The evolution of sexual difference in dispersal strategy sensitive to population density

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Abstract

Empirical studies reveal that dispersal behavior is dependent on local population density in different wild animals. Theoretical studies also pay much attention to modeling dispersal strategies sensitive to population density; however, the evolution of sex-biased dispersal has not been analyzed sufficiently by a model considering density-dependent dispersal. Therefore, a previous model where it is assumed that only genetic factors determine an individual’s dispersal timing was thoroughly modified. The resultant model assumes that dispersal timing is determined by the interaction of genetic factors with local population density and local habitat size. This model demonstrates that when females copulate before dispersal, they evolve to emigrate from their natal habitat earlier than males. A model where dispersal timing is dependent on the local sex ratio instead of population density was also analyzed. This model also results in the evolution of female early dispersal, but the resultant dispersal timing of both sexes is slightly different from the model sensitive to population density. This difference is related to sexual differences in factors affecting reproductive success. Local population density is associated with the intensity of resource competition among females, whereas local sex ratio is informative for mate competition among males.

Key words: Condition-dependent dispersal; phenotype plasticity; fluctuating environment; life history; simulation

INTRODUCTION

Many herbivores are agricultural pests. They disperse from damaged fields to the periphery and often have a serious economic impact. After the temporary elimination of pests by chemical control, herbivorous pests immigrate repeatedly from natural habitats. In particular, r-strategists spread in a short period (Wallner, 1987). Some imported herbivores have colonized almost a whole country within decades after invasion (Drew et al., 2005); therefore, understanding the evolutionary process of dispersal is useful for pest management.

Environmental conditions have an important influence on the dispersal decision over different taxa (Lambin et al., 2001). Theoretical models should incorporate condition-dependent dispersal into the discussion of the evolution of dispersal. Recently, much attention has been paid to theoretical models analyzing dispersal strategies sensitive to population density (Poethke and Hovestadt, 2002); however, the evolution of sex-biased dispersal has not been analyzed sufficiently using a model considering density-dependent dispersal.

Sex-biased dispersal is common among dispersing species, although the dispersing sex is different among species (Dobson, 1982; Greenwood and Harvey, 1982). Several theoretical studies have discussed the evolutionary process of sex-biased dispersal (Gandon, 1999; Perrin and Mazalov, 2000; Hirota, 2004); however, those models assumed that the dispersal rate and timing was determined completely by genes and ignored the phenotype plasticity sensitive to fluctuating conditions of the natal habitat. In the present study, therefore, previous models (Hirota, 2004, 2005) were thoroughly modified to evaluate whether sex-biased dispersal evolves, even when the dispersal pattern is determined not solely by genes but by the interaction of genetic factors with local population density.

Previous models (Hirota, 2004, 2005) demonstrated that pre-dispersal copulation facilitated the
evolution of female-biased dispersal under the fluctuating environment. Females should migrate and reproduce over habitats to spread their risk due to environmental fluctuation. On the other hand, males do not necessarily disperse, because their risk is spread by the dispersal of mating partners. Particularly when the dispersal cost is high, males should invest more reproductive effort in copulation in the natal habitat than in dispersal.

In the current model, the genetic system underlying dispersal behavior is designed based on Poethke and Hovestadt’s model (2002). This model defines that dispersal timing is a plastic phenotype sensitive to the population density and relative size of the natal habitat. Clutch size, dispersal mortality and mean patch capacity were varied in a number of simulation experiments. These experiments show that, even for a broad range of parameters, pre-dispersal copulation is always a sufficient condition for the evolution of sexual difference in density-dependent dispersal. In addition, the models are analyzed considering the phenotype plasticity to local sex ratio instead of population density and the sexual difference in response to the conditions of local habitats is discussed.

MODELS

The current model is an individual-based model simulating the evolution of dispersal strategies in a metapopulation. The generation is assumed to be discrete. Individual life history is shown in Fig. 1 and is based roughly on the life history of herbivorous insects (Hirota, 2004). Each component of the life history is accounted for as follows.

Dispersal. Individuals are assumed to disperse once in a lifetime towards an adjacent habitat. The dispersal direction is determined randomly, since it is assumed that individuals can not predict the population density of habitats except for the natal site before dispersal. Random numbers are generated by Mersenne Twister algorithm, as are the following processes (Matsumoto and Nishimura, 1998). In order to eliminate the difference in selection pressure between edge habitats and internal habitats, edge habitats at the opposite side are linked together. To evaluate the influence of dispersal cost, individuals are assumed to die at a constant rate by dispersal from the natal habitat to the next habitat. The mortality associated with dispersal (μ) is set as 0.0, 0.2, 0.4 or 0.8.

Four different diploid loci are responsible for dispersal behavior. Two loci are relevant to density dependence (p_{C_{m}}, p_{C_{t}}), and the other loci are relevant to patch-size dependence (p_{K_{m}}, p_{K_{t}}). P_{C_{m}} and P_{K_{m}} are expressed only in males, whereas p_{C_{t}} and p_{K_{t}} are expressed only in females. Dispersal timing (d) is determined by nonlinear model of Poethke and Hovestadt (2002):

\[
d = \begin{cases} 
0 & \text{if } C_{i} \leq C_{ih} \\
1 - (p_{C_{j}} - p_{K_{j}}/k_{j})/C_{i} & \text{if } C_{i} > C_{ih} \text{ and } C_{ih} > 0 \\
1 & \text{if } C_{ih} = 0 
\end{cases}
\]

with \( C_{i} \) = population density in patch \( i \), \( k_{i} = K_{i}/K_{\text{mean}} \) relative capacity of patch \( i \), \( K_{i} \) = capacity of patch \( i \), \( K_{\text{mean}} \) = mean capacity of patches in the landscape, and \( C_{ih} = p_{C_{j}} - (p_{K_{j}}/k_{j}) \) patch-size-dependent threshold density. d-value ranges from 0 to 1. When d = 0, individuals remain in the natal habitat and do not emigrate. When d = 1, males and females emigrate from the natal habitat just after sexual maturation and after copulation, respectively. When 0 < d < 1, they spend 1 − d of their lifetime in the natal habitat and spend d in the destination habitat after dispersal.

The individual values for \( p_{C_{j}} \) and \( p_{K_{j}} \) are determined by the arithmetic mean value of the two cor-
responding alleles. At initiation, the $p_{C,i}$ value is selected randomly from 0.00 to 2.00, and the $p_{K,i}$ value is selected randomly from -2.00 to 2.00. The values for these alleles are changed by mutation with a probability of $m$. The values of alleles are modified by a value drawn with uniform probability from an interval between -0.1 and +0.1. To promote greater variability of genotypes in the early generations and to reduce the influence of mutations on the stability of the final result, mutation rates are decreased exponentially from 0.1 to <0.0001 over the course of the simulation experiments:

$$m(t) = 0.1 \times \exp(-2.5 \times 10^{-4} t)$$

where $t$ is the generation number.

In addition, the model where the local sex ratio ($R_i$) is substituted for local population density ($C_i$) was also analyzed, since recent theoretical studies suggest that sex ratio is an important factor in the evolution of the dispersal pattern (Leturque and Rousset, 2004). $R_i$ is defined as having a similar range as $C_i$:

- Male: $R_i = (m_i + 1)/(f_i + 1)$
- Female: $R_i = (f_i + 1)/(m_i + 1)$

where $m_i$ and $f_i$ are the number of males and females born in the $i$-th patch, respectively. The model using $R_i$ is analyzed separately from that using $C_i$.

**Copulation.** Females are assumed to be monogamous. Females always copulate in the natal habitat before dispersal. A mating partner is selected from males that invest reproductive efforts in the females’ natal habitat. Although the mating partner is selected randomly, the competitive weight of males depends on the dispersal timing. The competitive weight increases with the time males spend in the habitat; that is, males who spend their life in a habitat will encounter females twice as frequently as males who spend half their life in the same habitat. In contrast to females, males are assumed to be polygamous, as observed in different taxa (Clutton-Brock, 1989; Ridley, 1990).

Since females are monogamous, late-dispersing males hardly encounter virgin females in the destination patches when adult emergence timing is synchronized with a metapopulation; however, larval development and adult emergence vary among individuals under laboratory conditions. In the field, the microclimate and habitat quality cause a large variance of adult emergence timing even within a generation. Consequently, late-dispersing males can also mate with females who emerge late; therefore, it is assumed that males can copulate in the destination patch after dispersal in the current models.

**Oviposition.** The clutch size ($\lambda$) is set as 3, 6 or 10. Females allocate their offspring before and after dispersal according to dispersal timing ($d$). When $d=0$, females reproduce all offspring in the natal habitat. When $d=1$, all offspring are reproduced after dispersal. When $0<d<1$, females reproduce $\lambda(1-d)$ offspring in the natal habitat and the rest ($\lambda d$) in the destination habitat after dispersal. The birth sex ratio is even, and offspring are male at the probability of 0.5. Four loci are segregated independently. Offspring develop into mature individuals with a density-dependent survival probability $s$:

$$s = \left(1 + \frac{\lambda(1-d)O_i}{\lambda K_i}\right)^{-1}$$

with $O_i$=offspring number in patch $i$.

The carrying capacity of each patch ($K_i$) is set randomly from certain ranges and changes with the alternation of generations. The range of $K_i$ is set as 1-19 (10), 1-99 (50) or 1-199 (100), where the numbers in parentheses are $K_{mean}$. To eliminate the influence of genetic drift, the overall metapopulation size is maintained almost the same among different $K_{mean}$ by adjusting the number of patches. When $K_{mean}$ is 10, 50 and 100, a metapopulation consists of $16 \times 16$, $7 \times 7$ and $5 \times 5$ local populations, respectively.

In the first generation, individuals of $K_{mean}$ are allocated to each habitat at an even sex ratio. Simulation is terminated at the 30,000th generation, since genetic parameters, $p_{C,i}$ and $p_{K,i}$, are stable after 20,000 or more generations. It is difficult to interpret the absolute values of $p_{C,i}$ and $p_{K,i}$, since individual $d$-values are determined by the interaction of both values with a local population density or sex ratio and relative carrying capacity, which fluctuate temporally (Poethke et al., 2003); therefore, mean $d$-values at 30,000th generation were used for statistical analysis. The simulation was replicated 10 times for each condition.

The resultant data were analyzed by linear model using statistical software R (R Development Core Team, 2006). The sexual difference of mean dis-
persal timing \((d_i - d_m)\) was considered as a dependent variable. Arcsine transformation is not applied to \(d_i - d_m\) because the \(d\)-value is not proportionate, \(d_i - d_m\) ranges to less than zero, and false interactions are often detected after angular transformation (Kasuya, personal communication). \(\mu\), \(\lambda\), \(K_{\text{mean}}\) and model type (using local density or sex ratio) were used as independent variables. The stepwise procedures selected a linear model whose AIC was lowest.

RESULTS

When the mean capacity (\(K_{\text{mean}}\)) and clutch size \(\lambda\) are small and dispersal cost \(\mu\) is high, metapopulations collapse in the early generation (Figs. 2 and 3). This is because a small \(\lambda\) slows down population growth, small \(K_{\text{mean}}\) enhances the extinction of patches, and high \(\mu\) reduces the chance of recolonization. Consequently, the extinction rate exceeds the immigration rate, and then a whole metapopulation becomes extinct.

When metapopulations are maintained long term, females evolve to disperse earlier than males under most conditions (Fig. 2). By contrast, males remain philopatric for a large part of their life and invest large reproductive effort in the natal habitat (Fig. 2), particularly when dispersers are put at mortal risk \((\mu \geq 0.2)\) and the mean capacity is large \((K_{\text{mean}} \geq 50)\). This tendency is consistent with the model considering a plastic phenotype sensitive to local sex ratio in stead of population density (Fig. 3).

The sexual difference in dispersal timing \((d_i - d_m)\) is slightly different between the two mod-

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**Fig. 2.** Mean dispersal timing \((d)\) at 30,000th generation under different conditions in the model considering phenotypic plasticity to local population density. Larger \(d\)-value shows earlier dispersal. Open and filled circles represent males and females, respectively. Error bars are unbiased standard deviations. The number in parentheses is the frequency of a whole metapopulation collapsing in the early generation in ten replications.

**Fig. 3.** Mean dispersal timing \((d)\) at 30,000th generation under different conditions in the model considering the phenotypic plasticity to local sex ratio. Larger \(d\)-value shows earlier dispersal. Open and filled circles represent males and females, respectively. Error bars are unbiased standard deviations. The number in parentheses is the frequency of a whole metapopulation collapsing in the early generation in ten replications.
els. When $\mu$ is small, males emigrate later in the model sensitive to population density than in the model sensitive to sex ratio, whereas female dispersal timing does not differ so largely between those models (Figs. 2 and 3). As a consequence, $d_f - d_m$ is larger in the former than the latter model. On the other hand, when $\mu$ is large, female dispersal timing is slightly earlier in the former model; nevertheless, $d_f - d_m$ is not largely different between models (Figs. 2 and 3). These results are consistent with the statistical model selected by stepwise linear models. Interactions among individual variables have a significant influence on $d_f - d_m$.

**DISCUSSION**

The early dispersal of females evolved in the current models assuming that individuals regulate dispersal timing according to the conditions of local populations, as observed in previous models that do not assume such a plastic phenotype (Hirota, 2004, 2005); however, the resultant dispersal timing is different among the previous and current models. This difference is caused by phenotype plasticity which realizes an adaptive dispersal pattern according to local conditions, and the sexual difference in essential factors affecting reproductive success. It is discussed how these factors affect the dispersal timing in the model sensitive to population density and to sex ratio, respectively.

**Dispersal strategy sensitive to local population density**

Under natural conditions the carrying capacity of habitats changes temporarily. The carrying capacity often fluctuates unpredictably, particularly when habitat conditions are dependent on many environmental factors. This study assumed that local carrying capacities change between generations. Consequently, individuals experience different local population densities between before and after sexual maturation. If a small number of individuals are born in the high quality patch, local population density is so low that resource competition is moderate and many of them can survive to adults; however, the quality of the same patch deteriorates before the generation of their offspring, and a large number of adults suffer from strong competition for offspring resources. By contrast, if patch quality is improved between generations, resource competition is relaxed among adults.

In previous models which assumed that dispersal timing is determined solely by genetic factors (Hirota, 2004, 2005), individuals could not respond immediately to temporal changes of local population density. In those models, maladaptive dispersal behaviors are often observed in a fluctuating environment, although the selected genetic traits are adaptive in the long term. On the other hand, in the current model, dispersal timing was determined by the interaction of genetic traits with local population density and patch size; therefore, even after genetic traits are fixed by stabilizing selection, individuals emigrate from the natal habitat at different times according to local conditions. In the present model, the variance of female dispersal timing at the 30,000th generation, when genetic variance is extremely low, is certainly larger than in previous models (Hirota, 2005); however, the variance of male dispersal timing is not so different from the previous model.

Local population density has a more important influence on female reproductive success than male mating success. In order to increase the survival rate of offspring, adult females should reproduce in patches where resources for offspring are abundant and female competitors are few. Consequently, female dispersal timing varies according to local population density. On the other hand, male mating success is dependent on the ratio of receptive females to male competitors, but not on the resource of offspring. Since in the current model the birth sex ratio is even and females always mate before dispersal, males are most likely to copulate at least once in the natal habitat regardless of local population density. Male reproductive success is also dependent on the survival rate of their offspring as well as the mating success; however, the mating partners of males emigrate after copulation and allocate their offspring to different patches. Consequently, males do not need to emigrate themselves, especially when dispersal is costly; therefore, mating dispersal timing does not vary significantly.

**Dispersal strategy sensitive to local sex ratio**

When dispersal timing is assumed to depend on the local sex ratio rather than population density, the resultant dispersal pattern is slightly different. When $K_{\text{mean}}$, $\mu$, and $\lambda$ are small, males emigrate
early and the variance of their dispersal timing is large. In the current model, the birth sex ratio was even, but individual sex is determined stochastically and the local sex ratio varies in a small population. When $K_{\text{mean}}$ is small, consequently, the local sex ratio is often biased and therefore male dispersal timing varies. Particularly when males are born in patches where there are no females, they can not encounter mating partners without emigrating, since females were assumed to copulate only in the natal habitat in the present study; therefore, males emigrate from the natal patch earlier when $K_{\text{mean}}$ is small. Small clutch size ($\lambda$) increases the variance of the local sex ratio, and small dispersal cost ($\mu$) facilitates male dispersal; thus, males can undergo adaptive dispersal by phenotypic plasticity to local sex ratio.

On the other hand, local sex ratio is not such an important factor for female reproductive success. Although the sex ratio correlates roughly with the number of females, it is not a good indicator of the ratio of female competitors to available resources for their offspring. Resource competition is not strong among adult females even in female-biased patches, unless the local population density is high; thus, local sex ratio is not informative for females to realize an adaptive dispersal strategy. Consequently, the resultant female dispersal timing is not largely different from the previous model where dispersal timing was determined solely by genetic factors.

**Implications for application**

Sexual differences and condition dependence on dispersal are important factors for pest management. In species with sedentary larvae, but not dispersing adults, that damage crops, such as lepidopterans, the dispersal of adult females is mainly responsible for expansion of the areas damaged by larvae. Although the dispersal of adult males reduces the inbreeding risk, female dispersal is more essential for larval distribution in the next generation. Consequently, the female dispersal rate should be paid more attention than the net dispersal rate. When pest dispersal is sensitive to local conditions, understanding the proximal factors stimulating emigration is useful for expecting the spatial distribution of pests. A shortage of food plants and essential nutrients results from strong intraspecific competition in high-density local populations. A shortage of proteins and salts facilitates mass migration in Mormon crickets (Simpson et al., 2006). The availability of pheromones and the encounter rate with other individuals are also possible indicators of population density. As a result of interspecific competition, predation and parasitism, the population density of other species is also a considerable factor to influence the dispersal behavior. Further empirical studies are necessary to reveal the cues stimulating pest dispersal, and further theoretical studies also suggest how these factors are utilized for pest management.

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**REFERENCES**


Sex-Specific Dispersal and Local Density


R Development Core Team (2006) *R: A Language and Environment for Statistical Computing.* Vienna, Austria.

