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Evolution of the density response of juvenile hormone concentration in the determination of wing type

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ABSTRACT

Question: What is the evolutionarily stable density-dependent juvenile hormone concentration that determines wing type in wing-polymorphic insects?

Key assumptions: An asexual species with larval and adult stages living in many patches. Larval growth rate depends on within-patch resources that are depleted by feeding larvae. Dispersal-type adults migrate out of the natal patch just before the reproductive stage, whereas reproductive-type adults do not disperse but are more fertile than dispersal types. The proportions of the two wing types are determined by juvenile hormone concentration, which follows a normal distribution with the mean decreasing linearly with density (larval biomass per unit resource). The carrying capacity of resources fluctuates between high and low values.

Method: We studied the evolution of three quantities controlling juvenile hormone concentration: (1) baseline value of the mean, γ_0; (2) density dependence of the mean, γ_1; and (3) variance, σ^2.

Results: If γ_0 and γ_1 evolved with σ^2 fixed, juvenile hormone production was high at low density and decreased with increasing density. If σ^2 evolved with γ_0 and γ_1 fixed, the variance evolved to be smaller for larger environmental fluctuations. If all three quantities (γ_0, γ_1, and σ^2) evolved simultaneously, the variance attained a minimum value when environmental fluctuation was large. In all three cases, evolution increased the proportion of dispersal-type individuals, which increased with density in an accelerating manner.

Keywords: density response of mean juvenile hormone concentration, environmental fluctuation, juvenile hormone, resource dynamics, wing polymorphism, variance of juvenile hormone concentration.

INTRODUCTION

The adults of some species of insects have two wing types, known as wing polymorphism (Roff, 1986; Zera and Denno, 1997). The flight-capable morph has fully developed wings (macropter or alate), while the flight-incapable morph has reduced wings (brachypter) or no wings (apter) (Zera and Denno, 1997). In general, the flight-capable morph is less fecund than the flight-incapable morph (Denno *et al.*, 1989; Mole and Zera, 1993). In some species, wing type is determined

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by environmental conditions including density (Kishimoto, 1956; Sutherland, 1969a; Roff, 1986). However, determination of wing type in response to density can vary among populations (Iwanaga *et al.*, 1985, 1987). In some plant hoppers and aphids, for example, the proportion of the flight-capable morph increases at high density (Kishimoto, 1956; Sutherland, 1969a), whereas in some crickets, the proportion of the flight-capable morph decreases under similar conditions (Zera and Tiebel, 1988). In the plant hopper *Nilaparvata lugens*, determination of wing type in response to density was shown to differ between local populations (Iwanaga *et al.*, 1985, 1987; Morooka *et al.*, 1988). The results of empirical studies suggest that environmental fluctuations in habitat might be the cause of the density response (Denno *et al.*, 1991, 1996; Denno, 1994).

Theoretical studies of dispersal evolution have concluded that dispersal is favoured in fluctuating environments (Roff, 1974; Cohen and Levin, 1991; McPeek and Holt, 1992). Evolution results in changes in dispersal in response to environmental conditions, including density (Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006; Hovestadt *et al.*, 2010; Rodrigues and Johnstone, 2014). In a previous paper, we studied a mathematical model for wing-polymorphic insects, in which we considered resource dynamics and growth processes explicitly, and analysed the evolution of wing type in response to density. We showed that positive density dependence of wing determination evolved when environmental fluctuation was high and that high rates of larval growth and resource recovery discouraged the production of dispersal-type adults, whereas a high rate of mortality enhanced the production of dispersal-type adults (Kamioka and Iwasa, 2017).

Previous physiological studies have focused on juvenile hormone (JH) and ecdysone as major regulators of wing determination (Southwood, 1961; Zera and Denno, 1997). Recently, insulin signalling has also been associated with the determination of wing type (Xu *et al.*, 2015; Guo *et al.*, 2016). The relationship between JH concentration and wing determination has been studied in detail (Hardie, 1980, 1981; Iwanaga and Tojo, 1986; Zera and Tiebel, 1988; Zera and Denno, 1997; Braendle *et al.*, 2006; Schwartzberg *et al.*, 2008; Ishikawa *et al.*, 2013; Ogawa and Miura, 2014). *Nilaparvata lugens* larvae develop into a flight-incapable morph when JH concentration is above a certain threshold during the sensitive larval stage, whereas it becomes a flight-capable morph if it is below that threshold (Iwanaga and Tojo, 1986; Bertuso and Tojo, 2002; Bertuso *et al.*, 2002). In some wing-polymorphic insects, density during the sensitive period affects wing determination. There is no direct evidence to show that increased density decreases JH concentration in wing-polymorphic insects. However, the topical application of juvenile hormone or a JH analogue increases the proportion of the short-wing (or alate) type (Hardie, 1980, 1981; Iwanaga and Tojo, 1986; Zera and Tiebel, 1988; Ayoade *et al.*, 1999), and the topical application of a JH antagonist increases the proportion of the flight-capable type (Ayoade *et al.*, 1996; Bertuso *et al.*, 2002). Juvenile hormone concentration was shown to decrease in response to environmental stimulation in insects that show other types of polymorphism (Watanabe *et al.*, 2011). Thus, JH concentration is expected to decrease as larval density increases in wing-polymorphic insects showing density-dependent dispersal.

The JH concentration of a larva varies with genetic and environmental factors (Zera, 2006). Empirical studies indicate that differences in mean JH esterase activity in a population are associated with the proportion of the flight-capable type in that population (Zera and Tiebel, 1989; Zera and Holtmeier, 1992; Fairbairn and Yadlowski, 1997; Roff and Fairbairn, 1999, 2007; Zera and Huang, 1999; Zera, 2006; Zera *et al.*, 2007). These results indicate that the JH concentration of individuals is the result of adaptive evolution to environmental conditions. However, the relationship between the density response of mean JH concentration and its variance remains unclear.

Here, we discuss the evolution of the density response of JH regulation, which is important for the determination of wing type. Specifically, we consider the case in which the rate of production of the dispersal type is regulated by JH concentration, which follows a normal distribution with a fixed variance and the mean decreases linearly with increasing density. We show that large fluctuations in environmental conditions promote the evolution of strong density dependence. We also discuss how this result depends on environmental factors and on parameters related to resource dynamics and insect growth.

MODEL POPULATION DYNAMICS

We considered an asexual population of insects living in many patches. In these patches, larvae grow to adults. There are two types of adults: the ‘dispersal-type’ and the ‘reproductive-type’. Dispersal-type adults migrate out of the natal patch just before the reproductive stage; reproductive-type adults cannot disperse but are more fertile than dispersal-type adults. The proportion of dispersal-type adults is affected by JH concentration, which, in turn, is mediated by density (per unit resource) encountered in the larval stage.

Stage-structured population

The population consists of I patches. The number of insects in the ith patch is denoted by N_i^j, where j is l, d or r, which represent ‘larvae’, ‘dispersal-type adults’ and ‘reproductive-type adults’, respectively. The dynamics of the number of larvae are represented as follows:

Larvae:
$$\frac{dN_i^l}{dt} = f^r N_i^r + f^d (1-m) \frac{1}{I-1} \sum_{k \neq i} N_k^d \times (R_i/\bar{R}) - (gR_i + u)N_i^l. \tag{1a}$$

The first and second terms on the right-hand side of equation (1a) represent the reproduction of adult insects. The number of larvae in patch i increases with the number of reproductive-type adults in patch i, and the number of dispersal-type adults immigrating from other patches. Dispersal-type adults suffer dispersal mortality (m). The fecundity of reproductive- and dispersal-type adults is denoted by f^r and f^d, respectively. The number of dispersal-type adults immigrating from other patches is greater when the resources available in the focal patch outweigh those in other patches. To be specific, we here assume that resources are proportional to $R_i/\bar{R}$, where $\bar{R}$ is the average of all the patches. The third term on the right-hand side of equation (1a) represents the transition from eggs to the larval stage with growth rate gR_i. The fourth term represents the death of eggs with mortality u, which is assumed to be the same for larvae, reproductive-type and dispersal-type adults.

The dynamics of reproductive-type adults and dispersal-type adults are given as follows:

Reproductive type:
$$\frac{dN_i^r}{dt} = gR_i(1-c_i)N_i^r - uN_i^r, \tag{1b}$$

Dispersal type:
$$\frac{dN_i^d}{dt} = gR_i c_i N_i^d - uN_i^d. \tag{1c}$$

Larvae develop into the dispersal type with proportion c ($0 \leq c_i \leq 1$), and into the reproductive type with proportion $1 - c$.

Density

We assume that the density in the ith patch affects the proportion of larvae that develop into the dispersal type, c_i. Here we denote biomass by B_i, which is defined as

$$B_i = \sum_j N_i^j \omega_j, \tag{2}$$

where ω_j is body mass in the jth stage. Density in patch i is defined as the biomass per unit amount of resources, and is given by B_i/R_i.

Larval growth rate

The rate of larval growth depends on the supply of resources (R_i). The dynamics of resource abundance (R_i) is described by:

$$\frac{dR_i}{dt} = rR_i\left(1 - \frac{R_i}{K_i}\right) - gB_iR_i. \tag{3}$$

The first term on the right-hand side of equation (3) represents the growth rate of resources, and the second term on the right-hand side represents the rate of resource consumption by insects in a patch, which is proportional to the biomass of insects, B_i.

Environmental fluctuations

We assumed that the carrying capacity of resources fluctuates periodically between a high value and a low value, each lasting for time T. We also assumed that patches do not fluctuate synchronously. The ratio of these two values indicates the magnitude of environmental fluctuation.

Juvenile hormone regulating wing type

An individual's JH concentration is affected by genetic and environmental factors (Zera, 2006). In individuals collected from field populations, the activity of JH esterase, which degrades juvenile hormone, followed a continuous distribution often with a single peak and some variance (Zera and Zhang, 1995; Zera, 2006).

Here we assume that the JH concentration of individual h in patch i during the larval sensitive period tends to decrease with density in that patch. To be specific, it is given as follows:

$$JH_{i,h} = \gamma_0 - \gamma_1 (B_i/R_i) + \xi_{i,h}, \tag{4}$$

where $\xi_{i,h}$ is a random variable that follows a normal distribution with a mean of zero and variance σ^2. The JH concentration of individual h decreases linearly with density within the same patch. The mean JH concentration of individuals at very low density is denoted by γ_0, and the rate of decrease in mean JH concentration with density is denoted γ_1. Juvenile hormone concentration is also affected by several other environmental factors, including feeding opportunities, which is represented by the random variable $\xi_{i,h}$, with variance σ^2.

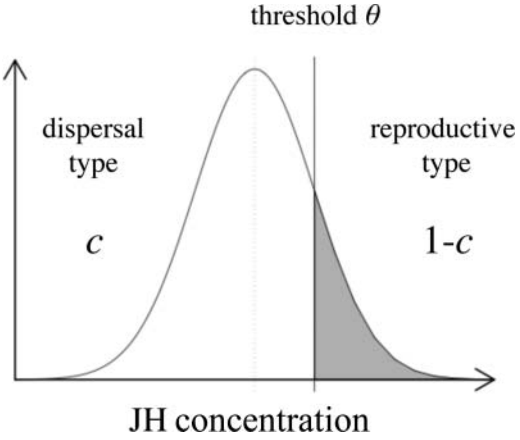

Fig. 1. Physiological process. Juvenile hormone (JH) concentration in the local population follows a normal distribution, $N(\gamma_0 - \gamma_1 B_i/R_i, \sigma^2)$. Larvae with a JH concentration above the threshold θ will develop into the reproductive type, whereas larvae with a JH concentration below the threshold will develop into the dispersal type.

Juvenile hormone concentration during the larval sensitive period for individuals in patch i follows a normal distribution, $N(\gamma_0 - \gamma_1 B_i/R_i, \sigma^2)$.

We assume that there is a threshold ($\theta = 1$) in JH concentration. Larvae with a JH concentration above the threshold will develop into the reproductive type, whereas larvae with a JH concentration below the threshold will develop into the dispersal type. A proportion c of larvae will develop into dispersal-type adults while the remainder (proportion $1 - c$) will develop into reproductive types. We summarize these assumptions in Fig. 1.

Here, we assume that γ_0, γ_1, and σ^2 are quantitative traits that evolve by natural selection.

EVOLUTIONARY DYNAMICS

We traced the evolutionary changes in three traits (γ_0, γ_1, and σ^2) that regulate JH concentration and control the proportion of larvae that develop into the dispersal type. Due to limited computational resources, we first studied the simultaneous evolution of γ_0 and γ_1 with σ^2 fixed, followed by the evolution of σ^2 with γ_0 and γ_1 fixed. Finally, we considered the simultaneous evolution of γ_0, γ_1, and σ^2. Evolutionary change was examined in the following steps:

1. *Initial population*. At first, all patches contained larvae of the resident type only with the three traits taking initial values. Then, the resident population was allowed to grow and disperse for a sufficiently long period.
2. *Introduction of a rare mutant*. Mutants were introduced into all patches at a low frequency. In the numerical analyses reported here, the initial proportion of mutants was 0.001, or 0.1% of the total population, which was common to all patches. The traits of mutants were distributed around those of the resident individuals. Specifically, we assumed that the traits of the mutant were those of the resident plus a normally distributed random variable with a mean of zero and standard deviation of 0.01.

3. *Invasibility of the mutant*. The population dynamics of the resident and the mutant were traced for a sufficiently long time. If the proportion of mutants exceeded 0.1% of the population as a whole after the evolutionary simulation runs, we judged the mutant capable of invading a population dominated by the resident. In contrast, if the proportion of mutants failed to reach 0.1% of the population as a whole, we judged the mutant to be incapable of invading the population.
4. *Simulation in the next round*. If the mutant successfully invaded the population, we considered that it would out-compete the resident and replace it. In the next round of evolutionary simulation, the mutant became the resident and a new mutant was chosen at random following the rules outlined above. If the mutant failed to invade, the resident continued as resident in the subsequent round, and a new mutant was chosen.

We repeated this procedure (i.e. generating a new mutant and examining its ability to invade or not) more than 5000 times for the evolution of mean traits γ_0 and γ_1, 1200 times for the evolution of variance σ^2, and over 30,000 times for the simultaneous evolution of γ_0, γ_1, and σ^2. After these procedures, the traits converged to a rather narrow range. We regarded this to be the evolutionary endpoint. As this procedure almost always resulted in convergence to the same set of values even when starting from different initial conditions, we concluded that this was the evolutionary endpoint. We then compared the behaviour derived from modelling with that of the organisms observed in nature.

OUTCOME OF THE EVOLUTIONARY DYNAMICS

Density-dependent juvenile hormone regulation

Below we summarize the effect of each parameter on the evolution of density-dependent juvenile hormone concentration.

Effect of environmental fluctuations

First, we studied the effect of the magnitude of environmental fluctuation on the evolution of γ_0 and γ_1 with σ^2 fixed. In these simulations, we fixed the value of the high carrying capacity (K_h) in the resource dynamics (eq. 3) while varying the value of the low carrying capacity (K_l). Figure 2a indicates the effect of ratio K_l / K_h on the standard deviation of available resources. A low K_l / K_h ratio suggests stronger environmental fluctuation. The values of γ_0 and γ_1 converged to a narrow range during the evolutionary simulation, regardless of initial values. The values of γ_0 and γ_1 averaged over the final 200 rounds of evolutionary simulation are shown in Fig. 3a.

When there was high environmental fluctuation ($K_l = 1$), both γ_0 and γ_1 evolved to be positive, while γ_0 evolved to be higher than the threshold ($\theta = 1$) value in JH concentration. When environmental fluctuation was lower ($K_l = 2$–4), both γ_0 and γ_1 evolved to be larger than when $K_l = 1$, and their values were highest when $K_l = 4$. When environmental fluctuation was markedly lower ($K_l = 5$–7), the values of γ_0 and γ_1 decreased and the fall in γ_1 was particularly pronounced (Fig. 3a). Figure 3b illustrates the functional shape of proportion c in response to density based on γ_0 and γ_1 at the evolutionary endpoint for different values of environmental fluctuation. When environmental fluctuation was high, the production of the dispersal type was low at low density, but increased rapidly as density increased. When environmental fluctuation was lower, the density above which the production of the

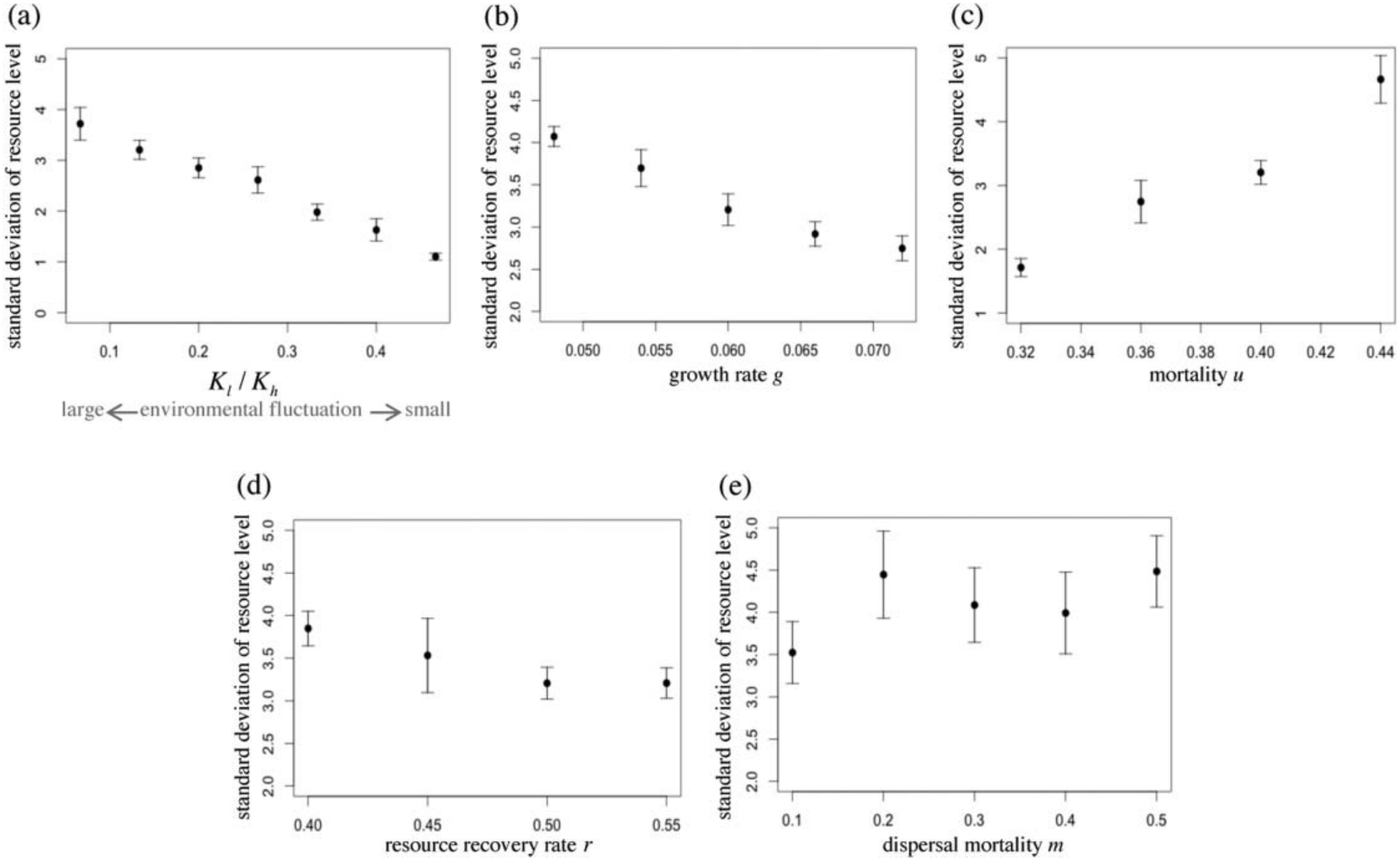

Fig. 2. Fluctuation in resources. (a) The horizontal axis represents K_l/K_h; the vertical axis shows fluctuation in resources, represented by the mean of the standard deviation of resources between years. Vertical bar represents the standard deviation of resource fluctuation between patches. (b) Growth rate, *g*. (c) Mortality, *u*. (d) Rate of recovery of resources, *r*. (e) Dispersal mortality, *m*.

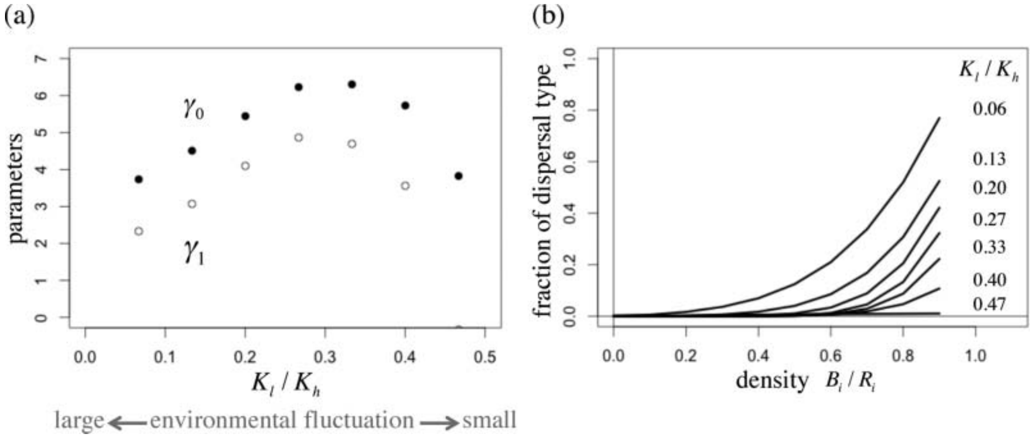

Fig. 3. Evolution of traits affecting mean JH concentration. (a) γ_0 and γ_1 for different magnitudes of environmental fluctuation. Solid circles indicate the evolution of γ_0; open circles indicate the evolution of γ_1. $\sigma^2 = 1.0$. (b) Proportion c_i of dispersal-type adults. Horizontal axis represents density. Other parameter values: $r = 0.5$, $g = 0.06$, $u = 0.4$, $m = 0.01$, $f^r = 0.9$, and $f^d = 0.6$.

dispersal type began to increase also increased, and total production of the dispersal type was reduced. When environmental fluctuation was reduced further, the proportion c in response to density became smaller. No dispersal types were produced with very low environmental fluctuation.

Second, we observed an effect of the magnitude of environmental fluctuation on the evolution of σ^2 with γ_0 and γ_1 fixed. Here, we assumed that a minimum value of σ^2 exists because very accurate regulation would require a high cost. In the evolutionary simulation, the value of σ^2 converged to a narrow range, regardless of initial values. We then calculated the average value of σ^2 over the final 200 rounds of simulation; the results are shown in Fig. 4. As the magnitude of environmental fluctuation increased, the value of σ^2 evolved

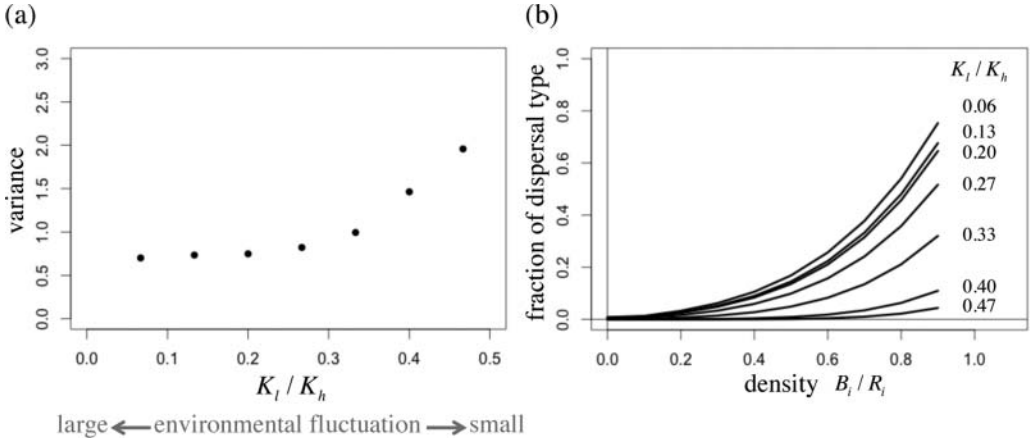

Fig. 4. Evolution of the variance in JH concentration. (a) σ^2 for different magnitudes of environmental fluctuation. $\gamma_0 = 4.0$, $\gamma_1 = 2.0$. (b) Proportion c_i of dispersal-type adults. Horizontal axis represents density for different values of σ^2. Other parameter values as for Fig. 3.

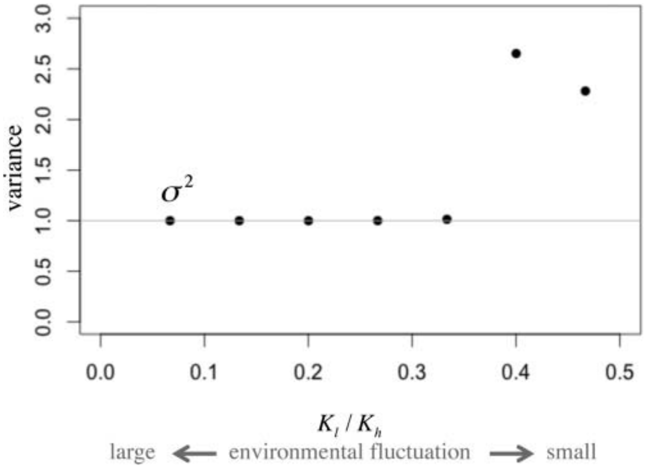

Fig. 5. Evolution of the variance in JH concentration when the mean and the variance were allowed to evolve simultaneously. Solid circles indicate the evolution of σ^2. The horizontal line indicates the minimum value of σ^2.

to be smaller (Fig. 4a). Figure 4b shows the functional shape of proportion c in response to density based on σ^2 at the evolutionary endpoint for different values of environmental fluctuation. When environmental fluctuation was high, the proportion of the dispersal type was small at low density, but increased rapidly as density increased. In contrast, when environmental fluctuation was low, the production of the dispersal type was similarly low, but the density response of the dispersal type was weak.

Finally, we observed the effect of the magnitude of environmental fluctuation for the simultaneous evolution of γ_0, γ_1, and σ^2. Due to limited computational resources, we assessed the convergence of γ_0, γ_1 for a limited number of cases. The results are shown in Fig. 5. The value of σ^2 converged to the minimum value when $K_l = 1$–4. The value of σ^2 evolved larger as K_l increased from 5 to 7.

Parameter dependence

We examined the dependence of the evolutionary outcomes of γ_0 and γ_1 on parameters affecting the resource dynamics and growth of organisms in the patch, such as growth rate (*g*), mortality (*u*), rate of recovery of resources (*r*), and dispersal mortality (*m*). Figures 2b–e show the effects of these parameters on the magnitude of fluctuation in available resources. The standard deviation of available resources was large if *g* was small, *r* was small, *u* was large, or *m* was large.

Figure 6 shows the effects of these parameters on the evolution of γ_0 and γ_1. Figure 6a shows the effect of growth rate on the evolution of γ_0 and γ_1. The horizontal axis represents growth rate (*g*) and the vertical axis γ_0 and γ_1. Parameter *g* had no effect on the evolution of γ_0, whereas γ_1 decreased with increasing *g*. Figure 6b shows the density response of the dispersal type with γ_0 and γ_1 evolving for different values of *g*. Production of the dispersal type and the density response during production of the dispersal type increased when *g* was smaller.

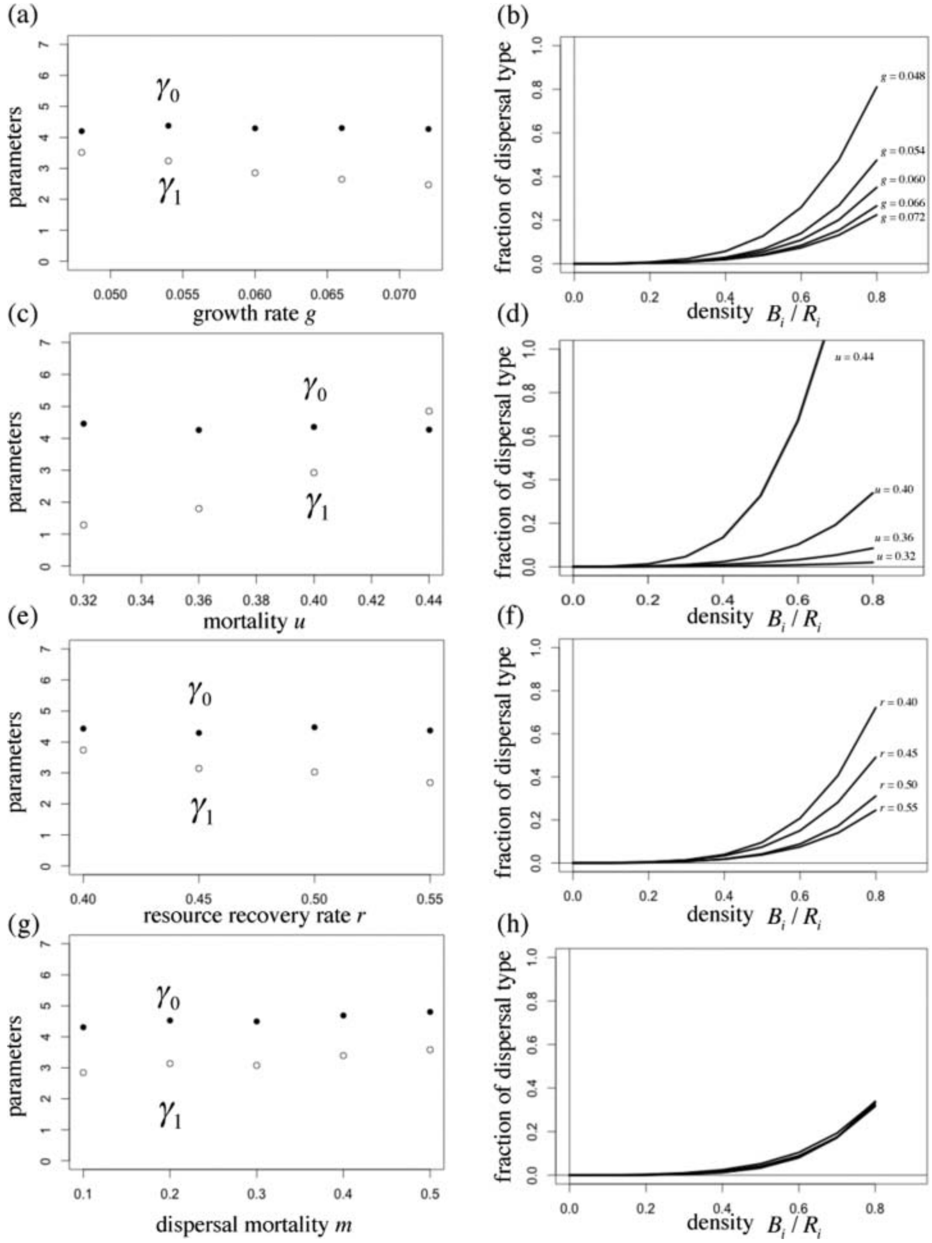

Fig. 6. Parameter dependence of the evolution of γ_0 and γ_1. (a) Solid and open circles indicate the evolution of γ_0 and γ_1, respectively. Horizontal axis represents growth rate, *g*. (b) Proportion c_i of dispersal-type adults. Horizontal axis represents density. Curves are for different *g* values. (c) Mortality, *u*. (d) Proportion c_i of dispersal-type adults. Horizontal axis represents density. Curves are for different *u* values. (e) Rate of recovery of resources, *r*. (f) Proportion c_i of dispersal-type adults. Horizontal axis represents density. Curves are for different *r* values. (g) Dispersal mortality, *m*. (h) Proportion c_i of dispersal-type adults. Horizontal axis represents density. Curves are for different *m* values. For all panels, $\sigma^2 = 1.0$. Other parameter values as for Fig. 3.

Figure 6c shows the effect of mortality (u) on the evolution of γ_0 and γ_1. At the evolutionary endpoint, parameter u had no effect on γ_0, whereas γ_1 increased with increasing u. Figure 6d shows the density response of the dispersal type during the evolution of γ_0 and γ_1. Production of the dispersal type and the density response during production of the dispersal type increased when u was large.

Figure 6e shows the effect of the rate of recovery of resources (r) on the evolution of γ_0 and γ_1. At the evolutionary endpoint, γ_0 was not affected by r; however, γ_1 decreased with increasing r. Figure 6f shows the density response of the dispersal type during the evolution of γ_0 and γ_1. Production of the dispersal type and the density response during production of the dispersal type increased when r was small.

Figure 6g shows the effect of dispersal mortality (m) on the evolution of γ_0 and γ_1. At the evolutionary endpoint, neither γ_0 nor γ_1 was affected by m. Figure 6h shows the density response of the dispersal type during the evolution of γ_0 and γ_1. Parameter m had no effect on either production of the dispersal type or the density response during production of the dispersal type.

We also examined the dependence of the evolutionary outcomes of σ^2 on parameters g, u, and r affecting resource dynamics and growth of organisms within the patch. Figure 7

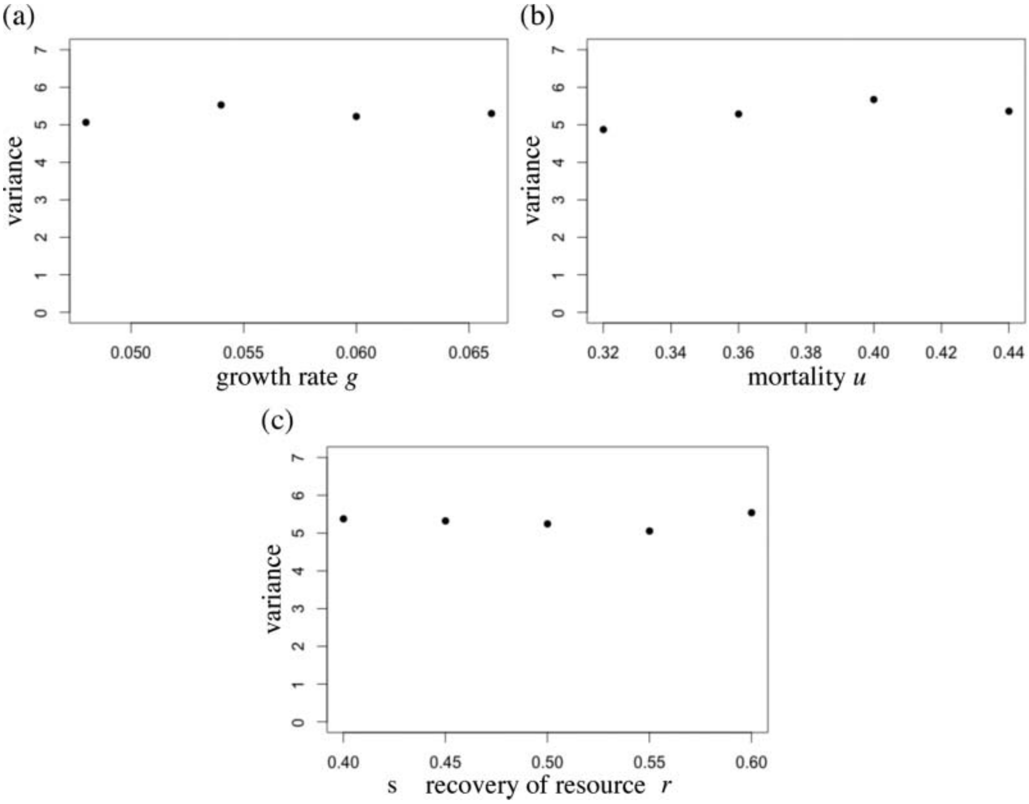

Fig. 7. The effect of growth rate, mortality, and rate of recovery of resources on the evolution of σ^2. Other parameter values as for Fig. 3.

shows the effects of these parameters on σ^2; none had any effect on the evolutionary outcome of σ^2.

DISCUSSION

Effect of environmental fluctuation

In this study, we first calculated the evolution of the mean and the variance of juvenile hormone (JH) concentration between individuals in the same patch. If mean JH concentration as a linear function of density evolved with the variance (σ^2) fixed, the baseline value of the mean (γ_0) evolved to be higher than the threshold ($\theta = 1$) value, and JH concentration decreased with density if environmental fluctuation was high. If the variance in JH concentration evolved with mean JH as a decreasing linear function of density, the variance became smaller when environmental fluctuation was high. In both cases, production of the dispersal type began to increase with density in an accelerating manner, and this response to density became stronger as environmental fluctuation became stronger.

In a previous study (Kamioka and Iwasa, 2017), we investigated the evolution of density dependence in wing-polymorphic insects without considering hormonal regulation, which mediates density in a patch and the production of the dispersal type. We demonstrated that the evolutionarily stable rate of production of the dispersal type was such that the proportion of dispersal-type adults was low at low density, but increased rapidly as density increased. The dispersal strategy we observed is consistent with the results of previous studies of density-dependent dispersal (Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006). We also showed that the density response was higher in a highly fluctuating environment than in a stable one (Kamioka and Iwasa, 2017). Therefore, the patterns of dispersal-type production observed in the present study, which considered JH concentration explicitly, are in line with those of our previous study in which density was shown to have a direct effect on the production of the dispersal type (www.evolutionary-ecology.com/data/3090Appendix.pdf, Fig. A1). Our results are also consistent with previous studies of dispersal evolution (Poethke and Hovestadt, 2002; Kun and Scheuring, 2006), in which dispersal rate was assumed to be a function of density without considering physiological mechanisms. Also, both the mean and variance of JH concentration evolved to achieve the pattern of the density response seen during production of the dispersal type. Hence, physiological studies of wing-polymorphic insects should take account not only of mean JH concentration but also the change in variance among individuals.

Parameter dependence

We also investigated the effects of growth rate and mortality of insects and the recovery of resources during evolution. If the growth rate of larvae (g) and the recovery of resources (r) were small, and the mortality of insects (m) was large, the density response of JH concentration became stronger, which resulted in a stronger density response during production of the dispersal type. We also showed that a low growth rate, high mortality rate, and low rate of recovery of resources enhanced fluctuations in resources, which also enhanced the density response of the production of the dispersal type.

Elsewhere, we studied the effects of growth rate, mortality, and rate of recovery of resources during evolution of density-dependent wing polymorphism in insects, without explicitly considering the dynamics of JH concentration (Kamioka and Iwasa, 2017). We observed that increases in growth rate and recovery of resources, and a decrease in mortality, enhanced the production of the dispersal type. The dependence of these parameters on the evolutionary outcome is in line with the model in the present study, in which JH regulation was modelled explicitly.

The relationship between JH regulation and ecological parameters, including mortality, growth of larvae, and resource recovery rate, has not previously been addressed. However, empirical research has demonstrated that the quality and nutrition of host plants have an effect on wing determination (Sutherland, 1969b; Denno *et al.*, 1986; Muller *et al.*, 2001), and that this effect differs among strains (Sutherland, 1969b). Future research should address the effect of these parameters on environmental fluctuations in a field population.

We also investigated the effect of dispersal mortality. The density response of the production of the dispersal type was not affected by dispersal mortality. High dispersal mortality enhanced the fluctuation in resources, which indicates that high dispersal mortality decreases the proportion of the dispersal type, but large environmental fluctuations offset that effect.

Some theoretical studies of the evolution of dispersal have concluded that high dispersal mortality decreases dispersal rate (Travis *et al.*, 1999; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006). However, none of these studies considered the resource dynamics or depletion by the insects explicitly. Interestingly, analysis of the model that explicitly included resource dynamics in the present study indicates that increased dispersal mortality does not always decrease the rate of dispersal.

Future work

In this study, we assumed that baseline JH concentration, the JH concentration in response to density, and the variance of JH concentration in the population evolved. The density response during the production of the dispersal type was regulated by the evolution of baseline JH concentration, the JH concentration in response to density, the variance of JH concentration, and by others factors. In this study, we did not consider the regulation of JH concentration via gene expression. Mathematical models that consider more detailed molecular mechanisms will help to further our understanding of wing-type determination in wing-polymorphic insects. Furthermore, it is possible that the sensitivity of individuals to JH concentration is affected by density, which varies in the population. Recently, the molecules that are downstream of the JH pathway, such as JH receptors, have been identified (Pursley *et al.*, 2000; Parthasarathy *et al.*, 2008). Further study is needed to determine the relative importance of JH concentration and sensitivity to juvenile hormone in wing determination.

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