

Modeling of self-organized competition hierarchy with body weight development in larval cricket, *Gryllus bimaculatus*

Shiro YANO¹, Yusuke IKEMOTO², Hitoshi AONUMA³, Takashi NAGAO⁴, and Hajime ASAMA²

Abstract Larval crickets develop a big body and high aggressiveness under isolated conditions, but develop a small body and low aggression under crowded conditions. Furthermore, their ensemble variance increases. It is known that the heavier cricket tends to win. Therefore, the two growth processes affect competition. We constructed a mathematical model for intraspecific competition based on the Bonabeau model, showing body weight effects on the winning rate. Results show that the population mean of body weight decreases under the condition of specific memory enhancement that places more emphasis on losing than winning. Furthermore, hierarchical effects in foraging efficiency increase the ensemble variance.

1 Introduction

It is essentially necessary for multirobot system to maintain community structure so as to perform the cooperative function. Recently some studies intend to transfer multirobot through bottlenecks with recalibrating the bilateral relations between community structure, and it is difficult to reconstruct the prior community structure after transit through the bottlenecks[1][2].

Reconstructing the prior community structure is important in many circumstances, for example, guard patrol and waitstaff: robots always deploy themselves close to security area or table whereas they go and return between narrow hallway, bottlenecks, frequently.

Graduate School of Engineering, The University of Tokyo, itano@race.u-tokyo.ac.jp
Research into Artifacts, Center for Engineering (RACE), The University of Tokyo, ikemoto@race.u-tokyo.ac.jp, asama@race.u-tokyo.ac.jp
Research into Electronic Science (RIES), Hokkaido University, aon@ncps.es.hokudai.ac.jp
Human Information System Laboratories, Kanazawa Institute of Technology, nagao@his.kanazawa-it.ac.jp

Now we focus attention to animals' strategy of territory. Most of animals guard and memorize own territory so once they are away from home, they'll be back again[3]. We specifically examine the competition of cricket *G. bimaculatus*.

G. bimaculatus also have territory behavior: they guard territory for foraging behavior and courtship behavior. It has never examined that cricket will be back to same place again or not when cricket is away from home. However, they remember the dominance between crickets in few hours and can reconstruct dominance hierarchy after an absence of few hours[4]. So territory behavior of cricket is thought as a primitive form of the way that multirobot reconstructs task distribution not spatial distribution.

It is known that agonistic behavior, such as aggressive behavior, constructs territory[3][5]. Cricket causes aggressive behavior to construct territory too, so we focus in the way how crickets fight to the finish.

Regarding the growth process of cricket *G. bimaculatus*, the adult insects' body size, activity, and aggression are strongly associated with alteration of their growth environment [8][9][10]. Moreover, they display distinctive and destructive intraspecific interaction and fighting behavior. Recent reports describe that crickets develop a large body and high aggressiveness under isolated conditions[8][11]. Conversely, they develop a small body and low aggressiveness under crowded conditions. Therefore, intraspecific competition seems to be an embedded ability that maintains variance among them.

In this paper, we present a mathematical model of intraspecific competition based on Bonabeau model[13], and clarify how competition affects individual body weight growth, ensemble variance, and the population mean of body weight. In order to understand the way territory is constructed, we would like to know about if crickets treat win or lose in the same manner or not. In this regard, we deduce which is the long-continued memory about win or lose. At last, we conclude that crickets' experience of loses is long-continued state.

2 Modeling of Body Size Development

A logistic function describes evolution of animal body weight growth of some types[6]. Two studies have examined body weight increases in relation to effects of population density in the cricket *G. bimaculatus*[8][9] and an evolutionary logistic equation fitting them(see fig. 1.1).

For this study, we use a logistic growth function written in the differential form as shown below:

$$\frac{dm_i}{dt} = \alpha(T, P_i)r_i m_i, \quad (1)$$

$$r_i = r_0 \left(1 - \frac{m_i}{M\beta(T, P_i)} \right) \quad (2)$$

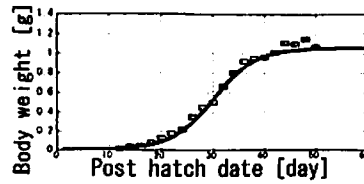


Fig. 1 Discrete body weight increase points are measured[8].

where $M = \text{const. [g]} > 0$ is the mature weight, $m_i(t)$ [g] > 0 is the current weight, $r_0 = \text{const. [s}^{-1}] > 0$ is the egg growth rate immediately after production, $r_i(t)$ [s⁻¹] > 0 is the growth rate, T [°C] is the temperature, P_i [g/s] is the foraging efficiency, and α and β respectively signify a weighting function on the growth rate and mature weight (see Fig. 1.2). Experience shows that α and β are important factors for development[12].

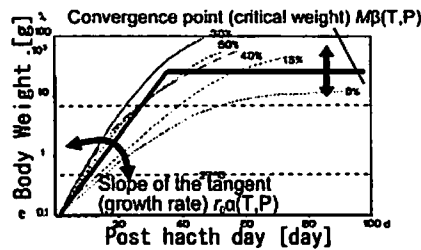


Fig. 2 Each curve shows growth hysteresis under five types of percentage of the protein rate in food. There are two other temperature data: 23 [°C] and 31 [°C]. All data are from an earlier study[9].

Equation (1.2) includes M ; however, an animal can not know its own mature weight at an interim period during growth. We redefine the weight growth equation without M as the following.

$$\begin{aligned} \frac{dr_i}{dt} &= -\frac{r_0}{M\beta} \frac{dm_i}{dt} \\ &= -\frac{r_0}{M\beta} \alpha r_i m_i = -r_0 \alpha r_i \left(1 - \frac{r_i}{r_0}\right) \end{aligned} \quad (3)$$

Regarding eq. (1.3), we must devote attention to the fact that the factor β was removed. The reason is the mode of formula development: we take the condition “ α and β as time-invariant if T and P_i are constant.” Consequently, $d\beta/dt = 0$. Such a condition is necessary for a logistic growth curve and construed as solitary growth or at a least low-crowd-density growth condition, effects of population density can be negligible. In contrast, it is compensated as eq. (1.4) when effects of the population density can not be negligible.

$$\frac{dr_i}{dt} = (r_i - r_0) \left(\alpha r_i - \frac{d(M\beta)/dt}{M\beta} \right) \quad (4)$$

In addition, $d(M\beta)/dt$ is expanded as follows

$$\begin{aligned} \frac{dM\beta}{dt} &= \frac{\partial M\beta}{\partial T} \frac{dT}{dt} + \frac{\partial M\beta}{\partial P_i} \frac{dP_i}{dt} \\ &= \frac{\partial M\beta}{\partial P_i} \frac{dP_i}{dt} \end{aligned} \quad (5)$$

The temperature is constant for the experiments[8][9].

According to eq. (1.5), the stabilization points of r_i are $r_i = r_0$ and $r_i = \frac{d(M\beta)/dt}{\alpha M\beta}$. The stable convergence point of m_i is

$$m_i^{\text{fix}} = M\beta \left(1 - \frac{1}{r_0} \frac{d(M\beta)/dt}{\alpha M\beta} \right). \quad (6)$$

Consequently, when we calculate the body weights under effects of population density, we must know the data of body weight and growth rate under low-density $M\beta$ and $r_0\alpha$, and the time variation of the foraging efficiency dP_i/dt .

3 Modeling of Intraspecific Competition

As computers became powerful and sophisticated, numerous studies of many-body systems using computer simulation increased rapidly during the 1990s. Bonabeau studied how the hierarchy emerges in the course of agonistic behavior in an intraspecific community using computer simulation[13]. A few studies derived from his model were later performed[14][15]. Lacasa studied the most primitive part of Bonabeau model using a discrete mean-field approximation approach[14]. In this section, we construct a model of time variation of the foraging efficiency dP_i/dt using the parameter of hierarchy from the modified competition model.

3.1 Modified Bonabeau model

The most primitive equation of the Bonabeau model is described as follows[14].

$$P_{ij}(t) = \frac{1}{1 + \exp(\eta(h_j(t) - h_i(t)))} \quad (7)$$

$$h_i(t+1) = (1 - \rho)(1 - \mu)h_i(t) + \frac{\rho(1 - \mu)}{N-1} \sum_{j: i,j/t}^N \{P_{ij}(t)(h_i(t) + 1) + (1 - P_{ij}(t))(h_i(t) - F)\}, \quad (8)$$

$\rho = N/S$, N: Number of animals, S: Field size [cm²]

In those equations, P_{ij} is the probability that attacker i will defeat individual j , time dependent variable $h_i(t)$ is the hierarchy (Lacasa calls it status), $\eta > 0$ is an adjustable strength of force parameter, ρ is the population density, $(1 - \mu)$ is a relaxation factor of status, which is interpreted as the fading memory of individuals. In this discussion, we treat h_i as the parameter reflecting a dominance hierarchy in the way that Bonabeau treated it in his study[13]. Equation (1.8) reflects that, after each combat, the winner's h_i increases by 1 and the loser's h_i decreases by F .

In their models, hierarchy emergently becomes differentiated between individuals at the point of critical density ρ_c with phase transition (see Fig. 1.3).

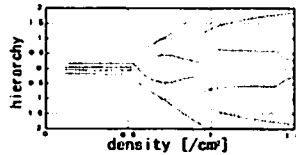


Fig. 3 Hierarchy organized by phase transition. (N=4, F=1)

That is to say, h_i yields instability under $\rho > \rho_c$. Therefore, minute fluctuations in the hierarchy trigger a phase transition. Minute fluctuations result from, for example, individual differences of agonistic behavior generated over time or innate individual differences of the body structure. Large individuals are known to tend to defeat small ones. We add this body size effect with hierarchical effect(see eq.(1.8) and fig.(1.8))

$$Q_{ij}^1(t) := \frac{1}{1 + \exp\{\eta_2 \left(\frac{1}{2P_{ij}(t)} - \frac{m_i}{m_j} \right)\}} \quad (9)$$

$$m_0 = m_i(0) = 0.7 \times 10^{-3}(1 + 0.5\xi), \quad (10)$$

where $0 < \xi < 1$ is a fluctuation factor.

In the equations above, m_0 is the initial weight after egg hatching. Furthermore, m_0 is affected by the mother's condition, so adoption of individual differences is completely natural.

3.2 foraging efficiency affected by hierarchy

Definition of social hierarchy includes that the dominant hierarchy is superior to that of the subordinate in foraging efficiency[7]. We define this tendency to the factor of foraging efficiency P_i in eq. (1.11);

$$\frac{dP_i}{dt} = \frac{\partial P_i}{\partial h_i} \frac{dh_i}{dt} \frac{\delta t}{dt} \quad (11)$$

where δt is the interval of time required for agonistic behavior; also,

$\delta t/dt$ is a frequency of fighting in a day.

In eq. (1.11), we construct $\partial P_i/\partial h_i$ as Fig. 1.4, where dh_i/dt is an outcome of eq. (1.8) under the condition " $\delta t = 1$ ".

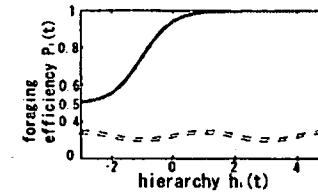


Fig. 4 How the foraging efficiency is affected by hierarchy, with the assumption that $\min(h_i)$, requires double the time to achieve foraging equal to solitary ones.

3.3 Parameter determination

In this section, we determine parameter $r_0\alpha$, $M\beta$, $\rho_j(m_i, m_j)$ and $\delta t/dt$ from experiments.

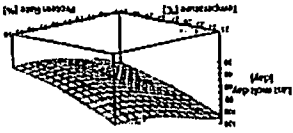


Fig. 7 Duration of growth period fitted to $2x_0 = t - \frac{Q_{10}}{T - T_0}$, $Q_{10} = 0.4$, $T_0 = 18.5$, $Q_{10} = 1 + \exp\left(-\frac{v}{x^2}\right)$, $v = 2.3$, $t = 2.5$, $\mu = 42$, $v = 15$, [9].

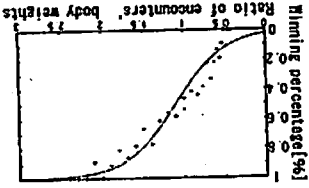


Fig. 8 Point distribution shows that the winning rate p_W is monotone increasing function of body weight ratio W . It is fitted by $p_W = \frac{1}{1 + \exp(-1.1W)}$.

3.3.4 determination of dt/dt

Herein, dt/dt represents the frequency of agonistic behavior per day. Aonuma conducted an experiment related to the recovery speed crawl back from a lost battle in *G. bimaculatus*, as shown in Fig. 19. We use $dt/dt = 1$ and $\mu = 4.47 \times 10^{-2}$ by this result.

4 Simulation and Analytic Prediction

First, we run a computer simulation of the model in Matlab and compare the results to experimental data. Second, we discuss the model analytically.

3.3.1 determination of $r_0\alpha$

From eq. (1.1)(1.2), we can approximately derive $r_0\alpha$ as follows.

$$\frac{dm_i}{dt} = \alpha(T, P)r_i m_i \approx \alpha(T, P)r_i m_i (1 - 0) m_i$$

$$\left(\text{for } i \approx 0, \frac{MB}{m_0} \approx \frac{MB}{m_0} \ll 1, m_0 \approx 0.7[\text{mg}]\right)$$

$$m_i = m_0 \exp(r_0\alpha t) = m_0 10^{(r_0\alpha \log e)t}$$

Therein, $r_0\alpha$ is the slope of the tangent (see fig. 1.2). We referred the value of that parameter from [9].

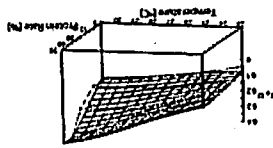


Fig. 6 Fitted by $r_0\alpha(T, P) = a + b \exp\left(-\frac{cT}{T-d}\right) - \frac{eP}{1+fP}$, $a = 0.055$, $b = 0.35$, $cT = 32.2$, $cP = 46$, $dP = 5.5$, $dP = 26$

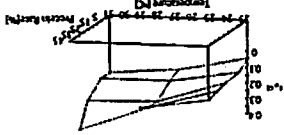


Fig. 5 Data referred from [9].

3.3.2 determination of MB

The analytical solution of eq.(1.3) is

$$r_i = \frac{1 + \exp(r_0\alpha(t - t_0))}{n_i} \tag{13}$$

and eq.(1.2)

$$MB = 1 + \exp(r_0\alpha t_0) \tag{14}$$

Here, t_0 is the half period from hatch to adult; we referred the value of this parameter from [9].

3.3.3 determination of p_W

Nagao performed an experiment related to the effect of body weight on the winning rate in *G. bimaculatus*, as presented in Fig. 1.8.

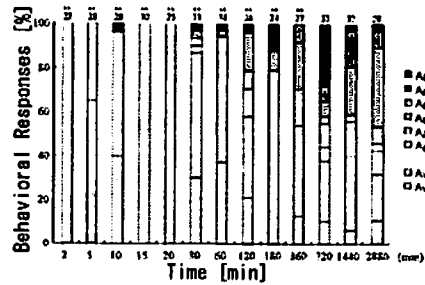


Fig. 9 Histogram showing that the avoidance rate requires 12 h to recover to 50[%].

4.1 Computer simulation

We determine other undefined parameters as $\eta = 1, F = 2, N = 4, \text{ and } S = 16$. Simulation 1 shows a variance increase of the body weight on the last molt day. Simulation 2 demonstrates decreased body weight in the final weight.

4.1.1 Simulation 1: Comparison of ensemble variance

This simulation is designed to compare the ensemble variance of the final weight under solitary growth and crowded growth. As discussed previously, we set $N = 4$. The ensemble variance of solitary growth has roots in the fluctuation factor on m_{hi} .

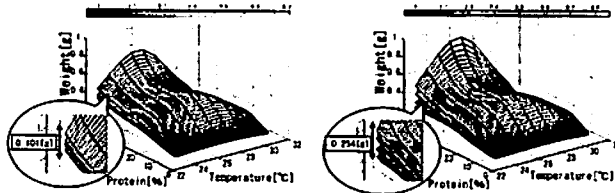


Fig. 10 Body weight of solitary individuals, Fig. 11 Self organization of body weight, which has root from initial fluctuation of body has a root from hierarchical foraging efficiency ($N=4, F=2$)

4.1.2 Simulation 2: Comparison of Population Means

This simulation compares the population means of the final weight under solitary growth and crowded growth. Bonabeau shows that the population mean of hierarchy becomes zero under ($F = 1$). We show ($F = 0.5$) and ($F = 2$) specifically. The mean

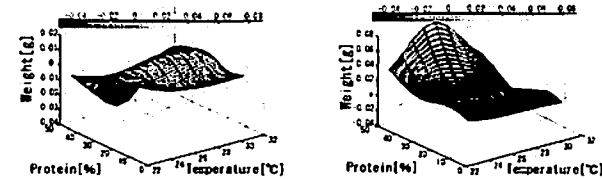


Fig. 12 Subtract the mean weight of group growth individuals from the mean weight of solitary ones under $0 < F < 1$ Fig. 13 Subtract the mean weight of group growth individuals from the mean weight of solitary ones under $F > 1$

weights under crowded growth is greater than under solitary growth in ($F = 0.5$), this is opposite to ($F = 2$).

4.2 Analytic approach: A qualitative feature from eq. (1.6)

Herein, $M\beta$ is the body weight of solitary growth of individuals, so $\delta_i = -\frac{1}{r_{hi}\alpha} \frac{d(M\beta)}{dt}$ are correction terms of the density effect (eq. (1.6)). In addition, $(\max(\delta_i) - \min(\delta_i))$ reflects the variance of individuals' body weights affected by the density effect. Furthermore, $\frac{1}{N} \sum_i \delta_i$ reflects the mean value of the individuals' body weights affected by the density effect. We discuss these two equations and make a qualitative prediction below.

4.2.1 Approach 1: Magnitude correlation of $\max(\delta_i)$ and $\min(\delta_i)$

$\{\max(m_i) - \min(m_i)\}_{crowded} - \{\max(m_i) - \min(m_i)\}_{solitary}$ shows that the ensemble variance of body weights. It is equivalent to $\{\max(\delta_i) - \min(\delta_i)\}$. The difference on δ_i arises from factor $\frac{d(M\beta)}{dt}$.

$$\frac{d(M\beta)}{dt} = \frac{d(M\beta)}{dP} \frac{dP}{dh} \frac{dh}{dt} \text{ and } \frac{dP}{dh} > 0, \tag{15}$$

so that difference on $\frac{dMB}{dt}$ originates from the factors $\frac{dMB}{dt}$ and $\frac{dh_i}{dt}$. Merkel reported that $\frac{dMB}{dt}$ shows positive and negative value[9]. To see qualitative trend on the ensemble variance, it is sufficient to show that any two terms are different (s.t. $\frac{dh_i}{dt} \neq \frac{dh_j}{dt} \mid i \neq j$). Moreover, it is readily apparent that the bifurcation of h_i satisfies $(\frac{dh_i}{dt} \neq \frac{dh_j}{dt} \mid i \neq j)$.

Consequently, the variance of individuals' body weights increases or decreases.

4.2.2 Approach 2: Discriminant positive and negative of $(-\frac{1}{N} \sum_{i=1}^N \delta_i)$

The discriminant positive and negative of $(-\frac{1}{N} \sum_{i=1}^N \delta_i)$ are equivalent to those of $(\frac{1}{N} \sum_{i=1}^N \frac{dh_i}{dt})$. The foregoing study demonstrated that $(\sum_{i=1}^N \frac{dh_i}{dt} < 0)$ when $(F > 1)$ [14].

Therefore, the mean value of an individual's body weight decreases when losing a game has a greater effect than that of winning a game $(F > 1)$.

5 Discussion and Conclusion

For the analyses described in this paper, we constructed a mathematical model of intraspecific competition based on the Bonabeau model[13] to clarify how competition affects individual body weight growth, ensemble variance, and population mean of body weight. We added the effect of body weight on the winning rate to the simplest Bonabeau model and the effect of the foraging rate, as influenced by the dominance hierarchy. Results demonstrated that fluctuation of initial body weight causes bifurcation of hierarchies. Using the analytical approach with eq. (1.6), we showed that hierarchical bifurcation increases the variance of body weight and that $F > 1$ causes a mean value decrease of body weight. Actually, $F > 1$ means that losing a game has a greater effect than winning a game, which is not improbable.

This study includes a quantitative comparison because biological data for *Gryllus bimaculatus* are lacking. For example, we substitute τ and $r_0\alpha$ from group individuals for those values from solitary ones. Actually, $r_0\alpha$ is probably fit in solitary ones because competition might be negligible in the neighborhood of $t \approx 0$. However τ might not. We expect to perform further laboratory experiments. Several studies have examined density effects on body size[16]. We expect to perform more simulations on other animals as well.

Initial individual differences (e.g., physical structure, informational imbalance, and so on) engender further diversity with time in general terms, as shown by developmental phenomena such as those occurring through evolutionary progress.

References

1. D. Kurabayashi, K. Otogawa(2005) J. Robotics Society of jap. 23:376-382
2. A. Ishiguro(2006) Robotics and Autonomous Systems 54:641-650
3. M. Cain, et al.(2002) W W Norton & Co Ltd; 2 Rev Ed.
4. SA Adamo et al.(1995) J. Exp. Biol. 198:1691-1700
5. C. Rutte, et al (2006) Trends in Ecology & Evolution 21:16-21
6. M. Grossman , B.B Bohren (1985) J. Heredity 76:459-462
7. E. O. Wilson(1982) Sociobiology. Harvard University Press
8. M. Iba, T. Nagao, A. Urano(1995) Zool. soc. jap. 12:695-702
9. G. Merkel (1977) Occol. 30:129-140
10. L.W. Simmons (1987) J. Anim. Ecol. 56:1015-1027
11. T. Nagao (1998) Proc. 69th Anim. Meeting of the Zool. Soc. Jap. 15:89
12. G. Davidowitz , D'Amico L.J., Nihout H.F.(2003) Evol. & Devel. 5:2,188-197
13. E. Bonabeau, G. Theraulaz, J.L. DENEUBOURG (1996) Bulletin of Mathe. Biol. 58:661-717
14. L. Lacasa, B. Luque(2006) Physc. A. 366:472-484
15. Ben-Naim E., Vazquez F.,Redner S (2006) European Physc. Jour. B. 49:531
16. C. M. Dash , K. A. Hota (1980) Ecol. 61:1025-1028