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ORIGINAL ARTICLE
Effective population size in eusocial Hymenoptera with worker-produced males

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In many eusocial Hymenoptera, a proportion of males are produced by workers. To assess the effect of male production by workers on the effective population size N_e, a general expression of N_e in Hymenoptera with worker-produced males is derived on the basis of the genetic drift in the frequency of a neutral allele. Stochastic simulation verifies that the obtained expression gives a good prediction of N_e under a wide range of conditions. Numerical computation with the expression indicates that worker reproduction generally reduces N_e. The reduction can be serious in populations with a unity or female-biased breeding sex ratio. Worker reproduction may increase N_e in populations with a male-biased breeding sex ratio, only if each laying worker produce a small number of males and the difference of male progeny number among workers is not large. Worker reproduction could be an important cause of the generally lower genetic variation found in Hymenoptera, through its effect on N_e.
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INTRODUCTION
Effective population size N_e is a crucial parameter in population, conservation and quantitative genetics, because this parameter determines both the rate of inbreeding and the amount of genetic drift in populations (Caballero, 1994; Falconer and Mackay, 1996; Frankham et al., 2002). In haplodiploid species, N_e has been predicted by applying Wright's (1933) standard formula for X-linked locus,

$$N_e = \frac{9N_f N_m}{2N_f + 4N_m},\qquad(1)$$

where N_f and N_m are the numbers of breeding females and males, respectively. This application is reasonable, as inheritance in haplodiploid species is effectively equivalent to sex-linked inheritance in diploid species (Yokoyama and Nei, 1979; Page and Marks, 1982).

Colonies of eusocial Hymenoptera are characterized by a reproductive division of labour. Colonies are founded by mated females (queens), who produce diploid daughters (workers and young queens) and haploid males. Workers do not mate, but they retain ovaries in many species. If workers are sterile, only queens should be counted as the breeding females in the computation of N_e. Furthermore, under monogamous mating system as in many Hymenopteran species, both the numbers of queens and males are approximated by the number of nests, giving from equation (1) an estimate of N_e as the number of nests multiplied by 1.5 (Ellis et al., 2006). In some species, as honey bees and army ants, a queen mates with more than one male, leading to a biased breeding sex ratio ($r = N_m/N_f$) from unity. In such species, assuming the absence of worker reproduction, N_e has been predicted from equation (1) as

$$N_e = \frac{9rN_f}{4r+2}$$

(Page and Marks, 1982). When r is large as in honey bees, $9N_f/4$, that is, the number of nests multiplied by 9/4, can be a good approximation of N_e (Page and Marks, 1982).

It is, however, known that under certain conditions, workers lay unfertilized eggs which develop into males (Crozier and Pamilo, 1996). This production of males by workers is widespread in the eusocial Hymenoptera, such as stingless bees, honey bees, bumble bees, vespine wasps and higher ants (Crozier and Pamilo, 1996). Worker reproduction has received much attention in the context of evolution of sociality and altruism. For example, the kin selection theory of Hamilton (1964) predicts that haplodiploidy and its consequent asymmetric relationship among colony members cause a conflict over male production between queens and workers (Trivers and Hare, 1976; Queller et al., 1997). The conflict will be intensively expressed in a monogamous colony, because the workers should prefer to rear their own sons and nephews over their brothers (queen-produced males). This conflict has motivated many researchers to carry out theoretical and experimental studies (for example, Brown et al., 2003; Tsuchida et al., 2003; Wenseleers et al., 2004). In many species, worker-laid eggs are killed (policed) by the queen or by other workers. The policing is an important mechanism for resolving the queen–worker conflict and maintaining social harmony (Wenseleers et al., 2004), and also provides a clue for solving a question whether worker altruism is voluntary or enforced (Wenseleers and Ratnieks, 2006).

As for the effect of worker reproduction on N_e, there are two contrasting views. Contel and Kerr (1976) considered that the presence of worker-produced males will increase N_e because of the increased number of 'genetically active' females. In contrast, Crozier and Pamilo (1996) predicted that worker reproduction decreases N_e, despite there being more breeding females, because an extra round of gametic sampling is introduced in each generation and the rate of genetic drift is enhanced. Owen and Owen (1989) derived an expression of N_e for the simplest case where each laying worker contributes exactly one breeding male. By numerical analysis with the

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obtained expression, they showed that if the breeding sex ratio is unity or female-biased, then N_e is reduced by the presence of worker-produced males, while with male-biased breeding sex ratio N_e is increased. For a more realistic situation where laying workers produce variable numbers of breeding males, they predicted using computer simulation that worker-produced males reduces N_e regardless of breeding sex ratio. However, due to lack of a general formula of N_e, the effect of worker-produced males on N_e has never been fully assessed.

In the present study, we derive a general expression of N_e for populations eusocial Hymenoptera with worker-produced males. The validity is checked by computer simulation, and the effect of worker-produced males on N_e is assessed by numerical analysis.

MATERIALS AND METHODS

Model and description of genetic drift

We assume a random mating population of eusocial Hymenoptera with a constant size of N_f queens, N_m (haploid) males and N_w laying workers. The N_m males consist of N_{m1} queen-produced and N_{m2} worker-produced males, thus the proportion (φ) of the worker-produced males being $\varphi = N_{m2}/N_m$. Subscripts $f, m, w, m1$ and $m2$ are used to specify the cohorts of queens, males, laying workers, queen-produced males and worker-produced males, respectively. The assumed breeding structure is illustrated in Figure 1.

There are two major definitions of N_e, the variance effective size ($N_{e(V)}$), which is defined by the accumulation rate of genetic drift, and the inbreeding effective size ($N_{e(I)}$), which is defined by the increasing rate of inbreeding (Crow and Kimura, 1970). Our derivation of expressions for N_e is based on the dentition of $N_{e(V)}$. Crow and Kimura (1970) has shown that $N_{e(V)}$ is approximately equal to $N_{e(I)}$ in a population with a constant mating system and a constant population size over generations. This view will be verified under the examined condition in this study by computer simulation in the later section.

We consider an allele on a neutral locus with the frequency in an arbitrary initial generation as follows:

Queens p_f
Laying workers p_w
Queen-produced males p_{m1}
Worker-produced males p_{m2}
All males $p_m = (1-\varphi)p_{m1} + \varphi p_{m2}$

Owing to genetic drift, the allele frequencies will be changed between generations. With subscripts u and v ($= f, m, w, m1$ or $m2$), the change through the gametic pathway from cohorts of u to v is expressed as Δp_{uv}. Furthermore, let Δp_f, Δp_{m1} and Δp_{m2} be the total change of gene frequency from the parental generation to queens, queen-produced males and worker-produced males in the next generation, respectively. From the mode of
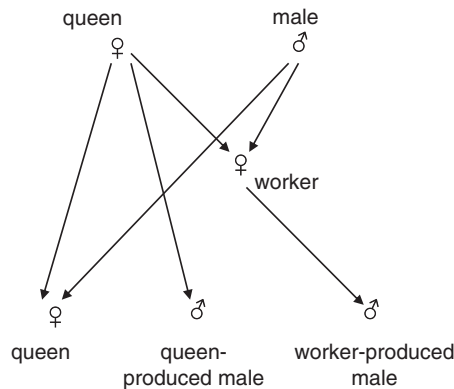
haplodiploid inheritance,

$$\Delta p_f = \frac{1}{2}(\Delta p_{ff} + \Delta p_{mf}) \tag{2}$$

$$\Delta p_{m1} = \Delta p_{fm1}$$

The change of gene frequency in worker-produced males (Δp_{m2}) is generated through two steps: step from parents (queens and males) to workers, and step from workers to their sons. Thus, Δp_{m2} is expressed as

$$\Delta p_{m2} = \frac{1}{2}(\Delta p_{fw} + \Delta p_{mw}) + \Delta p_{wm2} \mid p_w, \tag{3}$$

where $\Delta p_{wm2}|p_w$ is the change of gene frequency from workers to their sons for a given p_w. The total change of gene frequency in males (Δp_m) in the next generation is

$$\Delta p_m = (1-\varphi)\Delta p_{m1} + \varphi\,\Delta p_{m2} \tag{4}$$

Following Hill's (Hill, 1979) idea of the asymptotic contribution of a reproductive cohort in a given generation to remote future, which was introduced to define N_e with overlapping generations, we consider the asymptotic contributions of queens and males in a given generation, which are denoted by $c_{f(\infty)}$ and $c_{m(\infty)}$, respectively. As shown in Appendix A, they are expressed as

$$\begin{aligned} c_{f(\infty)} &= \frac{2-\varphi}{3-\varphi} \\ c_{m(\infty)} &= \frac{1}{3-\varphi}. \end{aligned} \tag{5}$$

Note that when $\varphi = 0$, $c_{f(\infty)} = 2/3$ and $c_{m(\infty)} = 1/3$, and these contributions are immediately attained. However, when $\varphi > 0$, the contributions asymptotically converge to $c_{f(\infty)}$ and $c_{m(\infty)}$. With the asymptotic contributions, the asymptotic contribution of the total change of gene frequency to remote future generations is expressed as

$$\Delta p = c_{f(\infty)}\Delta p_f + c_{m(\infty)}\Delta p_m = \frac{2-\varphi}{3-\varphi}\Delta p_f + \frac{1}{3-\varphi}\Delta p_m.$$

The variance of Δp among an infinite number of conceptual replicated populations is

$$V[\Delta p] = \left(\frac{2-\varphi}{3-\varphi}\right)^2 V[\Delta p_f] + \left(\frac{1}{3-\varphi}\right)^2 V[\Delta p_m].$$

According to Hill (1979), the effective population size (N_e) is obtained by equating $V[\Delta p]$ to $p(1-p)/2N_e$:

$$\frac{p(1-p)}{2N_e} = \left(\frac{2-\varphi}{3-\varphi}\right)^2 V[\Delta p_f] + \left(\frac{1}{3-\varphi}\right)^2 V[\Delta p_m] \tag{6}$$

where p is the asymptotic average gene frequency in the parental generation, defined by

$$p = \frac{2-\varphi}{3-\varphi}p_f + \frac{1}{3-\varphi}p_m. \tag{7}$$

This definition of average gene frequency was also adopted by Owen and Owen (1989) but without the detailed explanation.

Formulation of the effective population size

From the derivation in Appendix B, we obtain following approximated expressions of $V[p_f]$ and $V[p_m]$:

$$V[p_f] = \frac{p(1-p)}{8N_f}\left[1 + \sigma_{ff}^2 + 2\left(\frac{\sigma_{mf}^2}{\mu_{mf}}\right)\right] \tag{8a}$$

$$V[p_m] = \frac{p(1-p)}{2}\left\{\frac{(1-\varphi)^2}{N_{m1}}\left[1 + \frac{\sigma_{fm1}^2}{\mu_{fm1}}\right] + \frac{\varphi^2}{4N_w}\left[1 + \frac{\sigma_{fw}^2}{\mu_{fw}} + 2\left(\frac{\sigma_{mw}^2}{\mu_{mw}}\right)\right] + \frac{\varphi^2}{N_{m2}}\left[1 + \frac{\sigma_{wm2}^2}{\mu_{wm2}}\right]\right\}, \tag{8b}$$

where μ_{uv} and σ_{uv}^2 are the mean and variance of the number of progeny in cohort v from a parent in cohort u. Noting $\mu_{uv} = N_v/N_u$ and $N_{m1} = (1-\varphi)N_m$, and substituting (8) into (6) give a general expression of N_e of Hymenopteran

Figure 1 Assumed breeding structure and gametic pathways.

population with worker-produced males as

$$\frac{1}{N_e} = \frac{1}{(3-\varphi)^2}\left[\frac{(1-\varphi)^2}{N_f}\left(\frac{\sigma_{fm1}^2}{\mu_{fm1}^2}\right) + \frac{1-\varphi}{N_m} + \frac{\varphi^2}{4N_f}\left(\frac{1}{\mu_{fw}} + \frac{\sigma_{fw}^2}{\mu_{fw}^2}\right)\right.$$
$$+ \frac{\varphi^2}{2N_m}\left(\frac{\sigma_{mw}^2}{\mu_{mw}^2}\right) + \frac{\varphi}{N_w}\left(\frac{1}{\mu_{wm2}} + \frac{\sigma_{wm2}^2}{\mu_{wm2}^2}\right)$$
$$\left. + \frac{(2-\varphi)^2}{4N_f}(1+\sigma_{ff}^2) + \frac{(2-\varphi)^2}{2N_m}\left(\frac{\sigma_{mf}^2}{\mu_{mf}^2}\right)\right]. \quad (9)$$

When $\varphi = 0$, equation (9) reduces to

$$\frac{1}{N_e} = \frac{1}{9N_m}\left[1 + 2\left(\frac{\sigma_{mf}^2}{\mu_{mf}^2}\right)\right] + \frac{1}{9N_f}\left[1 + \sigma_{ff}^2 + \frac{\sigma_{fm}^2}{\mu_{fm}^2}\right],$$

agreeing with the formula obtained by Pollak (1980, 1990), except for omitting the term of covariance among female and male progeny numbers of female parents (queens), which can be neglected if female and male progeny are independently selected.

A compact expression comparable to the formula (1) could be obtained by assuming a Poisson distribution of the progeny number in each gametic pathway, which is a good approximation when the progeny are selected at random. Noting $\mu_{uv} = \sigma_{uv}^2$ under a Poisson distribution, we get from (9)

$$\frac{1}{N_e} = \frac{(2 + \mu_{wm2}\varphi)N_f + (2-\varphi)^2 N_m}{(3-\varphi)^2 N_m N_f}, \quad (10)$$

which reduces to the formula (1) when $\varphi = 0$. If the distribution of male progeny number of worker deviates from a Poisson distribution but in other gametic pathways the progeny numbers follow a Poisson distribution within each gametic pathway, N_e should be predicted by

$$\frac{1}{N_e} = \frac{\{2 - \varphi + (1 + CV_{wm2}^2)\varphi\mu_{wm2}\}N_f + (2-\varphi)^2 N_m}{(3-\varphi)^2 N_m N_f}, \quad (11)$$

where $CV_{wm2}(=\sigma_{wm2}/\mu_{wm2})$ is the coefficient of variation of male progeny number per laying worker.

Owen and Owen (1989) derived a formula of N_e for the special case where each laying worker produce exactly one male. In this case, $\mu_{wm2} = 1$ and $\sigma_{wm2}^2 = 0$. Assuming again Poisson distributions of the progeny numbers in the other gametic pathways, we obtain from (9)

$$\frac{1}{N_e} = \frac{2N_f + (2-\varphi)^2 N_m}{(3-\varphi)^2 N_m N_f}, \quad (12)$$

in accordance with the formula given by Owen and Owen (1989).

Computer simulation

Validity of the obtained equations was checked by computer simulation of genetic drift in the frequency of an allele on a neutral locus. Initial genotypes of N_f queens and N_m males were generated by randomly assigning A_1 and A_2 alleles with equal frequency ($p_m = p_f = 0.5$). To obtain the genotype of a young queen, a gamete (gene) picked at random with equal probability from a queen randomly sampled from N_f queens and a gamete from a male randomly sampled from N_m males was united. The sampling of parents (queen and male) and unification of their gametes were repeated until obtaining the genotypes of N_f young queens. In each repetition the sampling of parents was carried out with replacement, allowing both queens and males to have a chance of multiple mating, that is, 'polyandry–polygyny' model was simulated. The above process to generate young queens is conceptually equivalent to a situation where each parent contributes a large number of candidates for young queens, and young queens are randomly selected from the pooled candidates. The genotypes of N_w laying workers were generated in the same manner. For a queen-produced male, a gene picked at random with equal probability from a randomly sampled (with replacement) queen was assigned. This was replicated to obtain N_{m1} queen-produced males. In the basic model of simulation, N_{m2} worker-produced males were analogously generated from N_w laying workers. The above reproduction was repeated over a specified number of generations.

In each generation, the frequencies of A_1 allele in N_f queens and N_m males were computed. The average gene frequency (p_t) in generation t was calculated

with equation (7). The simulation was replicated 10 000 times, and the variance of the gene frequency among the replicates (σ_t^2) in generation t was computed. Following Spiess (1989), the variance effective population size ($N_{e(V),t}$) in generation t was obtained by

$$\frac{1}{2N_{e(V),t}} = \frac{\sigma_t^2 - \sigma_{t-1}^2}{p_0(1-p_0) - \sigma_{t-1}^2},$$

where $p_0 (=0.5)$ is the initial gene frequency.

As another measure of simulated effective population size, the inbreeding effective population size ($N_{e(I),t}$) in generation t was computed from the rate of inbreeding in young queens. The average inbreeding coefficient (F_t) of young queens in generation t was obtained by applying the coancestry method (Falconer and Mackay, 1996) with modification for haplodiploidy and presence of worker reproduction, as described in Appendix C. Following Crow and Kimura (1970), the rate of inbreeding (ΔF_t) was computed by

$$\Delta F_t = \frac{F_t - F_{t-1}}{1 - F_{t-1}}.$$

With the average ($\Delta \bar{F}_t$) over 10 000 replicates, the inbreeding effective population size ($N_{e(I),t}$) in generation t was obtained by $N_{e(I),t} = 1/2\Delta\bar{F}_t$.

Figure 2 shows the variance and inbreeding effective sizes ($N_{e(V),t}$ and $N_{e(I),t}$) observed over 30 generations in simulated populations with two sets of variables, set A: $N_f = N_m = 100$, $\varphi = 0.4$ and $\mu_{wm2} = 2$, and set B: $N_f = N_m = 100$, $\varphi = 0.8$ and $\mu_{wm2} = 5$. Because the first inbred young queens appear in generation 2, $N_{e(I),t}$ was computed after generation 2. After the initial sharp decline, $N_{e(I),t}$ essentially attained a steady value. Although $N_{e(V),t}$ showed a larger fluctuation, the fluctuation seems to be random deviation from an equilibrium value. In all the examined simulations with other sets of variables, similar tendency was observed in the behaviour of $N_{e(V),t}$ and $N_{e(I),t}$. In simulations with a small effective population size as in the variable set B, fixation (or extinction) of an allele occurred in a small proportion ($<0.1\%$) of the replicated populations after generation 25. Inclusion of such replicated populations into the computation of $N_{e(V),t}$ will result in an overestimation through an underestimation of change in the variance of gene frequency. Viewing these results, the simulated variance and inbreeding effective population sizes were expressed as the harmonic mean over generations 6–20.

In Table 1, the simulated N_e are compared with the prediction from equation (10) for several combination of N_f, N_m and φ. In all the cases
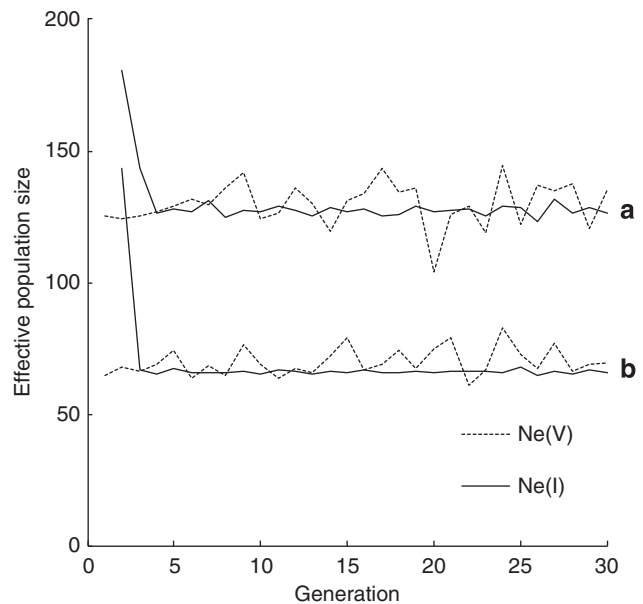

Figure 2 Variance and inbreeding effective population sizes ($N_{e(V)}$ and $N_{e(I)}$) observed during 30 generations of simulated populations with two sets of variables, set (a): $N_f = N_m = 100$, $\varphi = 0.4$ and $\mu_{wm2} = 2$, and set (b): $N_f = N_m = 100$, $\varphi = 0.8$ and $\mu_{wm2} = 5$.

Table 1 Simulated variance and inbreeding effective sizes ($N_{e(V)}$ and $N_{e(I)}$) and predicted ($N_{e(pre)}$) effective size of populations with various proportion (φ) of worker-produced males, when the progeny number in each gametic pathway follows a Poisson distribution

N_f	N_m	μ_{wm2}	φ	Effective size		
				$N_{e(V)}$	$N_{e(I)}$	$N_{e(pre)}$
100	100	2	0.2	140.5	142.1	139.0
			0.4	128.1	127.2	126.1
			0.8	101.3	98.6	96.0
		5	0.2	126.3	127.3	125.6
			0.4	105.5	104.3	103.0
			0.8	68.2	65.9	65.1
150	50	2	0.2	117.3	113.2	112.6
			0.4	95.7	92.6	92.5
			0.8	66.1	60.3	59.3
		5	0.2	103.2	99.3	96.1
			0.4	75.7	71.8	69.6
			0.8	41.9	38.4	37.3
50	150	2	0.2	100.1	97.7	97.0
			0.4	99.9	97.2	96.8
			0.8	94.8	92.4	91.7
		5	0.2	93.4	93.1	92.5
			0.4	91.3	87.5	86.8
			0.8	74.4	71.1	70.3

Abbreviations: N_f, number of queens; N_m, number of males; μ_{wm2}, average number of male progeny per laying worker.

Table 2 Simulated variance and inbreeding effective sizes ($N_{e(V)}$ and $N_{e(I)}$) and predicted ($N_{e(pre)}$) effective size of populations with various proportion (φ) of worker-produced males, when the male progeny number of laying worker follows a uniform distribution with the range from 1 to 5

N_f	N_m	N_w	φ	Effective size		
				$N_{e(V)}$	$N_{e(I)}$	$N_{e(pre)}$
100	100	5	0.15	144.1	140.8	139.5
		15	0.45	120.2	116.1	116.1
		30	0.90	82.4	79.3	78.6
50	150	10	0.2	99.6	95.7	96.0
		30	0.6	95.1	92.1	91.1
		40	0.8	89.9	86.9	85.9
150	50	5	0.3	97.7	96.3	96.9
		10	0.6	71.3	67.9	67.7
		15	0.9	49.1	45.9	45.9

Abbreviations: N_f, number of queens; N_m, number of males; N_w, number of laying workers.

Table 3 Simulated variance and inbreeding effective sizes ($N_{e(V)}$ and $N_{e(I)}$) and predicted ($N_{e(pre)}$) effective size of populations with various proportion (φ) of worker-produced males and monoandry–monogyny mating system

N_f	N_m	μ_{wm2}	φ	Effective size		
				$N_{e(V)}$	$N_{e(I)}$	$N_{e(pre)}$
100	100	2	0.2	142.5	140.2	139.0
			0.4	130.1	127.4	126.1
			0.8	99.3	96.6	96.0
		5	0.2	130.5	127.6	125.6
			0.4	105.7	104.4	103.0
			0.8	69.7	66.0	65.1
300	300	2	0.2	423.1	418.4	417.0
			0.4	383.0	386.9	378.4
			0.8	289.0	288.1	288.1
		5	0.2	383.7	390.2	376.9
			0.4	314.5	311.4	309.1
			0.8	196.6	191.9	195.2

Abbreviations: N_f, number of queens; N_m, number of males; μ_{wm2}, average number of male progeny per laying worker.

examined, $N_{e(V),t}$ and $N_{e(I),t}$ show an essentially same value, as expected from the relevant theory (Crow and Kimura, 1970). Equation (10) gives a good prediction of both the effective sizes, although it tends to slightly underestimate the simulated effective sizes.

Owen and Owen (1989) simulated two distribution models of the male progeny number per laying worker: the first model is that each laying worker exactly contributes one male, and the second model is that equal numbers of workers produce either 1, 2, 3, 4, or 5 males. Under the first model, they verified that their equation (that is, equation (12) in the present study) leads to a satisfactory prediction. In additional simulations, we checked the validity of our prediction under the second model of Owen and Owen (1989) by comparing simulated N_e with that predicted from equation (11). As shown in Table 2, we again found a good agreement between the simulated and predicted N_e.

In many eusocial Hymenopteran species, both queens and males mate only once or nearly so (Crozier and Pamilo, 1996; Hughes *et al.*, 2008), which could be approximated by 'monoandry–monogyny' model. Validity of the obtained equation was also checked under this model. In the simulation, an equal number ($N = N_f = N_m$) of queens and males were paired to form N fixed couples in each generation. A young queen (or a laying worker) was generated by uniting gametes from a randomly sampled (with replacement) couple. The sampling of couple and unification of their gametes were replicated to obtain N_f young queens (or N_w laying workers). Males were reproduced in the analogous way to the 'polyandry–polygyny' model. Predicted N_e from equation (10) is compared with the simulated N_e in Table 3. It is verified that under the 'monoandry–monogyny' model, equation (10) gives a satisfactory prediction of $N_{e(V),t}$ and $N_{e(I),t}$.

Numerical analysis

To assess the effect of male production by workers on N_e, numerical analysis was carried out. Assuming that the progeny numbers in all the gametic pathways but that from workers to males follow independent Poisson distributions, relative N_e with worker-produced males to that without male production by workers was computed. Using equations (1) and (11), the

relative effective size (R) is expressed as

$$R = \frac{2(3-\varphi)^2}{9} \cdot \frac{1+2r}{2-\varphi+(1+CV_{wm2}^2)\varphi\mu_{wm2}+(2-\varphi)^2 r}, \tag{13}$$

where $r = (N_m/N_f)$ is the breeding sex ratio. In Hymenopteran species, female-baiased breeding sex ratio are very rare, and even when they exists, they are not far from unity. To evaluate the effect of male production by workers on N_e under realistic situations, the low and high ends of r were set at 0.9 and 10, respectively, in the numerical analysis.

In Figure 3, R is plotted along the proportion of worker-produced males (φ) for the cases where each laying worker produces exactly one male ($\mu_{wm2} = 1$ and $CV_{wm2} = 0$). If the breeding sex ratio is unity or female-biased ($r \leqslant 1$), the effect of worker-produced males is to slightly reduce N_e. In contrast, when the breeding sex ratio is male-biased ($r > 1$), N_e is increased compared with the value with $\varphi = 0$. The increase in N_e is more prominent for a larger bias in the breeding sex ratio toward male.

A more realistic situation where some laying workers produce more than one male was examined by considering the combination of two values of μ_{wm2} ($=2$ and 4) and two values of CV_{wm2}: $CV_{wm2} = \alpha/\sqrt{\mu_{wm2}}$, where $\alpha = 1$ (variation expected under Poisson distribution) and 2 (variation twice that expected under Poisson distribution). Values of R for the breeding sex ratio $r = 1, 5$ and 10 are plotted along φ in Figures 4a, b and c, respectively. As a case with female-biased breeding sex ratio, the breeding sex ratio of $r = 0.9$ was computed, but the result was omitted because it did not largely depart from the result from the unity breeding sex ratio. When the breeding sex ratio is unity (Figure 4a), male production by workers always reduces N_e. Note that the reduction is considerably greater than that in the case of no variation of male progeny number per worker (cf. Figure 3). For example, with the breeding sex ratio $r = 1$ and $\varphi = 0.5$, N_e is reduced by 2.0% when each worker produces a single male (Figure 3), whereas when the male progeny numbers of workers follow a Poisson distribution with $\mu_{wm2} = 2$, the reduction is 20.6% (Figure 4a). The reduction in N_e is enhanced by an increase in μ_{wm2} and/or CV_{wm2}. If the breeding sex ratio is male-biased (Figures 4b and c), a prominent increase in N_e by worker reproduction is observed only for smaller μ_{wm2} and CV_{wm2}. Unless the breeding sex is extremely biased toward male, the presence of worker-produced males may reduce N_e when μ_{wm2} and/or CV_{wm2} become larger, as seen in Figure 4b.

RESULTS AND DISCUSSION

Crozier and Pamilo (1996) predicted that male production by workers inevitably reduces N_e due to the enhanced genetic drift induced by extra reproduction by workers. The present study, however, showed that a reduction in N_e is not an inevitable consequence of worker reproduction. In a population with male-biased breeding sex ratio, worker reproduction may increase N_e if each laying worker produce a small number of males and the difference of male progeny number among workers is not large.

The honeybee *Apis cerana* is a good illustrative example for the increased N_e by worker reproduction. Using microsatellite markers, Takahashi (unpublished data) estimated the proportion of worker-produced males (φ) in this species to be 34.3% (average over eight colonies). By dissection of workers, he found that 10.2% (average over 8 colonies) of workers per colony have highly developed ovary, but most of them have at most one mature egg in their ovaries. This observation suggests that most of the worker-produced males are from different workers, that is, $\mu_{wm2} \approx 1$ and $\sigma^2_{wm2} \approx 0$. Koyama *et al.* (2009) estimated that a queen of this species mates nine drones on average. As each drone mates only once, the breeding sex ratio is estimated to be $r = 9$. Substituting these estimated values into (13) gives a relative effective size of 1.12. Thus, the male production by workers in *A. cerana* increases N_e by 12%, compared with the population without worker-produced males.

In populations with unity or female-biased breeding sex ratio, worker reproduction always reduces N_e. Even in population with male-biased breeding sex ratio, N_e may be reduced by worker reproduction when laying workers contribute highly variable numbers of males. The reduction in N_e could be illustrated with a population of the wasp *Polistes chinensis*. From the data given by Tsuchida *et al.* (2003); Wenseleers and Ratnieks (2006) estimated the proportion of worker-produced males (φ) to be 51.1%. Assuming unity breeding sex ratio ($r = 1$) and a Poisson distribution of the progeny number in each gametic pathway, the reduction in N_e predicted from (13) is 21.2% for $\mu_{wm2} = 2$. The reduction increases to 34.0% when $\mu_{wm2} = 4$.

The bumblebee *Bombus sylvarum* could be another example to illustrate the importance for incorporating the effect of worker
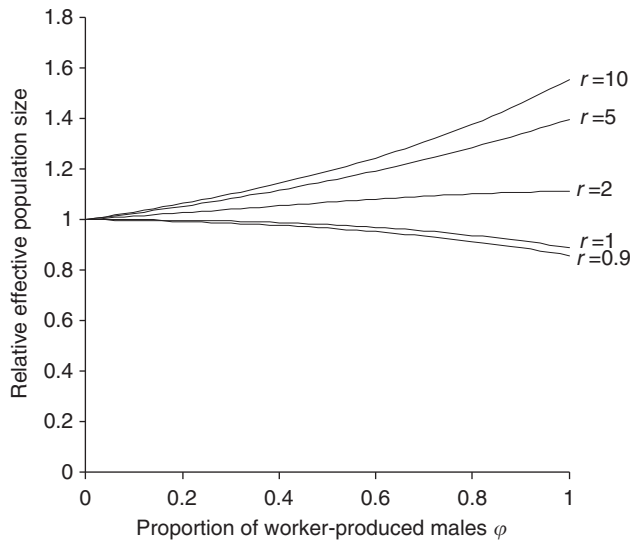

Figure 3 Relative effective size of populations with worker-produced males to that without male production by workers ($\varphi = 0$), when each laying worker exactly produces one male. r, breeding sex ratio (N_m/N_f).
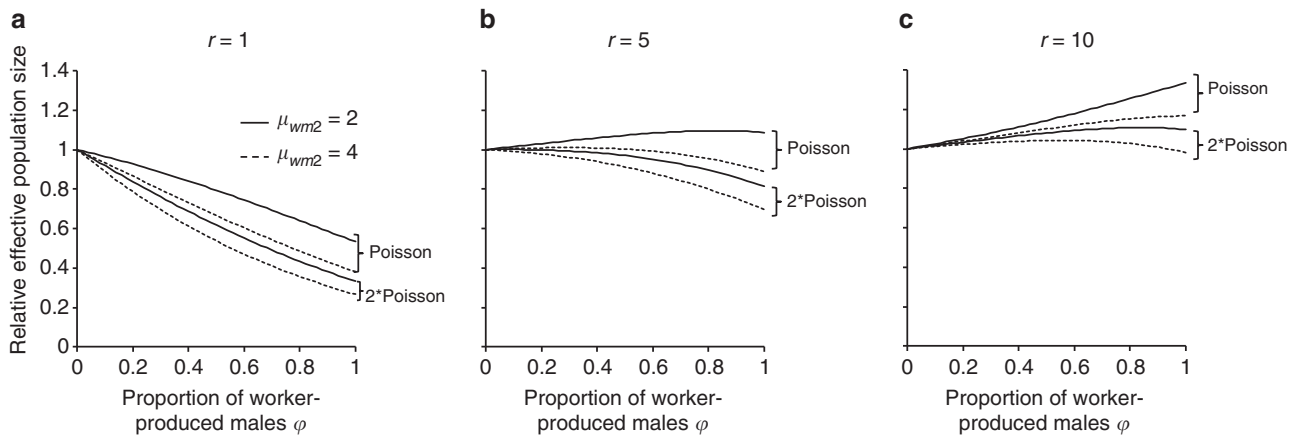

Figure 4 Relative effective size of populations with worker-produced males to that without male production by workers ($\varphi = 0$), when laying workers produce variable numbers of males. r, breeding sex ratio (N_m/N_f); μ_{wm2}, average number of male progeny per laying worker; Poisson, male progeny number per laying worker distributes with the coefficient of variation expected under a Poisson distribution; $2 \times$ Poisson, male progeny number per laying worker distributes with the coefficient of variation twice that expected under a Poisson distribution. Results for $r = 1, 5$ and 10 are shown in panels **a**, **b** and **c**, respectively.

reproduction into the estimation of N_e. Assuming monogamous mating and $N_f = N_m = 32$ (which is the estimated number of nests), and using formula (1), Ellis *et al.* (2006) estimated N_e of an isolated population (Castlemartin) of *B. sylvarum* in UK to be 48, whereas a three times less estimate (16.4) of N_e was obtained for this population from the changes in allele frequency at microsatellite loci. Although the proportion (φ) of worker-produced males in this species is not known, significant levels (20–80%) of worker-produced males have been reported in many *Bombus* species (Crozier and Pamilo, 1996; Brown *et al.*, 2003). Assuming $N_f = N_m = 32$ and $\mu_{wm2} = 4$, equation (10) gives estimates of $N_e = 35.1$ for $\varphi = 0.4$, and $N_e = 23.3$ for $\varphi = 0.8$. In a recent work, Huth-Schwarz *et al.* (2011) reported that the proportion of worker-produced males in the neotropical bumblebee *B. wilmattae* is 96.7%. When this proportion is assumed, the estimate of N_e is further reduced to 19.1. These estimates suggest that a large part of the difference between the two estimates (48 *vs* 16.4) of N_e reported by Ellis *et al.* (2006) might be ascribed to the effect of worker reproduction.

Hymenopteran species usually exhibit lower levels of genetic variation, when compared with diploid species (reviewed by Packer and Owen (2001)). Crozier and Pamilo (1996) predicted that although male production by workers may lead to lower levels of genetic variation by its effect on N_e, it is unlikely that the effect is larger. However, as shown in the present study, worker reproduction could be a critical source to limit genetic variation through a reduction in N_e.

N_e has a special importance in Hymenopteran species with complementary sex determination (CSD), because it determines allelic diversity at the CSD locus (Yokoyama and Nei, 1979; Page and Marks, 1982; Zayed, 2009). Populations with a smaller N_e maintain less alleles at the CSD locus, and consequently produce higher frequencies of sterile or effectively lethal diploid males. As suggested by Zayed and Packer (2005), this phenomenon can lead to 'an extinction vortex'. Furthermore, Zayed (2004) showed that CSD itself may drastically reduce N_e by the loss of breeding males through diploid male production. The present study suggests that worker reproduction could be an additional factor to critically reduce N_e and should be incorporated into population and conservation genetic models of Hymenopteran populations with CSD.

DATA ARCHIVING
Data have been deposited at Dryad: doi: 10.5061/dryad.7p838r83.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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APPENDIX A
Derivation of equation (5)
Let π_{uv} be the contribution of parents of cohort u ($=$m or f) to progeny of cohort v ($=$m or f). Clearly,

$$\pi_{ff} = \pi_{mf} = \frac{1}{2}.$$

The contribution π_{fm} consists of two components: the direct contribution of queens, and the contribution through laying workers,

which are expected to be $1 - \varphi$ and $\varphi/2$, respectively. Thus,

$$\pi_{fm} = 1 - \varphi + \frac{\varphi}{2} = 1 - \frac{\varphi}{2}.$$

As males contribute to male progeny only through laying workers,

$$\pi_{mm} = \frac{\varphi}{2}.$$

We define a transition matrix $\mathbf{P}$ and vectors $\mathbf{c}_{f(0)}$ and $\mathbf{c}_{m(0)}$ as

$$\mathbf{P} = \begin{bmatrix} \pi_{ff} & \pi_{mf} \\ \pi_{fm} & \pi_{mm} \end{bmatrix} = \begin{bmatrix} 1/2 & 1/2 \\ 1-\varphi/2 & \varphi/2 \end{bmatrix},$$

$$\mathbf{c}'_{f(0)} = \begin{bmatrix} 1 & 0 \end{bmatrix}., \mathbf{c}'_{m(0)} = \begin{bmatrix} 0 & 1 \end{bmatrix}., and$$

The contributions of queens in a given generation (generation 0) to queens and males in generation t, $c_{ff(t)}$ and $c_{fm(t)}$, respectively, are obtained as

$$\begin{bmatrix} c_{ff(t)} \\ c_{fm(t)} \end{bmatrix} = \mathbf{P}^t \mathbf{c}_{f(0)}.$$

Similarly, the contribution of males in generation 0 to queens and males in generation t, $c_{mf(t)}$ and $c_{mm(t)}$, respectively, are

$$\begin{bmatrix} c_{mf(t)} \\ c_{mm(t)} \end{bmatrix} = \mathbf{P}^t \mathbf{c}_{m(0)}.$$

Since $\mathbf{P}$ is a stochastic matrix describing a two-state Markov chains, from the relevant theory of stochastic process (for example, Bhat, 1984), $\mathbf{P}^t$ is expressed as

$$\mathbf{P}^t = \begin{bmatrix} \frac{2-\varphi}{3-\varphi} + x & \frac{1}{3-\varphi} - x \\ \frac{2-\varphi}{3-\varphi} - y & \frac{1}{3-\varphi} + y \end{bmatrix},$$

where

$$x = \pi_{mf} \frac{(1-\pi_{mf}-\pi_{fm})^t}{\pi_{mf}+\pi_{fm}} \text{ and } y = \pi_{fm} \frac{(1-\pi_{mf}-\pi_{fm})^t}{\pi_{mf}+\pi_{fm}}$$

Since $x \to 0$ and $y \to 0$ for $t \to \infty$,

$$\mathbf{P}^\infty = \begin{bmatrix} \frac{2-\varphi}{3-\varphi} & \frac{1}{3-\varphi} \\ \frac{2-\varphi}{3-\varphi} & \frac{1}{3-\varphi} \end{bmatrix}.$$

Then,

$$\begin{bmatrix} c_{ff(\infty)} \\ c_{fm(\infty)} \end{bmatrix} = \mathbf{P}^\infty \mathbf{c}_{f(0)} = \begin{bmatrix} \frac{2-\varphi}{3-\varphi} \\ \frac{2-\varphi}{3-\varphi} \end{bmatrix},$$

giving

$$c_{f(\infty)} \equiv c_{ff(0)} = c_{fm(0)} = \frac{2-\varphi}{3-\varphi}.$$

Analogously, we get from $\mathbf{P}^\infty \mathbf{c}_{m(0)}$

$$c_{m(\infty)} \equiv c_{mf(0)} = c_{mm(0)} = \frac{1}{3-\varphi}.$$

APPENDIX B
Derivation of equation (8)
From (2), the variance of Δp_f is

$$V[\Delta p_f] = \frac{1}{4} V[\Delta p_{ff}] + \frac{1}{4} V[\Delta p_{mf}]. \tag{A1}$$

Take $V[\Delta p_{ff}]$ as an example of the derivation. Following the approach described by Crow and Denniston (1988) and Caballero (1994), let k_{ffi} be the number of young queens contributed by queen i, with the mean (μ_{ff}) and variance (σ_{ff}^2),

$$\mu_{ff} = \sum_{i=1}^{N_f} k_{ffi}/N_f = 1$$

$$\sigma_{ff}^2 = \sum_{i=1}^{N_f} (k_{ffi}-1)^2/N_f,$$

and x_{fi} ($=0$, 1/2 or 1) be the gene frequency in queen i. The gene frequency in queens is

$$p_f = \frac{1}{N_f} \sum_{i=1}^{N_f} x_{fi}$$

and the gene frequency in N_f genes of young queens contributed by queens is

$$p_{ff} = \frac{1}{N_f} \sum_{i=1}^{N_f} \left(k_{ffi}x_{fi} + \sum_{j=1}^{k_{ffi}} \delta_{ij} \right),$$

where δ_{ij} is the difference in gene frequency between jth sampled gene and its parental value x_{fi} (δ_{ij} is zero if queen i is a homozygote, or $\pm 1/2$ if a heterozyote). Then,

$$V[\Delta p_{ff}] = V[p_{ff} - p_f]$$
$$= \frac{1}{N_f^2} \left\{ V\left[\sum_{i=1}^{N_f} (k_{ffi}-1)x_{fi} + V\left[\sum_{i=1}^{N_f} \sum_{j=1}^{k_{ffi}} \delta_{ij} \right] \right] \right\}.$$

Following the retrospective approach in defining the effective population size from the observed numbers of progeny per parent (Crow and Kimura, 1970; Caballero, 1994), we regard k_{ffi} as a fixed variable. This gives

$$V[\Delta p_{ff}] = \frac{1}{N_f} \left\{ \sigma_{ff}^2 V[x_{fi}] + V[\delta_{ij}] \right\}.$$

According to Caballero (1994), approximated expressions of $V[x_{fi}]$ and $V[\delta_{ij}]$ are $V[x_{fi}] = p_f(1-p_f)/2$ and $V[\delta_{ij}] = p_f(1-p_f)/2$. With these expressions, we obtain

$$V[\Delta p_{ff}] = \frac{p_f(1-p_f)}{2N_f} (\sigma_{ff}^2 + 1). \tag{A2}$$

Applying a similar approach and noting that males are haploids, we obtain an expression of $V[\Delta p_{mf}]$ as

$$V[\Delta p_{mf}] = \frac{p_m(1-p_m)}{N_f} \left(\frac{\sigma_{mf}^2}{\mu_{mf}} \right). \tag{A3}$$

Approximating p_f and p_m by the average gene frequency p, that is,

$$p = p_f = p_m \tag{A4}$$

and substituting (A2) and (A3) into (A4) give equation (8a) in the text. Approximation (A4) is reasonable, because the difference of gene frequency between queens and males in a generation asymptotically disappears, as predicted from the deterministic analysis by Owen (1980).

Next, consider the variance of Δp_m. From (4), the variance is expressed as

$$V[\Delta p_m] = (1-\varphi)^2 V[\Delta p_{m1}] + \varphi^2 V[\Delta p_{m2}]. \tag{A5}$$

The derivation applied to obtain (A2) gives

$$V[\Delta p_{m1}] = \frac{p_f(1-p_f)}{2N_{m1}} \left(\frac{\sigma_{fm1}^2}{\mu_{fm1}} + 1 \right). \tag{A6}$$

From (3), $V[\Delta p_{m2}]$ is written as

$$V[\Delta p_{m2}] = \frac{1}{4} \left\{ V[\Delta p_{fw}] + V[\Delta p_{mw}] \right\} + E[V[\Delta p_{wm2}|p_w]], \tag{A7}$$

where $E[\ ]$ is the expectation taken for p_w. With the analogous derivation applied to (A2) and (A3), we have

$$V[\Delta p_{fw}] = \frac{p_f(1-p_f)}{2N_w} \left(\frac{\sigma_{fw}^2}{\mu_{fw}} + 1 \right) \tag{A8}$$

and

$$V[\Delta p_{mw}] = \frac{p_m(1-p_m)}{N_w}\left(\frac{\sigma_{mw}^2}{\mu_{mw}}\right). \tag{A9}$$

Furthermore, applying an approximation $E[p_w(1-p_w)] = p(1-p)$ and an analogous derivation to (A2), we have an expression of the final term in (A7) as

$$E[V[\Delta p_{wm2}|p_w]] = \frac{p(1-p)}{2N_{m2}}\left(\frac{\sigma_{wm2}^2}{\mu_{wm2}} + 1\right). \tag{A10}$$

Substituting (A8–10) into (A7) and applying the approximation (A4) give

$$V[\Delta p_{m2}] = \frac{p(1-p)}{2}\left[\frac{1}{4N_w}\left\{1 + \frac{\sigma_{fw}^2}{\mu_{fw}} + 2\left(\frac{\sigma_{mw}^2}{\mu_{mw}}\right)\right\} + \frac{1}{N_{m2}}\left\{1 + \frac{\sigma_{wm2}^2}{\mu_{wm2}}\right\}\right]. \tag{A11}$$

Finally, substituting (A6) and (A11) into (A5), and again applying the approximation (A4) lead to equation (8b) in the text.

APPENDIX C

Modified coancestry method applied to computation of inbreeding coefficient in simulated populations

For the computation of inbreeding coefficients of young queens, the coancestry method described by Falconer and Mackay (1996) was applied with modifications for haplodiploidy and presence of worker reproduction. We first define a coancestry matrix among young queens and males in generation t as

$$\mathbf{\theta}_t = \begin{bmatrix} \mathbf{\theta}_{ff,t} & \mathbf{\theta}_{fm,t} \\ \mathbf{\theta}'_{fm,t} & \mathbf{\theta}_{mm,t} \end{bmatrix},$$

where $\mathbf{\theta}_{ff,t}$ is a matrix (with order $N_f \times N_f$) containing coancestries among N_f young queens, $\mathbf{\theta}_{mm,t}$ is a matrix (with order $N_m \times N_m$) containing coancestries among N_m males, $\mathbf{\theta}_{fm,t}$ is a matrix (with order $N_f \times N_m$) containing coancestries between N_f young queens and N_m males, and $\mathbf{\theta}'_{fm,t}$ is the transposed matrix of $\mathbf{\theta}_{fm,t}$. For the initial generation ($t = 0$), $\mathbf{\theta}_{fm,0}$ is a null matrix, and $\mathbf{\theta}_{ff,0}$ and $\mathbf{\theta}_{mm,0}$ are diagonal matrices:

$$\mathbf{\theta}_{ff,0} = \text{diag}[\,1/2 \quad 1/2 \quad \cdots \quad 1/2\,] \text{ and } \mathbf{\theta}_{mm,0} = \text{diag}[\,1 \quad 1 \quad \cdots \quad 1\,].$$

When parentages of young queens and males are known, all the elements of $\mathbf{\theta}_t$ can be expressed with elements of $\mathbf{\theta}_{t-1}$.

Take elements of $\mathbf{\theta}_{mm,t}$ as an example. As males are haploid, self-coancestry ($\theta_{m(i)m(i),t}$) of a male (m(i); $i = 1, 2, \ldots, N_m$), which is a diagonal element of $\mathbf{\theta}_{mm,t}$, is apparently

$$\theta_{m(i)m(i),t} = 1.$$

To obtain expressions for coancestry among different males (m(i) and m(j); $i, j = 1, 2, \ldots, N_m$ and $i \neq j$), following four cases should be considered.
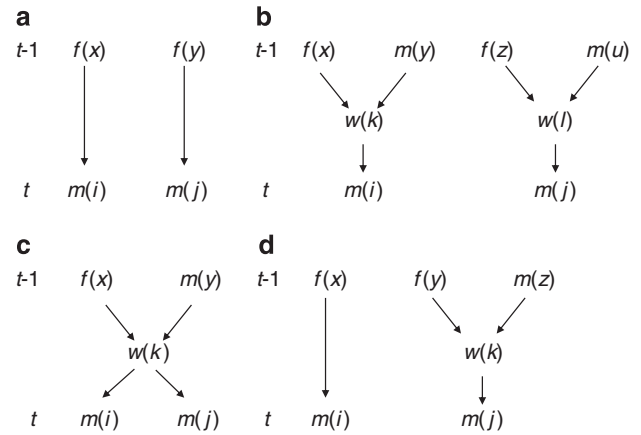
Case a: Two queen-produced males (Figure C1a).

Figure C1 Four cases of relationship among two males (m(i) and m(j)) to be considered in construction of coancestry matrix in generation t. (a) Two queen-produced males; (b) Two worker-produced males from different workers; (c) Two worker-produced males from same worker; (d) Queen-produced and worker-produced males. f and m, queen and male in generation $t-1$; w, laying worker.

By definition, coancestry among m(i) and m(j) is equal to coancestry among their mothers (f(x) and f(y)):

$$\theta_{m(i)m(j),t} = \theta_{f(x)f(y),t-1}.$$

Case b: Two worker-produced males from different workers (Figure C1b)

Coancestry among m(i) and m(j) is equal to coancestry among their mothers (workers w(k) and w(l)). Then, with the standard rule of coancestry (Falconer and Mackay, 1996),

$$\theta_{m(i)m(j),t} = \theta_{w(k)w(l)} = \frac{1}{4}(\theta_{f(x)f(z),t-1} + \theta_{f(x)m(u),t-1} + \theta_{m(y)f(z),t-1} + \theta_{m(y)m(u),t-1}).$$

Case c: Two worker-produced males from same worker (Figure C1c)

Coancestry among m(i) and m(j) is equal to self-coancestry of the common mother (worker w(k)). Then

$$\theta_{m(i)m(j),t} = \theta_{w(k)w(k)} = \frac{1}{2}(1 + \theta_{f(x)m(y),t-1}).$$

Case d: Queen-produced and worker-produced males (Figure C1d)

Coancestry among m(i) and m(j) is equal to coancestry among their mothers (queen f(x) and worker w(k)). Then

$$\theta_{m(i)m(j),t} = \theta_{f(x)w(k)} = \frac{1}{2}(\theta_{f(x)f(y),t-1} + \theta_{f(x)m(z),t-1}).$$

With an analogous way, the remaining elements of $\mathbf{\theta}_t$ can be related to elements of $\mathbf{\theta}_{t-1}$. The inbreeding coefficient ($F_{f(i),t}$) of a young queen in generation t is obtained by coancestry among their mother and father (f(x) and m(y)) as $F_{f(i),t} = \theta_{f(x)m(y),t-1}$, which is an element of $\mathbf{\theta}_{fm,t-1}$.