Persistence conditions of symmetric social hybridogenesis in haplo-diploid hymenoptera

Atsushi Yamauchi*, Norio Yamamura

Center for Ecological Research, Kyoto University, Hirano 2-509-3, Otsu 520-2113, Japan

Abstract

In eusocial Hymenoptera species, females variably develop into either alate females (queens) or workers, and in most cases, caste differentiation is determined environmentally. Recently, however, female castes in two harvester ant species, *Pogonomyrmex rugosus* and *P. barbatus*, were found to be determined genetically in hybrid zones of these two species. In the hybrid populations, homozygous females (e.g. *AA* or *BB*) and heterozygous females (*AB*) develop into alate females and workers, respectively. This genetic caste determination system is called symmetric social hybridogenesis (SSH). It is clear that populations with SSH can persist only if all four genotypes (*AA* and *BB* females, and *A* and *B* males) coexist simultaneously. However, it is not obvious that these populations are always persistent when the four genotypes simultaneously exist. Here, we examined the stability and persistence of an SSH population using a simple mathematical model. According to the analysis of the model, the SSH population persists only when some conditions are satisfied: (1) each female mates with more than two males, and (2) male production increases less steeply than linearly with increasing numbers of workers in a colony, and alate female production increases more steeply than linearly with increasing numbers of workers, or (2′) male production increases more steeply than linearly with increasing numbers of workers in a colony, and alate female production increases much more steeply than male production. Therefore, it is not obvious that SSH populations are maintained and are stable for long periods. We discuss whether these conditions are satisfied in real SSH populations.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: Symmetric social hybridogenesis; Harvester ant; Genetic caste determination; Population dynamics

1. Introduction

Hymenoptera species generally have a haplo-diploid sex determination system in which unfertilized haploid eggs develop to male individuals, and fertilized diploid eggs become females. In eusocial species, females variably develop into either alate females (next generation queens) or workers. In most species, differentiation of the female caste is determined environmentally, for example, by food or nutrient supplies. Recently however, the determination of female castes in some species was found to occur by other mechanisms. For example, in local populations of the ant *Cataglyphis cursor*, the female caste is determined via the maternal reproduction mode, such that workers and

new queens result from sexual reproduction and parthenogenesis, respectively (Pearcy et al., 2004).

On the other hand, in the harvester ant species *Pogonomyrmex rugosus* and *P. barbatus*, female caste is determined genetically in hybrid zones of these two species (Helms Cahan et al., 2002; Julian et al., 2002; Ashe and Oldroyd, 2002; Volny and Gordon, 2002). These species possess marker loci for caste determination. In allopatric areas where one species lives in the absence of the other, female caste is not determined genetically; the marker loci are homo- and heterozygous independently of female caste. In contrast, in sympatric areas where both species cooccur, female caste in both species is clearly determined genetically; the marker loci are homozygous in alate females and heterozygous in workers. Parker (2004) termed this genetic caste determination system 'symmetrical social hybridogenesis' (SSH). Helmes Cahan and Keller (2003) showed that this system evolved through hybridization events

*Corresponding author. Tel.: +81 77 549 8259; fax: +81 77 549 8201.
E-mail address: a-yama@ecology.kyoto-u.ac.jp (A. Yamauchi).

between *P. rugosus* and *P. barbatus*, resulting in four hybrid lines, H1, H2, J1 and J2. According to phylogenic analysis, H1 and J1 are closely related to *P. rugosus*, while H2 and J2 are closely related to *P. barbatus*. Crosses between the lineages H1 and H2 and between J1 and J2 tend to give rise to workers only, whereas mating within the lineage tends to produce alate females only.

The genetic background of SSH can be schematized as follows (Helms Cahan et al., 2002; Julian et al., 2002; Ashe and Oldroyd, 2002; Volny and Gordon, 2002). Consider two types of genomes, *A* and *B*. Because the Hymenoptera possess a haplo-diploid sex determination system, individuals with haploid genotypes *A* or *B* are male, while those with diploid genotypes *AA*, *BB* or *AB* are female. In the SSH system, *AB* females become workers, while *AA* and *BB* females become alate females. Accordingly, colonies founded by *A* male(s) and an *AA* female (or by *B* male[s] and a *BB* female) can neither grow nor reproduce because they cannot produce workers with the *AB* genotype. To found a colony containing both daughter queens and daughter workers, a mother queen must mate multiple times with both *A* and *B* males.

Parker (2004) pointed out that this system requires four types of reproductive individuals (*A*, *B*, *AA* and *BB*) to maintain the population, and considered the SSH system as a new sexual system involving more than two sexes. It is explicit that all four genotypes (*A*, *B*, *AA* and *BB*) are necessary for maintenance of the population under SSH. However, it is not obvious that the population is always persistent when the four genotypes exist simultaneously. Since the SSH system is observed only in a hybrid zone of two species, gene flows from original allopatric populations may be intuitively considered to play an important role in its maintenance. However, remarkably, mating between *AA* (or *BB*) queen and *A* (or *B*) male reproduces both alate females and workers in original populations, but alate female only in SSH populations. This indicates that the original strains have different genes from SSH strains, which allows homozygous females (*AA* or *BB*) to develop into workers. Accordingly, the gene flows would alternate reproduction pattern in SSH system, probably resulting in a degeneration of the system. Our interest here is the possibility of maintenance of SSH, assuming no effective gene flows from the original populations. We examine the condition for the maintenance by investigating the stability and persistence of an SSH population using a simple mathematical model.

2. Mathematical model

We considered an SSH species with a haplo-diploid sex determination system with two genomes, *A* and *B*. The combination of these genomes determines female caste, where *AA* and *BB* individuals are reproductive females, and *AB* individuals are workers. We were unable to locate a paper that precisely reported the number of colony founders in *P. rugosus* and *P. barbatus*. However, Johnson (2004) stated that in *Pogonomyrmex*, colony foundation by

multiple females was observed only in local populations of *P. californicus*. This implies that colonies are mainly founded by a single female in *P. rugosus* and *P. barbatus*. We also assumed that mating between an *A* (or *B*) male and a *BB* (or *AA*) female never produces alate females. According to crossing experiments, alate females rarely arise from mating between lineages (Julian et al., 2002; Helms Cahan et al., 2002; Helmes Cahan and Keller, 2003). If such rare events were effective in producing progeny, the established lineages could disappear gradually due to mixing of the genomes. The fact that there are clear lineages without mixtures implies that production of alate females by inter-lineage mating does not play an important role in natural environments. Accordingly, in this analysis, we ignored production of queens by mating between lineages. In addition, we assumed that an increment in the worker fraction in a colony positively affects production of both alate females (queens) and males (kings).

Thus, we characterized the population by the following life history: (1) a female founds a colony following multiple matings with k males, (2) the female produces m sons (alate males) and n daughters (alate females + workers) in the colony, (3) if sperm includes both *A* and *B* genotypes, daughters comprise qn alate females (*AA* or *BB* genotypes) and $(1-q)n$ workers (*AB* genotypes), (4) the production of alate females or males in the colony increases with the number of sister workers in the colony, of which the functional form is represented by $\alpha\{(1-q)n\}^{\beta}$, (5) the number of colonies (i.e. queens) in the habitat can not exceed a carrying capacity, K.

In the model, we assumed that the fractions of alate females and workers in the colony (q and $1-q$, respectively) proportionally reflect the fraction of sperm genotypes that are provided by k parent males. If a colony is originated by jA and $k-jB$ fathers, $q=j/k$ and $1-q=(k-j)/k$ when the mother is *AA*, whereas $q=(k-j)/k$ and $1-q=j/k$ when the mother is *BB*. It should be remarked that the fraction of *A* and *B* genotypes in fathers (j and $k-j$) follows a random, i.e. binomial distribution. Before mating of generation t, the numbers of *AA* and *BB* queens and *A* and *B* males in the population are denoted as $F_A(t)$, $F_B(t)$, $M_A(t)$ and $M_B(t)$, respectively. After mating, the queens found colonies, and all males die after contributing to sperm to the queens' spermathecae. At colony foundation, if the total number of queens (i.e. number of colonies in the habitat) exceeds the carrying capacity, K, the queen number is regulated at the carrying capacity. Accordingly, the numbers of females change as

$$F'_A = \begin{cases} F_A(t) & \text{if} \quad F_A(t)+F_B(t) \leqslant K, \\ \dfrac{F_A(t)}{F_A(t)+F_B(t)}K & \text{if} \quad F_A(t)+F_B(t) > K, \end{cases} \quad \text{(1a)}$$

$$F'_B = \begin{cases} F_B(t) & \text{if} \quad F_A(t)+F_B(t) \leqslant K, \\ \dfrac{F_B(t)}{F_A(t)+F_B(t)}K & \text{if} \quad F_A(t)+F_B(t) > K. \end{cases} \quad \text{(1b)}$$

Because surviving females reproduce, consuming sperm stocked in the spermatheca, the numbers of new alate

females and males can be formulated by

$$F_A(t+1) = \sum_{j=0}^{k-1}\left\{\alpha\left(\frac{k-j}{k}n\right)^{\beta_f}\left(\frac{j}{k}n\right)F'_A P(k,j)\right\}, \quad (1c)$$

$$M_A(t+1) = \sum_{j=0}^{k-1}\left\{\alpha\left(\frac{k-j}{k}n\right)^{\beta_m}mF'_A P(k,j)\right\} \quad (1d)$$

$$F_B(t+1) = \sum_{j=1}^{k}\left\{\alpha\left(\frac{j}{k}n\right)^{\beta_f}\left(\frac{k-j}{k}n\right)F'_B P(k,j)\right\}, \quad (1e)$$

$$M_B(t+1) = \sum_{j=1}^{k}\left\{\alpha\left(\frac{j}{k}n\right)^{\beta_m}mF'_B P(k,j)\right\}, \quad (1f)$$

where

$$P(k,j) = {}_kC_j\left(\frac{M_A(t)}{M_A(t)+M_B(t)}\right)^j\left(\frac{M_B(t)}{M_A(t)+M_B(t)}\right)^{k-j}. \quad (1g)$$

Here, β_f and β_m represent the worker dependency of the production of alate females and males, respectively. $P(k,j)$ represents a probability that among all k fathers, j males possess genotype A, and $k-j$ possess genotype B.

We analyzed the properties of these dynamics; for some special cases, we could obtain important characteristics of the dynamics. With either $\beta_f = 1$ or $k = 2$, the dynamics always satisfy $F_A(t+1)/\{F_A(t+1) + F_B(t+1)\} = F_A(t)/\{F_A(t) + F_B(t)\}$. This implies that the ratio of AA and BB queens is constant over generations, maintaining the initial ratio. However, in general cases (i.e. $\beta_f \neq 1$ and $k \neq 2$), the dynamic characteristics of this system cannot be derived analytically. Consequently, we examined the behavior of the system using computer simulations. The above result suggests that the behavior is critically influenced by a level of multiple mating, k, and worker dependency of the production of reproductive castes β_f and β_m. Accordingly, we investigated characteristics of the dynamics by varying the parameters k, β_m and β_f.

Fig. 1 summarizes consequences of simulations with various combinations of k, β_m and β_f. In this figure, white
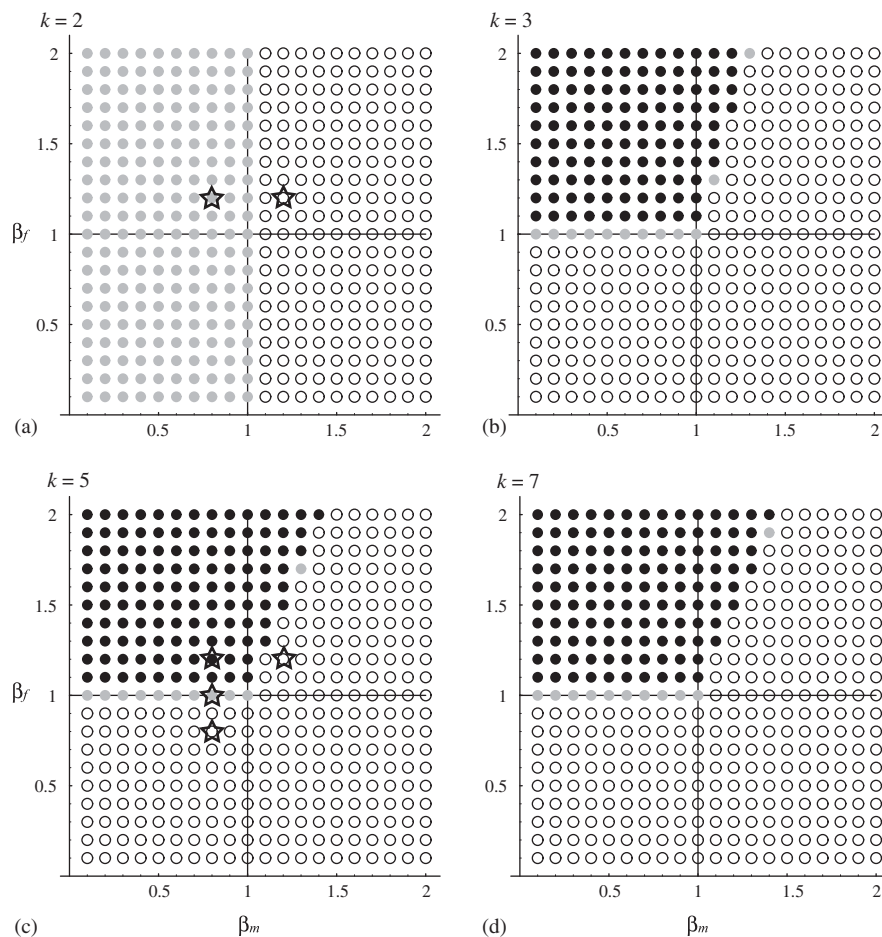

Fig. 1. Classification of parameter regions that result in different consequences. White circles indicate extinction of population, while both gray and black circles represent persistence of SSH population. At gray circles with $\beta_m \leqslant 1$, the population persists, maintaining the initial frequency of queen genotypes. On the other hand, at gray circles with $\beta_m > 1$, the population persists with continuous oscillations of genotypic frequencies of both male and queen around 0.5. At black circles, the population persists, with convergence of the genotypic frequency of both queens and males to 0.5. Stars indicate that substantial dynamics are illustrated in the following figures under those parameter sets.

circles indicate extinction of SSH population, while both gray and black circles represent persistence of the population. It is remarkable that there are two patterns in cases where SSH population persists. Under parameter sets of black circles, the population persists with convergence of the genotypic frequency of both queens and males to 0.5. On the other hand, under parameter sets of gray circles with $\beta_m \leqslant 1$, the population persists, maintaining the initial frequency of queen genotypes.

In follows, substantial dynamics are shown for parameter sets that are marked by stars in Fig. 1. First, we examined dynamics with $k = 2$, where a single queen mates with exactly two males. According to Fig. 1a and additional simulations, in this case, qualitative characteristics of the dynamics change with varying worker dependency of male production β_m, but not with that of alate female production, β_f. Fig. 2a illustrates a typical consequence with $\beta_m \leqslant 1$, where the population persists, remaining at the initial frequency of queen genotypes. In contrast, Fig. 2b shows a consequence with $\beta_m > 1$, in

which male genotypic frequency oscillates with growing amplitude over generations, resulting in complete alternation of the dominant male genotype, and extinction due to the absence of colonies including both alate females and workers.

Next, we assumed that a single queen mates with more than two males ($k > 2$). In Fig. 1b–d, white circles represent extinction of SSH population with $k > 2$. According to simulations, however, there are two different patterns in extinction in such cases, depending upon whether β_m is smaller than 1 or not. Fig. 3a illustrates a typical dynamic pattern with $\beta_m < 1$, where the initially small asymmetry of the allelic ratio gradually grows and one allele is finally lost, resulting in population extinction due to the absence of heterozygous workers. In contrast, Fig. 3b indicates a typical dynamic pattern with $\beta_m \geqslant 1$, where an amplitude of oscillations in male genotypic frequency grows with generations. After many generations, the dominant male genotype completely alternates every generation, resulting in extinction due to the absence of colonies including both
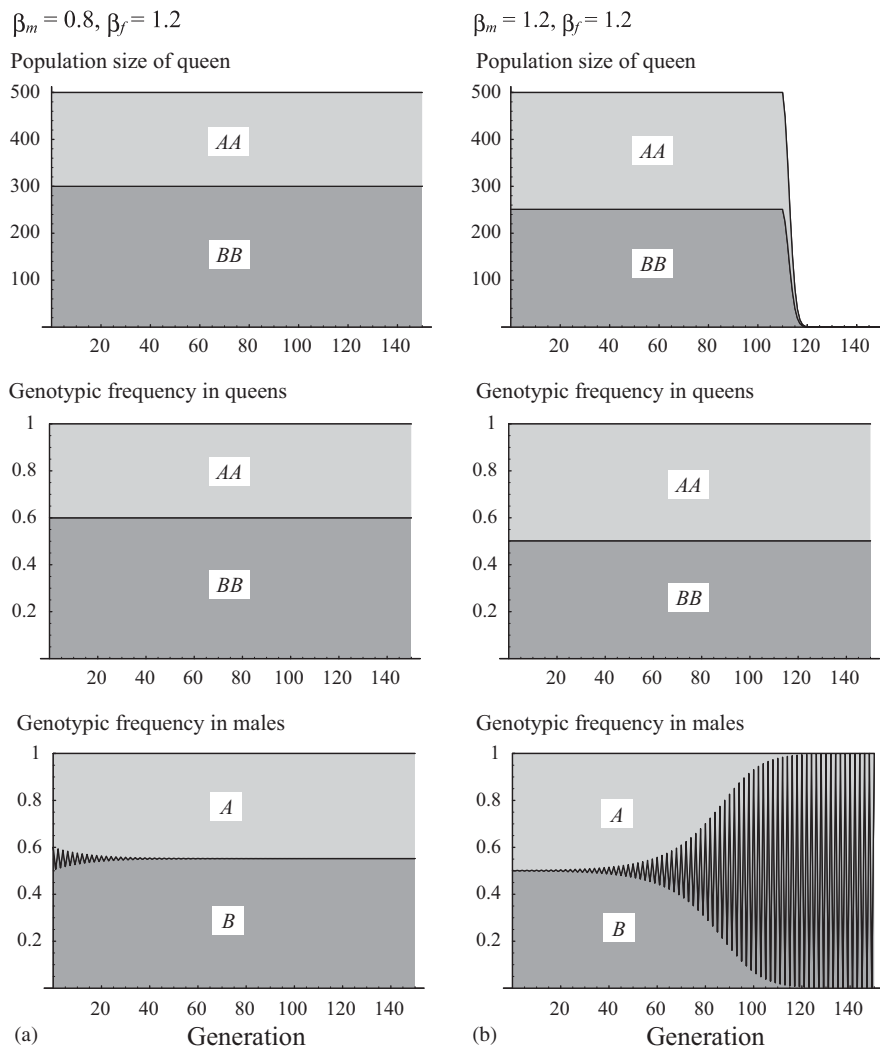

Fig. 2. Typical population and genotypic dynamics with $k = 2$, in which combinations of β_m and β_f correspond to stars in Fig. 1a. Parameter set is $n = 30$, $m = 10$, $\alpha = 0.1$ and $K = 500$.

$\beta_m = 0.8, \beta_f = 0.8$

Population size of queen

$\beta_m = 1.2, \beta_f = 1.2$

Population size of queen

Genotypic frequency in queens

Genotypic frequency in queens

Genotypic frequency in males

Genotypic frequency in males
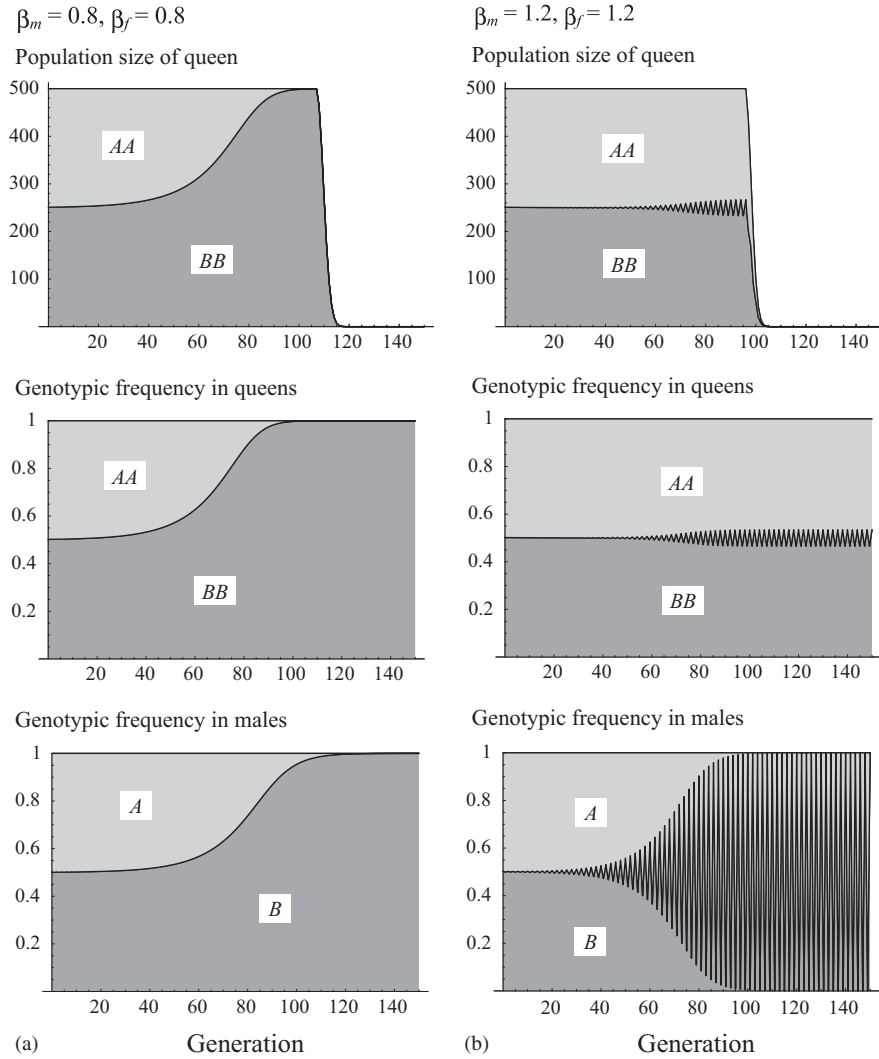
(a)   Generation

(b)   Generation

Fig. 3. Typical population and genotypic dynamics with $k = 5$, in which combinations of β_m and β_f correspond to stars with white circle in Fig. 1c. In these cases, SSH population finally becomes extinct. Other parameters are as in Fig. 2.

alate females and workers. On the other hand, when $k > 2$, there are also two different patterns of persistence of SSH population. According to Figs. 1b–d, when $\beta_m \leqslant 1$ and $\beta_f > 1$, and when $\beta_m > 1$ and $\beta_f \gg \beta_m$, the population persists with convergence of the genotypic frequency of both queens and males to 0.5 (i.e. black circles in Fig. 1). A typical dynamic behavior of such cases is illustrated in Fig. 4b. In addition to this, with $\beta_m \leqslant 1$ and $\beta_f = 1$ the population persists, maintaining the initial frequency of queen genotypes (i.e. gray circles with $\beta_m \leqslant 1$ in Fig. 1), of which typical dynamics is shown in Fig. 4a.

With $k > 2$ and $\beta_m < 1$, the population cannot persist if $\beta_f < 1$, due to gradually growing asymmetry in genotypic frequencies (see Fig. 3a), although the population persists if $\beta_f \geqslant 1$ (see Figs. 4a and b). The differences in the behavior of the system between $\beta_f < 1$ and $\beta_f \geqslant 1$ relates to advantages and disadvantages concerning the increment of workers in a colony. The advantage of increasing workers is an increase in the production of offspring,

whereas the disadvantage is a decrease in production of alate females due to the allocation of potential female production n. When $\beta_m < 1$ and $\beta_f < 1$ (Fig. 3a), the contribution of workers to increasing alate production is likely weak, implying that the advantage of an increment of workers is small. In such a case, a decrement of workers (i.e. an increment of alate females) is advantageous for the colony. Therefore, once A and AA (or B and BB) genotypes are dominant in the population, they tend to achieve a higher advantage due to the production of more alate females, which causes an increment of AA (or BB) queens in the next generation, resulting in increasing asymmetry in allelic frequency. On the other hand, when $\beta_f \geqslant 1$ (Figs. 4a and b), the advantage of increasing workers tends to be high, which suppresses the above unstabilizing effect and results in persistence of the dynamics.

With $k > 2$ and $\beta_m \geqslant 1$, the population cannot persist if β_f is relatively small, owing to growing oscillations in male genotypic frequency (see Fig. 3b). Since $\beta_m \geqslant 1$ in this case,
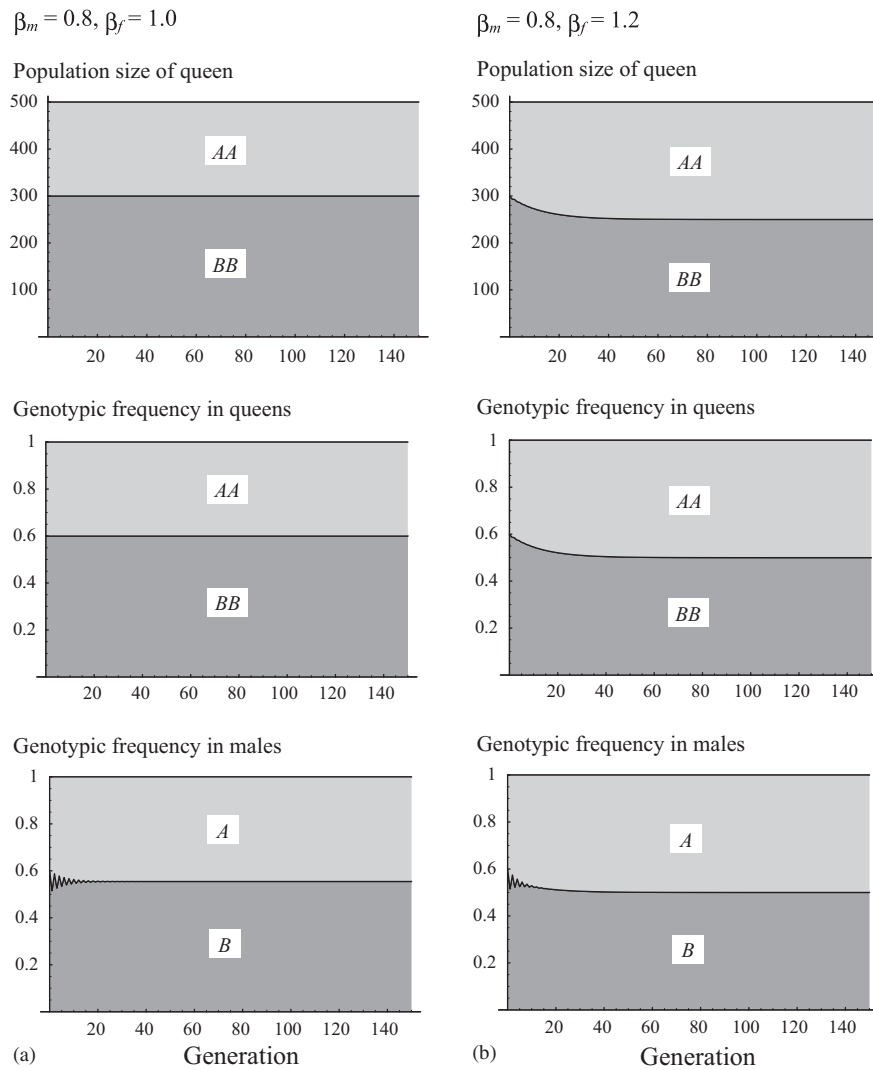
Fig. 4. Typical population and genotypic dynamics with $k = 5$, in which combinations of β_m and β_f correspond to stars with gray and black circles in Fig. 1c. In these cases, SSH population can persist. Other parameters are as in Fig. 2.

male production in the colony tends to increase with increasing worker number. Recall that queens mating with more males with different genotypes can produce more workers. If genotype A (or B) is dominant among males, BB (or AA) queens tend to produce more sons due to more workers, resulting in more B (or A) males in the next generation. This process results in the oscillation in male genotypic frequency. Despite such a tendency, the population can continuously persist when β_f is relatively large, with convergence of the genotypic frequency of both queens and males to 0.5 (see Figs. 1b–d). When β_f is relatively large, alate female production in the colony tends to increase with increasing worker number. Accordingly, under $\beta_m \geqslant 1$ and $\beta_f \gg \beta_m$, if A (or B) male is dominant, BB (or AA) queens produce more sons and alate females due to more workers, resulting in higher production of both B (or A) males and BB (or AA) queens in the next generation. However, when B males and BB queens (or A males and AA queens) become simultaneously dominant, B (or A)

males can not sufficiently contribute to A (or B) male production because mating between B (or A) males and AA (or BB) queens occur with lower probability. Consequently, when β_f is relatively large, growing oscillation in male genotype is likely suppressed by the synchronous changes of frequencies of B males and BB queens (and also A males and AA queens), resulting in persistence of SSH system.

3. Discussion

According to the analyses, the consequences of population dynamics under the SSH system can be classified into three categories, as summarized in Table 1. The first category is population persistence with convergence of genotypic frequencies of both queens and males toward 0.5. The second category is population persistence with maintenance of the initial frequency of the queen genotypes. The third category is population extinction

Table 1
Consequences of population dynamics of various SSH models

	$\beta_f < 1$	$\beta_f = 1$	$\beta_f > 1$
$k = 2$			
$\quad \beta_m \leqslant 1$	$\pm$	$\pm$	$\pm$
$\quad \beta_m > 1$	$-$	$-$	$-$
$k > 2$			
$\quad \beta_m \leqslant 1$	$-$	$\pm$	$+$
$\quad \beta_m > 1$	$-$	$-$	$-, +$

The characters '$-$', '$\pm$' and '$+$' indicate extinction, persistence with multiple equilibria and persistence with convergence to a single equilibrium, respectively. When $\beta_m > 1$ and $\beta_f > 1$, the results are '$+$' only for $\beta_f \gg \beta_m$, they are '$-$' otherwise (see also Fig. 1).

with two typical patterns: either the initial asymmetry in male genotypic frequency gradually increases, or male genotypic frequency oscillates with growing amplitude.

Both the first and second set of consequences realise population persistence under SSH, although some considerations may reduce the plausibility of the second category. The second category tends to appear with $\beta_m \leqslant 1$ under $k = 2$, or $\beta_m \leqslant 1$ and $\beta_f = 1$ under $k > 2$. Namely, the second category of persistence condition is $k = 2$ (with $\beta_m \leqslant 1$) or $\beta_f = 1$ (with $k > 2$). These conditions are quite special cases, which may not be satisfied generally. Furthermore, the second category results in population persistence at the initial frequency of queen genotypes indicating that an infinite number of equilibria exist in the dynamics, and they are neutrally stable. In such a case, if dynamics are accompanied by stochasticity, the frequency of queen genotypes will fluctuate without any stabilizing force, which may ultimately result in population extinction owing to an extreme bias in genotypic frequency or loss of an allele, i.e. a fixation by genetic drift.

Thus, the first category of consequences, where the population persists with convergence of genotypic frequency toward 0.5, may be a single explanation of persistence of SSH populations. The conditions for persistence of SSH populations are that (1) each female mates with more than two males ($k > 2$), and (2) male production increases less steeply than linearly with increasing numbers of workers in a colony ($\beta_m \leqslant 1$), and alate female production increases more steeply than linearly with increasing numbers of workers ($\beta_f > 1$), or (2′) male production increases more steeply than linearly with increasing numbers of workers in a colony ($\beta_m > 1$), and alate female production increases much more steeply than male production ($\beta_f \gg \beta_m$). Condition (1) may be justified, because the effective mate numbers of *Pogonomyrmex* spp. were estimated between 3.13 (*P. rugosus*: Helms Cahan et al. 2002) and 6 (*P. occidentalis*: Cole and Wiernasz 1999).

In both conditions (2) and (2′), we predicted that the production of alate females is an increasing function of the number of workers in the colony, and the functional form

is steeper than linear. Therefore, to justify the presented conditions, it is important to examine the effect of workers on colony productivity in empirical studies. Importantly, our model considered that all queens possess the same ability to produce daughters, n, which is allocated into qn alate females and $(1 - q)n$ workers. This condition may be approximately satisfied at the initial stages of colony foundation. However, during colony establishment, the substantial production of daughters is enhanced by workers, with the result that queens initially rearing more workers tend to produce more daughters (both alate females and workers) after establishment. Here, we included this effect on alate female production into the model by representing its functional from as $\alpha\{(1 - q)n\}^\beta$. To determine the functional form, observations of both initial numbers of workers and final production of alate females are required. Furthermore, in conditions (2) and (2′), we predicted that the enhancement effect of workers on male production must be less than that on alate female production. If this condition is true, variation in production of males among colonies may be smaller than that of female production. In other words, the condition may be approximately justified if the numbers of males are relatively constant compared to variations in alate female number among colonies.

In eusocial ant species, sex ratio often notably varies among colonies, which is considered to the optimal response to relatedness within each colony, called sprit sex ratio (Boomsma and Grafen, 1990, 1991). This conditional behavior must have established through evolution. Split sex ratio may influence the maintenance of SSH, although such an evolutionary issue exceeds a scope of the present paper. Role of the split sex ratio in SSH system should be studied in a future work, expanding the formulation of the present study that combined genetic dynamics with population dynamics.

Here, we pointed out that the persistence of populations with SSH is not obvious and may occur only under certain conditions. To understand both the evolution and population dynamics of SSH, more detailed behavioral information of the species concerned are necessary.

References

Ashe, A., Oldroyd, B., 2002. Genetic determination of caste in harvester ants. Trends Ecol. Evol. 17, 448–452.

Boomsma, J.J., Grafen, A., 1990. Intraspecific variation in ant sex ratios and the Trivers–Hare hypothesis. Evolution 44, 1026–1043.

Boomsma, J.J., Grafen, A., 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. J. Evol. Biol. 3, 383–407.

Cole, B.J., Wiernasz, D.C., 1999. Expected relatedness: correction. Science 286, 52.

Helmes Cahan, S., Keller, L., 2003. Complex hybrid origin of genetic caste determination in harvester ants. Nature 424, 306–309.

Helms Cahan, S., Parker, J.D., Rissing, S.W., Johnson, R.A., Polony, T.S., Weiser, M.D., Smith, D.R., 2002. Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. Proc. R. Soc. B 269, 1871–1877.

Johnson, R.A., 2004. Colony founding by pleometrosis in the semiclaustral seed-harvester ant Pogonomyrmex californicus (Hymenoptera: Formicidae). Animal Behav. 68, 1189–1200.

Julian, G.E., Fewell, J.H., Gadau, J., Johnson, R.A., Larrabee, D., 2002. Genetic determination of the queen caste in an ant hybrid zone. Proc. Natl Acad. Sci.,USA 99, 8157–8160.

Parker, J.D., 2004. A major evolutionary transition to more than two sexes? Trends Ecol. Evol. 19, 83–86.

Pearcy, M., Aron, S., Doums, C., Keller, L., 2004. Conditional use of sex and parthenogenesis for worker and queen production in ants. Science 306, 1780–1783.

Volny, V.P., Gordon, D.M., 2002. Genetic basis for queen-worker dimorphism in a social insect. Proc. Natl Acad. Sci. USA 99, 6108–6111.