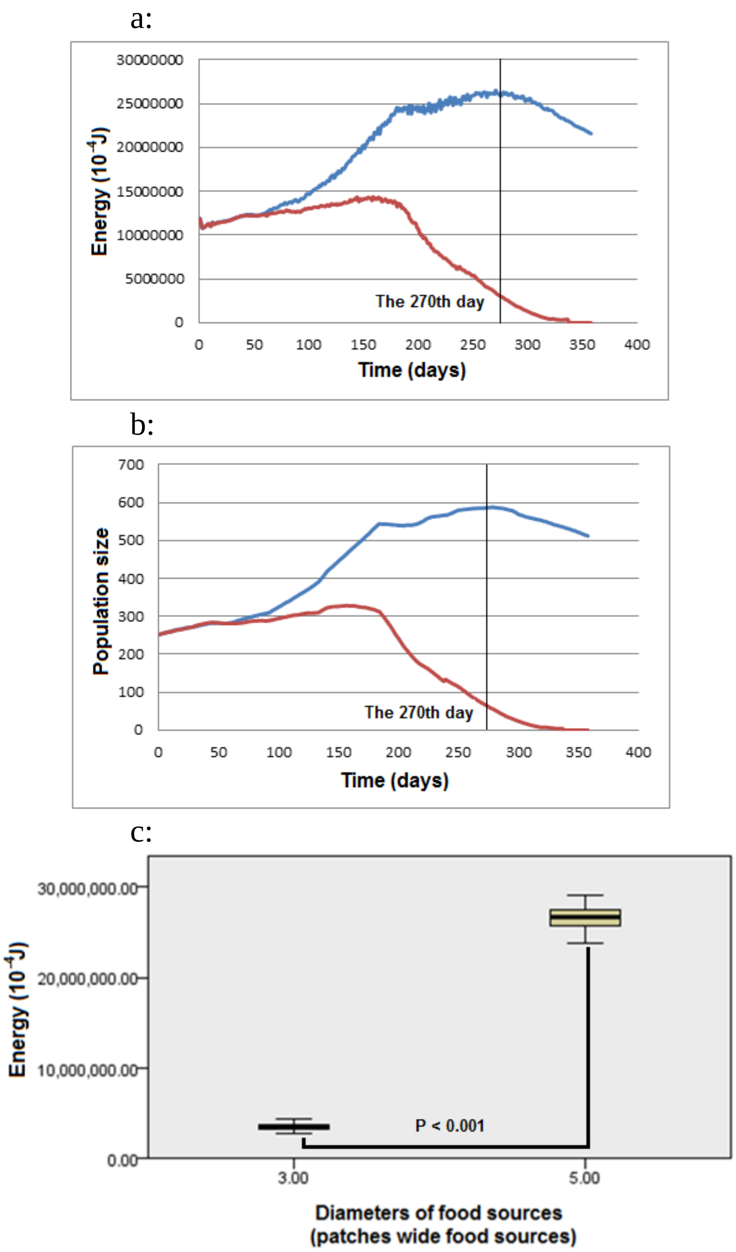


Figure 17 (continued on the next page). Effects of high temperature and food richness on (a) energy of colonies, (b) population size of colonies, (c) energy of colonies on the 270th day (Red line: 3-patch wide food sources; blue line: 5-patch wide food sources). *p*-value based on pairwise test using the Kruskal-Wallis test (*N=39, d.f.=2*).

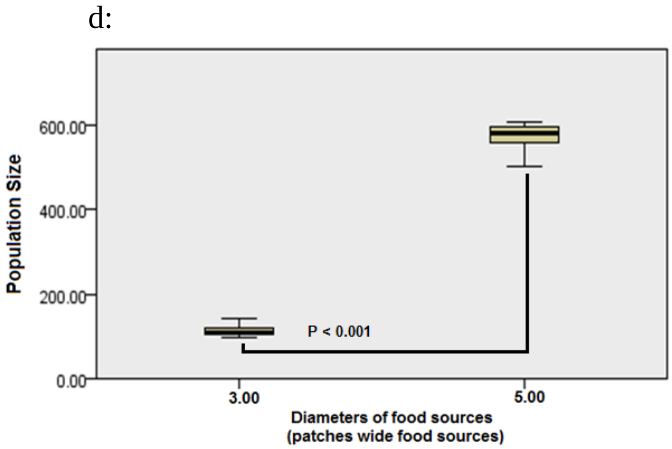


Figure 17 (continued). Effects of high temperature and food richness on (d) population of colonies on the 270th day. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=39, d.f.=2*).

In the 3-patch wide food sources group, the declining population is determined by significant lower birth rate and higher hunger rate of workers (R_{hunger}) than in 5-patch wide food richness group (*Kruskal-Wallis pairwise test*, $p < 0.001$, *N=40, d.f.=1*) (Fig. 18-19). In the environment with richer food supply, significantly higher foraging and nursing efficiency help colonies meet the energy demand than in lower food richness group (*Kruskal-Wallis pairwise test*, $p < 0.001$, *N=40, d.f.=1*) (Fig. 20-21).

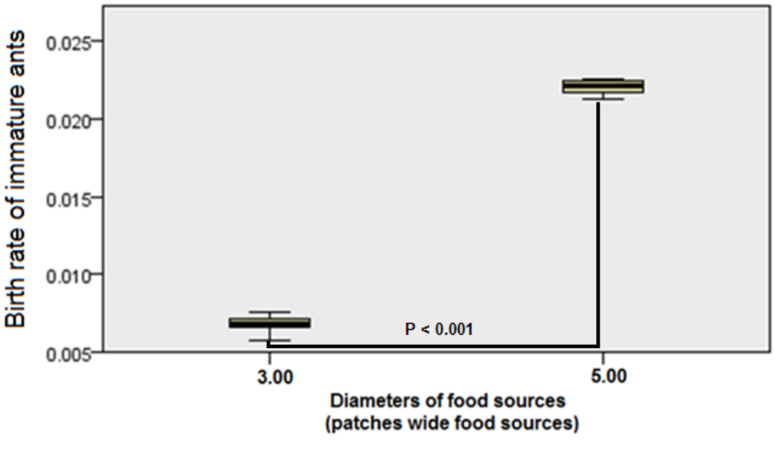


Figure 18. Effects of high temperature and food richness on birth rate of immature ants. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=40, d.f.=2*).

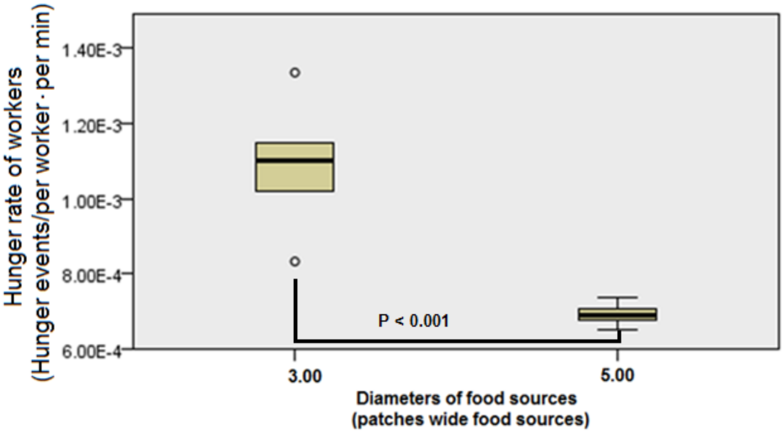


Figure 19. Effects of high temperature and food richness on hunger rate of workers. *p*-value based on pairwise test using the Kruskal-Wallis test (*N=40, d.f.=2*).

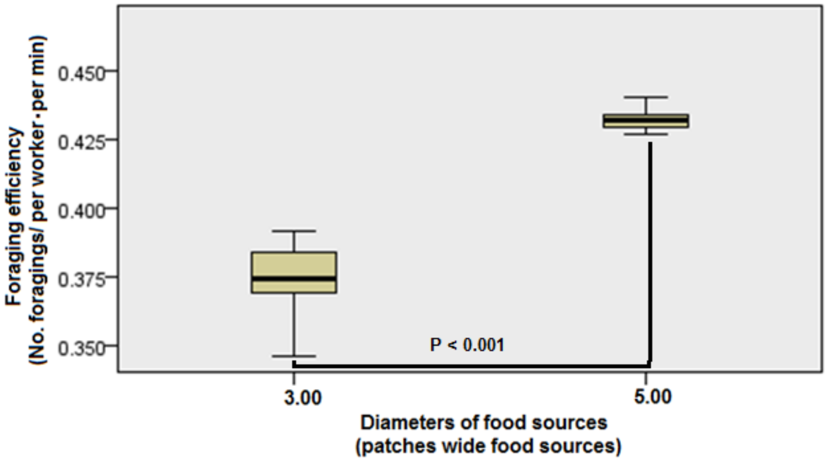


Figure 20. Effects of high temperature and food richness on foraging efficiency. p-value based on pairwise test using the Kruskal-Wallis test (N=40, d.f.=2).

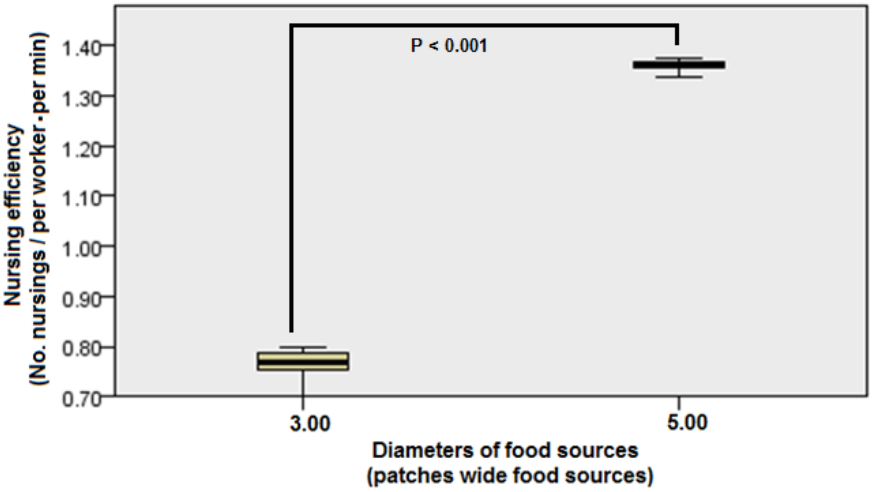


Figure 21. Effects of high temperature and food richness on nursing efficiency. p-value based on pairwise test using the Kruskal-Wallis test (N=40, d.f.=2).

CHAPTER 4

DISCUSSION

Seasonal Dynamics of Ant Colonies

Our model predicted that the size of a colony varies seasonally under dynamic temperature conditions (Fig. 3a). As in our study, Tschinkel (1999) reported that worker density of the Florida Harvester ant (*Hymenoptera: Formicidae*) in the Apalachicola National Forest clearly varied with the seasons, reaching a high point in the autumn and winter and a low at the end of spring or beginning of summer. In the simulations the growth patterns of colonies in constant and dynamic temperature conditions demonstrates that they grow logistically and may be food dependent. Tschinkel (1987) also indicated that the colony size is food determined, as in the seasonal cycles of in fire ants, *Solenopsis invicta*, in Tallahassee Florida. We also found that mass of workers increases steadily through the beginning of summer to middle of autumn and declines over the winter (Fig. 3). The mass content of workers in the model was accumulated and consumed in body fat. Tschinkel (1993) observed the dynamics of fat content in workers fire ants, *Solenopsis invicta*, and found patterns similar to that predicted in the model. Seasonal variation in the foraging efficiency of workers comes from seasonal temperature change that was considered as one of the considerably significant factor (Fig. 4d) affecting a worker's foraging behavior (Porter and Tschinkel 1987). They suggested that the foraging rate of workers might be determined by an underground tunnel system of colonies independent of external relative humidity, saturation deficits, soil moisture, and wind. The colonies in the model do not have underground tunnel systems, but the workers still perform at different foraging rates in different seasons, probably because of different movement rates, the workforce size, and trail pheromone networks. High temperature tends to promote foraging efficiency by accelerating workers' movement directly. Hurlbert et al. (2008) estimated the positive relationship between temperature and workers speed from 19 ant species from 22 different studies in which the fast movement of workers could facilitate foragers in finding and carrying food back to the nest. Indirectly, Bruce and Burd (2012) found an exponential relationship between the size of workers and foraging rate (number of resource-laden ants returning to the nest per unit time) that scaled at the 0.93 power of worker numbers. Apart from that, foraging rate was also determined by pheromone trail networks scaling at the –1.02 power of total trail length and the 0.65 power of trail width. The authors suggested that the number of foragers recruited by trail pheromones would determine how many workers could carry food back to the nest successfully. If more workers forage outside the nest, then pheromone trail could be maintained and strengthened faster to recruit more workers.

Effects of Temperature on Population and Energy Dynamic of Ant Colony

Pimm and Bartell (1980) used the number of cold and hot days to calculate fire ant propagation rate. They successfully predicted the northern limits of the fire ant range. Stoker et al. (1994) developed a model to find the "reproductive" border, which describes queen fecundity, mating flights, and the dependence of developmental rates and mortality on air temperature. The model ran with daily air temperature normally distributed around monthly means. Killion and Grant (1995) applied the temperature to find a "growth" border in space where a fire ant colony ceases to grow. Other temperature-dependent models were also built later relying on soil temperature (Korzukhin et al. 2001). When considering the predictive model for ant colony spatial distribution, temperature is a primary parameter.

The results we obtained reveal that temperature has a significant impact on dynamics of ant colony populations and energy through birth rate, developmental time, hunger of workers, and foraging and nursing efficiency. First of all, increased temperature has positive impacts on ant colonies by shortening developmental time (Figs. 8, 10). Poter (1988) found the developmental time of the fire ant to decrease with temperature. The total developmental time of fire ant was estimated under different temperature ranging from 23 days at 35^{o}C to 55 days at 24.5^{o}C. In the model we compressed 3 developmental stages (egg, larvae, and pupa) into one under the name of immature ant. However, the developmental time of immature ants in the model still decreased exponentially, ranging from 32 days at 14^{o}C elevation ($\overline{\mathrm{T}} = 27^{o}\mathrm{C}$) to 57 days at 0^{o}C elevation ($\overline{T} = 13^{o}C$). Theoretically, the decaying pattern of developmental time results from the basic energetic processes. The developmental time is determined by the reciprocal of development metabolic rate scaling to temperature by $e^{-1/T}$ (equ. 2, 23).

$$t_{development} \propto 1/(e^{-1/T}) \quad \text{(equ. 23)}$$

In other words, as temperature increases, more energy will be consumed for development and basic maintenance per unit time. When energy consumption is larger than energy intake, the energy intake would be used for basic maintenance primarily so that no more energy could be allocated to development. The exponential regression relationship over temperature in the model (Fig. 8) is different from the theoretical one probably because the temperature variable in the model is identified as the temperature elevation but not absolute temperature.

Elevated temperature plays a double role by affecting birth rate and foraging efficiency of workers. Abril et al. (2008) found the Argentine ant queen (*Linepithema humile* Mayr) at the southern edge of the Gavarres massif near the village of Castell d’Aro (Northeast Iberian peninsula) had a temperature preference for egg laying at 28^{o}C and was subjected to the upper and lower temperature limits on oviposition rate. The upper and lower temperature limits of oviposition rate were caused by the amount of the food the queen ingested. The oviposition rate of the queen in the model had the same performances (Fig.7). The birth rate of immature ants peaked at a mean temperature 17 °C ~19°C and the population and energy state of colonies on the 270th day peaked at the maximum mean temperature as well. (Fig. 5) The results of birth rate of immature ants suggest that the energetic effects of temperature on the egg-laying behavior of queens because moderate temperature elevations promote follicle and ovarian development (Phoofolo et al. 1995). In contrast, the high temperature will cut down the energy allocations for follicle and ovarian development. As regards workers' foraging behaviors, high temperature tends to promote foraging efficiency by speeding workers' movement directly and strengthening pheromone trail networks indirectly depicted above. In the 14°C elevation the declination of foraging efficiency was caused by decaying size of workforce probably to offset speeding impacts of high temperature (Fig. 10).

Temperature elevations have negative impacts on population size and energy of colonies in the energetic way: more energy intake would be needed to meet basic metabolic demands in terms of maintaining, moving, growing, and producing. Kaspari (2005) estimated that average worker mass across 49 ant communities. It decreased (partial $r^2 = 0.36$) with ambient temperature T, which supported the hypothesis that higher mean monthly temperatures, T, reduced worker mass by increasing metabolic costs. In the model the highest temperature occurs on the 200th day, and we predicted the average mass of workers on the 200th day decreased typically at the high level of temperature elevations (Fig. 11b). On the other hand, the average hunger rate of workers (R_{hunger}) we monitored increased exponentially with levels of temperature elevations ($y = 0.0005e^{0.0425x}$, $R^2 = 0.442$, $p < 0.0001$) (Fig. 10). However, workers' mass appears to be insensitive to the moderate temperature elevations because there are no significant differences among 0°C, 2 °C, 4 °C, and 6 °C elevation groups on the 200th day. Workers might have some special behaviors to resist losing mass, for example, speeding movement to increase foraging efficiency.

In the model for simplicity we set our ant as a monomorphic species: workers have the same size and physiology and they show only 2 behavioral profiles: foraging and nursing. In both cases workers only respond to saturation of food storage in the nest by switching tasks. In fact, in some ant species, such as harvester ants, *Pogonomyrmex barbatus*, were found to engage in 4 activities outside the nest: foraging, patrolling, nest maintenance, and upkeep of colony refuse pile (Gordon 1984). Different groups of workers could change their preferring behavior based on information of event from other groups of workers (Gordon 1989). In those groups of labors they can offset energy cost by efficient performing the specialized tasks (Wilson 1976; Lighton et al. 1987; Kay and Rissing 2005; Powell and Franks 2005; Powell 2009). For example, within nests workers (especially specialized castes) typically remain idle, becoming active only when exposed to a specific stimulus of sufficient strength (Wilson 1968, 1976; Robinson and Page 1989; Detrain and Pasteels 1991; Gordon 2002; Beshers and Fewell 2001; Fewell et al. 2009). In red harvester ant, *Pogonomyrmex barbatus*, it was found that the return of the patrollers stimulates the onset of foraging, and later the rate at which foragers return affects the rate at which foragers continue to leave the nest (Gordon 2002). It was the effective strategy to avoid foraging outside at high temperature and to economize the energy consumption. Apart from keeping idle inside nest, some ant species, such as *Leptothorax albipennis*, have particular worker group to store lipid during winter as a secondary energy resource (Blanchard et al. 2000). Albeit no matter how many energetic saving strategies exists in nature, the ant colonies still can’t escape from impacts of the air temperature once workers forage outside nest. The evidences from those results support our hypothesis that a large elevation of temperature will increase the energy cost to maintain energetic balance for surviving, although the impacts of temperature elevations depend on the temperature baseline.

Effects of Food Richness on Population and Energy Dynamic of Ant Colony

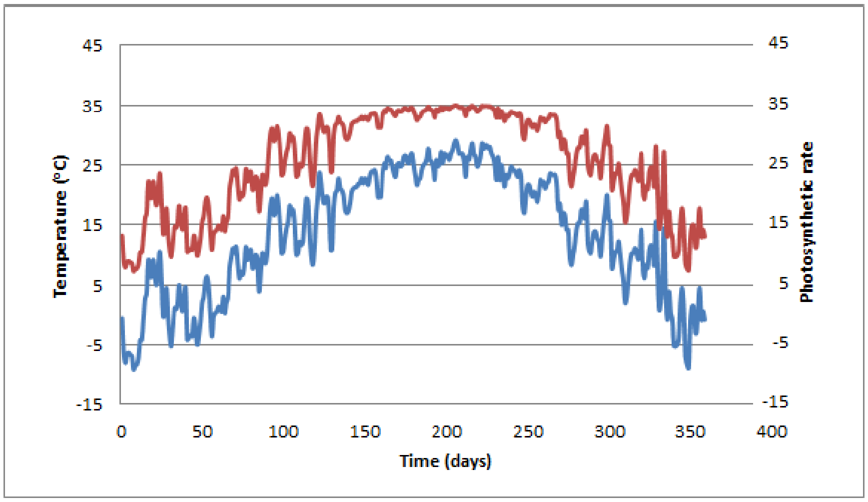
In the model the diameter of food source is used to estimate food availability. The food distributes evenly at the same density in the food source. Therefore, when food source is larger, there would be more food. The significant differences of energy and population at 3 levels of food availability support the hypothesis that ant colonies respond to the food availability (Fig. 13). Our observation that food availability affected the population size and energy intake of the colonies is similar to Macomi and Poter's (1995) findings on fire ant workers. In their fire ant colonies, doubling the cricket biomass caused an approximate doubling in colony biomass for colonies receiving only crickets, and colonies receiving sugar and crickets grew 65 and 40% larger with doubling of crickets from 1 to 2 and 2 to 4, respectively. Our model predicts that the foraging efficiency increases with food quantity (Fig.15). Schafer et al. (2006) found that the rate at which foragers return to the nest is linked to food availability: when food is easy to find, foragers return more quickly.

Under the predation pressure caused by food shortage and starvation, some ant species evolved several strategies to offset detrimental impacts of scattering and rare food sources. For example, granivorous ants select nest positions based on food availability (Sudd and Franks 1987, 206 p). Fire ants workers have different preferred diet depending on their status of starvation (Howard and Tschinkel 1981). Foraging ants regulate their activity rhythms on time of food availability (Hunt 1974; Hansen 1978). However, no matter what strategies the ant workers select, the colonies need basic energy to sustain themselves under the strong correlation between energy intake and colonies' biomass (Macomi and Porter 1995).

Effects of Both Food and Temperature on Population and Energy Dynamic of Ant Colony

In the model we have predicted how ant colonies responded to food and temperature. However, those results also suggest that temperature associate with food availability to determine colonies' dynamic. Firstly, when we considered the effects of temperature caused by climate change on ant colonies, symbolized by rising global CO_2 concentration and temperature, plant growth accounting for photosynthesis rate also exhibits temperature and CO_2 dependency. Photosynthetic rates increase with a short-term increase in CO_2 concentration and are related parabolically to leaf temperature (Von Caemmerer 2000). Based on the photosynthesis equations (Appendix 5) and the daily temperature in Johnson City the photosynthetic rate fluctuates (Fig.22a). As the temperature increases the photosynthetic rate increases as well (Fig.22b). In the light of temperature and food impacts on ant colony, temperature elevations increasing photosynthetic rate will facilitate plants to grow more food. If rich food patch could compensate starvation of colonies caused by the increased metabolism due to high temperature, then it could stabilize the population and energy dynamics of colonies that otherwise would die out. As expected, in the "experiment of climate change", the ant colonies died out in the 3-patch wide food source group because high temperature caused significantly higher hunger rate of workers, lower foraging and nursing efficiency and birth rate of immature ants. However, the population size and energy of colonies in 5-patch wide food source group peaked at almost 600 and 2.5KJ under the high ambient temperature (Fig. 17).

a:



b:

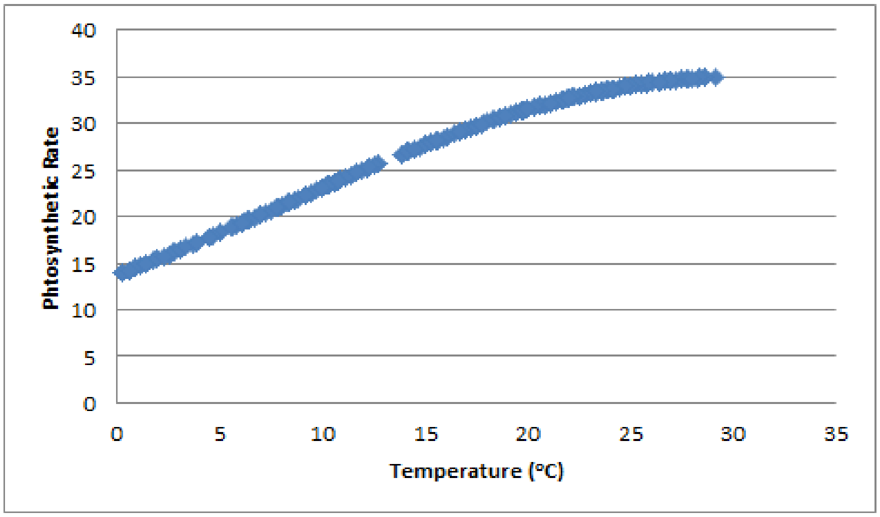


Figure 22. Relationship between photosynthetic rate and temperature. (a) the distribution of photosynthetic rate based on temperature in Johnson City: red line: photosynthetic rate; blue line: air temperature; (b) photosynthetic rate as the function of temperature.

Apart from interactions between food availability and temperature, Lienart et al. (2014) suggested that individuals in low physiological condition because of limited food availability are more susceptible to increased temperature. And the thermo-regulatory behavior of workers indicate that the growth curve for well-fed colonies was strongly skewed toward warmer temperature, and food limited colonies apparently grew larger at cooler temperatures because metabolic costs of workers were reduced (Porter and Tschinkel 1993). In the energetic explanation, with temperature elevations, individual metabolic rate increases exponentially so that more and more food and energy are consumed for basic energy maintenance. Ultimately, the well-feeding colonies might transfer to food limited colonies that are very susceptible to high temperature. In this process the food availability and temperature work under the networks (Fig. 23).

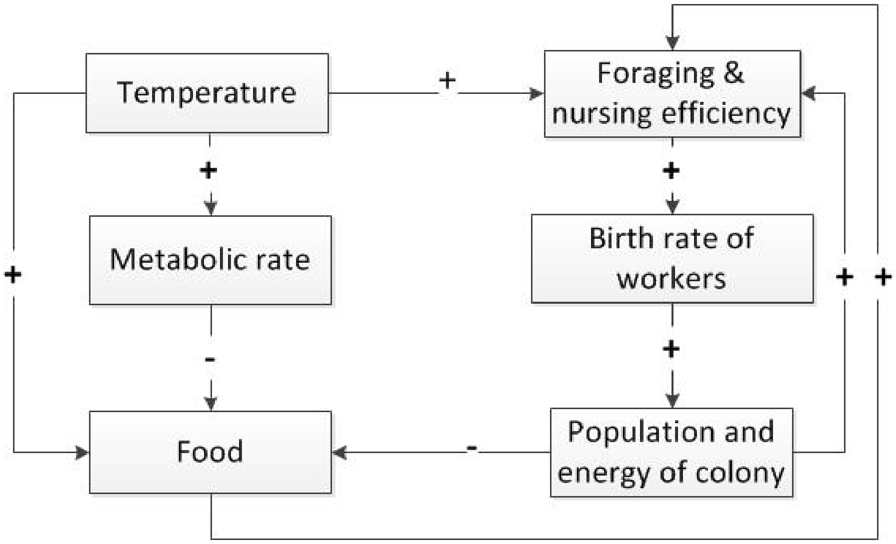


Figure 23. Feedbacks' networks of ant colony (+, positive feedback; -, negative feedback).

CHAPTER 5

CONCLUSIONS

By changing temperature and food availability, our model revealed the significant impacts of temperature and food on ant colonies’ population and energy dynamics. Moderate temperature elevation could boost colony growth by speeding workers’ foraging speed and increasing the energy allocations for reproduction of queen and development speed of immature ants. However, very high temperature elevation would cause the degeneration of energy and population of colonies because high temperature elevation increases ants’ metabolic rate. And ants may consume more energy to sustain themselves comparing with ants in moderate air temperature. In the environment with same air temperature, ant colonies could respond to the changes of food availability by adjusting their biomass to the food intake. The scarce food sources would increase colonies’ risk for dying out. Nevertheless, the rich food sources could protect ant colonies from food shortage and starvation. The equilibriums between food intake and consumption broken in low food richness could be saved in case of more available food. Temperature associates food availability has important impacts on ant colonies. Under the high temperature, a colony is more likely to change from the food-well one to food-limited one. The complicated feedback networks of the ant colony tell us that it is a very complex network of processes involved to estimate the effect of climate change on dynamics of population and energy of ant colonies.

REFERENCES

Abensperg-Traun M. 1996. The Effects of Habitat Fragmentation and Livestock-Grazing on Animal Communities in Remnants of Gimlet Eucalyptus salubris Woodland in the Western Australian Wheatbelt. I. Arthropods. Journal of Applied Ecology 33(6): 1281-1301.

Abril S, Oliveras J and Gómez C. 2008. Effect of temperature on the oviposition rate of Argentine ant queens (*Linepithema humile Mayr*) under monogynous and polygynous experimental conditions. Journal of insect physiology 54(1): 265-272.

Andersen AN. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. Proceedings of the Ecological ociety of Australia 16: 347–357.

Andersen AN. 1997. Using ants as bioindicators: multi-scale issues in ant community ecology[online]. Conservation Ecology 1: 8.

Ashton DH. 1979. Seed harvesting by ants in forests Eucalyptus rengans F. Muell. in central Victoria. Australian Journal of Ecology 4: 265–277.

Beattie AJ. 1985. The Evolutionary Ecology of Ant–Plant Mutualisms. New York: Cambridge University Press.

Beshers SN and Fewell JH. 2001. Models of division of labor in social insects. Annual review of entomology 46(1): 413-440.

Blanchard GB, Orledge GM, Reynolds SE and Franks NR. 2000. Division of labour and seasonality in the ant *Leptothorax albipennis*: worker corpulence and its influence on behaviour. Animal Behaviour 59(4): 723-738.

Blaustein AR. 2001. Amphibian Breeding and Climate Change. Conservation Biology 15.

Borjigidai A, Hikosaka K, Hirose T, Hasegawa T, Okada M, and Kobayashi K. 2006. Seasonal changes in temperature dependence of photosynthetic rate in rice under a free-air CO_2 enrichment. Ann Bot 97(4): 549-557.

Brian MV. 1973. Feeding and Growth in the Ant Myrmica. Journal of Animal Ecology 42(1): 37-53.

Brown KS. 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. Journal of Insect Conservation 1.

Bruce AI and Burd M. 2012. Allometric scaling of foraging rate with trail dimensions in leaf-cutting ants. Proceedings of the Royal Society B: Biological Sciences 279(1737): 2442-2447.

Calabi P, and Porter SD. 1989. Worker longevity in the fire ant *Solenopsis invicta*: Ergonomic considerations of correlations between temperature, size and metabolic rates. Journal of Insect Physiology 35(8): 643-649.

Campbell AJ and Tanton MT. Effects of fire on the invertebrate fauna of soil and litter of a eucalypt forest. In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. Canberra, Australia: Australian Academy of Sciences. 1981. 215–241 p.

Carvalho KS and Vasconcelos HL. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biological Conservation 91(2): 151-157.

Cassill DL and Tschinkel WR. 1995. Allocation of liquid food to larvae via trophallaxis in colonies of the fire ant, *Solenopsis invicta*. Animal Behaviour 50(3): 801-813.

Cassill DL and Tschinkel WR. 1999. Information flow during social feeding in ant societies. In Information processing in social insects. Birkhäuser Basel 69-81.

Cummins KW and Wuycheck JC. 1971. Caloric equivalents for investigations in ecological energetics.

Detrain C and Pasteels JM. 1991. Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant, Pheidole pallidula (Nyl.) (Hymenoptera: Myrmicinae). Journal of insect behavior 4(2): 157-176.

Dunn RR, Agosti D, Andersen AN, Arnan X, Bruhl CA, Cerda X, Ellison AM, Fisher BL, Fitzpatrick MC and Gibb H et al. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. Ecology letters 12(4): 324-333.

Fewell JH. 2003. Social insect networks. Science, 301(5641): 1867-1870.

Fewell JH, Schmidt SK and Taylor T. 2009. Division of labor in the context of complexity. In: Gadau J, Fewell J. (eds) Organization of insect societies: from genome to sociocomplexity. Cambridge: Harvard University Press. 483-502 p.

Gillooly JF, Brown JH, West GB, Savage VM and Charnov EL. 2001. Effects of size and temperature on metabolic rate. Science 293(5538): 2248-2251.

Glancey BM. 1981. Filtration of microparticles from liquids ingested by the red imported fire ant Solenopsis Invicta Buren. Insectes Soc 28(4): 395-401.

Gordon DM. 1984. Species-specific patterns in the social activities of harvester ant colonies (Pogonomyrmex). Insectes sociaux 31(1): 74-86.

Gordon DM. 1989. Dynamics of task switching in harvester ants. Animal Behavior, 38: 194-204.

Gordon, D.M. 2002. The regulation of foraging activity in red harvester ant colonies. The American Naturalist 159(5): 509-518.

Gordon DM. 2010. Ant encounters: interaction networks and colony behavior. Princeton: Princeton University Press. 30 p.

Griffiths D. 1991. Food Availability and the Use and Storage of Fat by Ant-Lion Larvae. Oikos, 60,(2): 162-172.

Grimbacher PS and Hughes L. 2002. Response of ant communities and ant–seed interactions to bush regeneration. Ecological Management & Restoration 3(3): 188-199.

Hansen SR. 1978. Resource utilization and coexistence of three species of Pogonomyrmex ants in an Upper Sonoran grassland community. Oecologia 35(1): 109-117.

Hasegawa E. 1993. Nest defense and early production of the major workers in the dimorphic ant Colobopsis nipponicus (Wheeler) (Hymenoptera: Formicidae).Behavioral ecology and sociobiology 33(2): 73-77.

Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. Nature 405(6789): 907-913.

Hölldobler B and Wilson, E.O. The ants. Cambridge: Belknap. 1990. 143 p.

Hölldobler B and Wilson, E.O. The ants. Cambridge: Belknap. 1990. 228 p.

Hölldobler B and Wilson, E.O. The ants. Cambridge: Belknap. 1990. 259 p.

Hölldobler B and Wilson, E.O. The ants. Cambridge: Belknap. 1990. 271 p.

Hoffmann BD and Andersen AN. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology 28(4): 444-464.

Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH and West GB. 2008. Energy uptake and allocation during ontogeny. Science 322(5902): 736-739.

Howard DF and Tschinkel WR. 1981. The flow of food in colonies of the fire ant, *Solenopsis invicta*: a multifactorial study. Physiological entomology 6(3): 297-306.

Humphreys GS. 1981. The rate of ant mounding and earthworm casting newar sydney, New South Wales. Search 12(5): 129-131.

Hunt JH. 1974. Temporal activity patterns in two competing ant species (Hymenoptera: Formicidae). Psyche 81(2): 237-242.

Hurlbert AH. 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecological Entomology 33: 144-154.

Huxley JS. 1924. Constant differential growth-ratios and their significance. Nature 114(2877): 895-896.

Huxley JS. 1932. Problems of relative growth. Methuen, London.

Jenkins CN., Sanders, N.J., Andersen, A.N., Arnan, X., Brühl, C.A., Cerda, X. and Dunn, R.R. 2011. Global diversity in light of climate change: the case of ants. Diversity and Distributions 17(4): 652-662.

Jensen TF. 1978. Annual Production and Respiration in Ant Populations. Oikos 31(2): 207-213.

Josens RB. 1998. Nectar feeding by the ant Camponotus mus: intake rate and crop filling as a function of sucrose concentration. Journal of Insect Physiology 44: 579–585.

Kaspari M. 2005. Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. Proceedings of the National Academy of Sciences of the United States of America 102(14): 5079-5083.

Kay A and Rissing SW. 2005. Division of foraging labor in ants can mediate demands for food and safety. Behavioral Ecology and Sociobiology 58(2): 165-174.

Keller L and Passera L. 1989. Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). Oecologia 80(2): 236-240.

Kennedy AD. 1995. Antarctic terrestrial ecosystem response to global environmental change. Annual Review of Ecology and Systematics 26(1): 683-704.

Killion MJ and Grant WE. 1995. A colony-growth model for the imported fire ant: potential geographic range of an invading species. Ecological Modellingn77(1): 73-84.

Kleiber M. 1932. Body size and metabolism. Hilgardia 6(11): 315-332.

Kondoh M. 1968. Bioeconomic studies on the colony of an ant species, Formica japonica Motschulsky. 2. Allometric study of the body weight and the corpulency relating to the body size of workers. Japanese Journal of Ecology 18: 171-179.

Korzukhin MD, Porter SD, Thompson LC and Wiley S. 2001. Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. Environmental Entomology 30(4): 645-655.

Lal R. 1988. Effects of macrofauna on soil properties in tropical ecosystems. Agriculture, Ecosystems, and Environment 24: 101–116.

Levieux J. 1983. The soil fauna of tropical savannas. IV. The ants. In: Bourliere, F. (Ed.), Tropical Savannas. Amsterdam: Elsevier. 525–540.

Lienart GD, Mitchell MD, Ferrari MC and McCormick MI. 2014. Temperature and food availability affect risk assessment in an ectotherm.Animal Behaviour 89: 199-204.

Lighton JR, Bartholomew GA and Feener Jr DH. 1987. Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant atta Colombica guer. Physiological Zoology 60(5): 524-537.

Lighton JRB. 1989. Individual and Whole-Colony Respiration in an African Formicine Ant. Functional Ecoloy 3(5): 523-530.

Lobry de Bruyn LA and Conacher AJ.1994. The bioturbation activity of ants in agricultural and naturally vegetated habitats in semi-arid environments. Australian Journal of Soil Research 32 (3): 555–570.

MacKay WP. 1985. A Comparison of the Energy Budgets of Three Species of Pogonomyrmex Harvester Ants. Oecologia 66(4): 484-494.

Macomi TE and Porter SD. 1995. Food and energy requirements of laboratory fire ant colonies

(Hymenoptera: Formicidae). Environmental Entomology 24(2): 387-391.

Majer JD. 1983. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental Management 7: 375–385.

Majer JD. 1984. Short-term responses of soil and litter invertebrates to a cool autumn burn in jarrah (Eucalyptus marginata) forest in Western Australia. Pedobiologia 26(4): 229-247.

Meer V. 1992. A comparison of queen oviposition rates from monogyne and polygyne fire ant, Solenopsis invicta, colonies. Physilogical Entomology 17: 384-390.

Miller LJ and New TR. 1997. Mount Piper grasslands: pitfall trapping of ants and interpretation of habitat variability. Memoirs of the Museum of Victoria 56(2): 377-81.

Moyano M. 2013. From colonies to communities: Nest relocation and resource discovery in ants [Doctoral dissertation]. The University of Utah.

National Research Council. 2010. Advancing the Science of Climate Change. Washington, DC: The National Academies Press. 25 p.

Parmesan C and Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918): 37-42.

Perfecto I and Vandermeer J. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108(3),: 577-582.

Perrin N. 1995. About Berrigan and Charnov's Life-History Puzzle. Oikos73(1): 137-139.

Phoofolo MW, Obrycki JJ and Krafsur ES. 1995. Temperature-dependent ovarian development in Coccinella septempunctata (Coleoptera: Coccinellidae). Annals of the Entomological Society of America 88(1): 72-79.

Pimm SL and Bartell DP. 1980. Statistical model for predicting range expansion of the red imported fire ant, Solenopsis invicta, in Texas.Environmental Entomology 9(5): 653-658.

Porter SD and Tschinkel WR. 1985. Fire ant polymorphism: the ergonomics of brood production. Behavioral Ecology and Sociobiology 16(4): 323-336.

Porter SD and Tschinkel WR. 1987. Foraging in Solenopsis invicta (Hymenoptera: Formicidae): effects of weather and season. Environmental Entomology 16(3): 802-808.

Porter SD. 1988. Impact of temperature on colony growth and developmental rates of the ant, Solenopsis invicta. Journal of Insect Physiology 34(12): 1127-1133.

Porter SD and Tschinkel WR. 1993. Fire ant thermal preferences: behavioral control of growth and metabolism. Behavioral Ecology and Sociobiology 32(5): 321-329.

Powell S and Franks NR. 2005. Caste evolution and ecology: a special worker for novel prey. Proceedings of the Royal Society B: Biological Sciences 272(1577): 2173-2180.

Powell S. 2009. How ecology shapes caste evolution: linking resource use, morphology, performance and fitness in a superorganism. Journal of evolutionary biology 22(5): 1004-1013.

Reyes-López JL and Fernández-Haeger J. 2002. Food Storage in the Nest and Seed Selectivity in the Harvester Ant Messor barbarus. Sociobiology 39(1).

Rissing SW. 1984. Replete caste production and allometry of workers in the honey ant, Myrmecocystus mexicanus Wesmael (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 347-350.

Robinson SW, Moser JC, Blum MS and Amante E. 1974. Laboratory investigations of the trail-following responses of four species of leaf-cutting ants with notes on the specificity of a trail pheromone of *Atta texana* (Buckley). Insectes sociaux 21(1): 87-94.

Robinson GE and Page RE. 1989. Genetic basis for division of labor in an insect society. The genetics of social evolution 61-80.

Roura-Pascual N, Suarez AV, Gomez C, Pons P, Touyama Y, Wild AL and Peterson AT. 2004. Geographical potential of Argentine ants (Linepithema humile Mayr) in the face of global climate change. Proc. Biol. Sci. 271(1557): 2527-2535.

Savage VM, Gillooly JF, Brown JH, West GB and Charnov EL. 2004. Effects of body size and temperature on population growth. The American Naturalist 163(3): 429-441.

Schafer RJ, Holmes S and Gordon, D.M. 2006. Forager activation and food availability in harvester ants. Animal Behaviour 71(4): 815-822.

Schilman PE and Roces F. 2005. Energetics of locomotion and load carriage in the nectar feeding ant, Camponotus rufipes. Physiological Entomology 30(4): 332-337.

Stoker RL, Ferris DK, Grant WE and Folse LJ. 1994. Simulating colonization by exotic species: a model of the red imported fire ant (*Solenopsis invicta*) in North America. Ecological Modelling 73(3): 281-292.

Sudd JH and Franks NR. 1987. The behavioural ecology of ants. Blackie & Son Ltd., 206.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Hughes L, Huntley B and Van Jaarsveld AS et al. 2004. Extinction risk from climate change. Nature 427(6970): 145-148.

Tschinkel WR and Howard DF. 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. Behavioral ecology and sociobiologyb3(3): 297-310.

Tschinkel WR. 1987. Seasonal life history and nest architecture of a winter active ant Prenolepis Imparis. Insectes Soc. 34(3): 143-164.

Tschinkel WR. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, Solenopsis invicta. Behavioral Ecology and Sociobiology 22: 103-115.

Tschinkel WR. 1993. Sociometry and sociogenesis of colonies of the fire ant Solenopsis invicta during one annual cycle. Ecological Monographs 63(4): 425-457.

Tschinkel WR. 1998. Sociometry and sociogenesis of colonies of the harvester ant, Pogonomyrmex badius: worker characteristics in relation to colony size and season. Insectes Soc. 45: 385-410.

Tschinkel WR. 1999. Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera: Formicidae). Annals of the Entomological Society of America 92(1): 80-89.

Underwood EC and Fisher BL. 2006. The role of ants in conservation monitoring: If, when, and how. Biological Conservation 132(2): 166-182.

Vogt JT. and Appel AG. 1999. Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass, and caste. Journal of insect physiology 45(7): 655-666.

Von Caemmerer S. 2000. Biochemical models of leaf photosynthesis (No. 2). Collingwood: Csiro publishing. 29 p.

West GB. 1997. A General Model for the Origin of Allometric Scaling Laws in Biology. Science 276(5309): 122-126.

West GB. 1999. The Fourth Dimension of Life: Fractal Geometry and Allometric Scaling of Organisms. Science 284(5420): 1677-1679.

West GB. 2001. A general model for ontogenetic growth. Nature 413: 628-631.

White EP, Ernest SK, Kerkhoff AJ and Enquist BJ. 2007. Relationships between body size and abundance in ecology. Trends in ecology & evolution 22(6): 323-330.

Wilson EO. 1968. The ergonomics of caste in the social insects. American Naturalist 41-66.

Wilson EO. 1974. The population consequences of polygyny in the ant Leptothorax curvispinosus. Annals of the Entomological Society of America 67(5): 781-786.

Wilson EO. 1976. The organization of colony defense in the ant Pheidole dentata Mayr (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology 1(1): 63-81.

Zheng D, Hunt Jr ER and Running SW. 1993. A daily soil temperature model based on air temperature and precipitation for continental applications.Climate Research 2(3): 183-191.

APPENDICES

APENDIX A

Standard Metabolic Rate

The standard metabolic rates of several ants species were estimated and the relationship between mass and metabolic rate was regressed in equation 1(Vogt and Appel 1999).

$$Standard\ Metabolic\ Rate = 753(\pm 1.39)Mass^{0.799(\pm 0.077)} \quad (\mu w) \qquad \text{equ. 1}$$

In the model, the standard metabolic rate of ants could be calculated based on their mass (equ. 1).

Table 3. Standard metabolic rate of ants.

Agent	*Mass*	*Metabolic*
Queen	*20mg*	*19.77*$(10^{-4}$ *J/min)*
Immature ant	*0.8mg*	*1.51*$(10^{-4}$ *J/min)*
Forager(Nurse)	*2mg*	*3.13*$(10^{-4}$ *J/min)*

APENDIX B

Metabolic Rate for Locomotion

Schilman (Schilman and Roces 2005) measured the net cost of transport (NCOT) for unladen locomotion in nectar-feeding ant, *Camponotus rufipes*.

$$NCOT_{body\ mass}=212.3\pm34.5\ (J\ kg^{-1}m^{-1})$$

We assume the NCOT is the universal parameter for calculating the metabolic rate of locomotion ($M_{locomotion}$) based on mass (equ.2).

$$M_{locomotion} = NCOT_{body\ mass} \cdot mass \cdot velocity \qquad \text{equ. 2}$$

Table 4. Initial metabolic rate of ant worker for locomotion.

$NCOT_{body\ mass}$	$Initial\ mass$	$Initial\ velocity$	$Initial\ M_{locomotion}$
212.3 (J kg -1m-1)	*2mg*	*120cm/min*	*5.09*(10^{-4}*J/min)*

APENDIX C

Metabolic Rate for Growth, Reproduction, and Biosynthesis

Chen (Hou et al. 2008)estimated energy allocation to storage for somatic growth during ontogeny in equation 3 and energy for biosynthesis in equation 4.

$$S = \gamma \cdot (B_0 m^{3/4} - B_0 M^{-1/4} m) \qquad \text{equ. 3}$$

Here, S is the rate of energy stored for development; γ is the storage coefficiency; B_0 is the standard metabolic rate; m is the mass at larvae size; M is the mass at adult size. We assume this equation is valid for ant development (Table 5):

Table 5. Immature ants' metabolic rate for somatic growth and biosynthesis.

Parameters	Estimate	References
B_0	*451.8*(10^{-4} *J/min*)	(Vogt 1999)
m	*0.8mg*	(Brian 1973)
M	*2mg*	(Jensen 1978)
γ	*9*	(Hou et al. 2008)
S	*3.95*(10^{-4} *J/min*)	Equ. 3

In the model, queen is designed to consume energy and store it for laying eggs. We assume the "immature ant" (0.8mg) develops from vitellogenic follicles (10ug). The energy for development of per follicle stored by queen could be calculated in equ. 3. In a medium sized colony , about 2,000 vitellogenic follicles were found in ovaries of the queen(Porter 1985). The total energy for development of follicles stored by queen and energy for queen's biosynthesis are listed in table 6.

Table 6. The rate of energy storage for reproduction.

Parameters	Estimate	References
B_0	*451.8*(10^{-4}*J/min)*	(Vogt 1999)
m	*0.01mg*	(Meer 1992)
M	*0.8mg*	(Reyes-López 2002)
γ	*9*	(Hou et al. 2008)
n	*2000*	(Porter 1985)
$S_{per\ follicle}$	*0.48*(10^{-4}*J/min)*	Equ. 3
$S_{total\ follicles}$	*960*(10^{-4}*J/min)*	$n \cdot S_{\text{per follicle}}$

A worker consumes energy to synthesize and accumulate the fat body, which was described in equation 4(Hou et al. 2008). Here, B_{syn} is energy consumed for biosynthesis; *m* is the mass of a worker; *M* is the mass' upper threshold of worker.

$$B_{syn} = \left(B_0 m^{3/4} - B_0 M^{-1/4} m\right) \qquad \text{equ. 4}$$

Table 7. The rate of energy for workers' biosynthesis.

Parameters	Estimate	References
B_0	*451.8*(10^{-4}*J/min)*	(Vogt 1999)
m	*2mg*	(Jensen 1978)
M	*5mg*	
B_{syn}	*0.874* (10^{-4}*J/min)*	Equ. 4

APENDIX D

Amount of the Food per One Bite

In the infrabuccal pellets of larvae, 1435-1760 food particles were counted, and the maximum size of food particles swallowed by larvae was 45.8 um, which is approximately corresponds to the diameter of the esophagus (Glancey 1981). We assume the food particle is a protein sphere with diameter 45.8 um and density 1.35 g/cm^3 (Cummins 1971), and ants have the same volume of infrabuccal pellets. Every bite, the weight and energy of food in pellets of ants, could be calculated in equation 5, 6 (Table 8).

$$W_{food} = N_{food} \cdot \left(\frac{4 \cdot \pi \cdot (D/2)^3}{3}\right) \cdot D_{food} \quad (mg) \qquad \text{equ. 5}$$

$$E_{food} = W_{food} \cdot c \qquad (10^{-4} J) \qquad \text{equ. 6}$$

W_{food} is the weight of food in one bite; N_{food} is the number of food particles in the pellets; D is the diameter of food particle that is approximately corresponds to diameter of the larvae esophagus; D_{food} is the density of food particles; E_{food} is the equivalent energy of the food in one bite; c is the weight-energy conversion factor.

Table 8. The amount of food per feeding event.

N_{food}	$R(um)$	D_{food} $(10^{-9} mg/um^3)$	c $(10^{-4} J/mg)$	W_{food} (mg)	E_{food} $(10^{-4} J)$
1435	*45.8*	*1.35*	*190000*	*0.023*	*4420*

APENDIX E

Relationship among Photosynthesis, Temperature, and CO_2

The relationships among photosynthesis, temperature and CO_2 concentration could be quantified in equ. 26, 27, 28 (Borjigidai et al. 2006):

$$P_c = \frac{V_{cmax}(C_i - \tau^*)}{C_i + K_c(1 + {}^{O}/_{K_o})} - R_d \qquad \text{equ.26}$$

$$P_r = \frac{J_{max}(C_i - \tau^*)}{4C_i + 8\tau^*} - R_d \qquad \text{equ.27}$$

$$f(T_k) = f(25)exp\left[\frac{E_a(T_k - 298)}{298RT_k}\right] \qquad \text{equ.28}$$

Where V_{cmax} is maximum rate of ribulose-1,5-bisphosphate (RuBP) carboxylation; J_{max} is maximum rate of electron transport; P_c is the photosynthetic rate limited by the RuBP Activity; P_r is the photosynthetic rate limited by RuBP regeneration; C_i is the concentration of CO_2 at intercellular space, τ^* is the CO2 compensation point in the absence of day respiration (Rd); K_c and K_o are Michaelis constants of RuBP carboxylase for CO_2 and O_2, respectively, and O is the O2 concentration; f is the value of a parameter; f(25) is f at 25^oC; E_a is the activation energy, R is the gas constant; T_k is leaf temperature in K; The photosynthetic rate is the minimum of P_c and P_r.

VITA

XIAOHUI GUO

Education:	MS Biology, East Tennessee State University, Johnson City, Tennessee, 2014. BSc. Biological Sciences, China Agriculture University, China, 2005.
Experience:	Teaching Associate, Department of Biological Sciences, East Tennessee State University, Johnson City, TN 2011-2013.
Awards and Grants:	Thesis Scholarship, Graduate of School, East Tennessee State University, Johnson City, Tennessee 2013.
Conferences:	Attended Appalachian Student Research Forum, East Tennessee State University, Johnson City, TN 2012; Appalachian Student Research Forum, East Tennessee State University, Johnson City, TN 2013; Appalachian Student Research Forum, East Tennessee State University, Johnson City, TN 2014.
Technical Skills:	SPSS, Netlogo, Anylogic, StarlogoTNG, MEME.