

Evolution of extraordinary female-biased sex ratios: The optimal schedule of sex ratio in local mate competition

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Received 24 January 2005; received in revised form 1 April 2005; accepted 4 April 2005

Available online 1 June 2005

Abstract

Female-biased sex ratio in local mate competition has been well studied both theoretically and experimentally. However, some experimental data show more female-biased sex ratios than the theoretical predictions by Hamilton [1967. *Science* 156, 477–488] and its descendants. Here we consider the following two effects: (1) lethal male–male combat and (2) time-dependent control (or schedule) of sex ratio. The former is denoted by a male mortality being an increasing function of the number of males. The optimal schedule is analytically obtained as an evolutionarily stable strategy (ESS) by using Pontrjagin's maximum principle. As a result, an ESS is a schedule where only males are produced first, then the proportion of females are gradually increased, and finally only females are produced. Total sex ratio (sex ratio averaged over the whole reproduction period) is more female-biased than the Hamilton's result if and only if the two effects work together. The bias is stronger when lethal male combat is severer or a reproduction period is longer. When male–male combat is very severe, the sex ratio can be extraordinary female-biased (less than 5%). The model assumptions and the results generally agree with experimental data on *Melittobia* wasps in which extraordinary female-biased sex ratio is observed. Our study might provide a new basis for the evolution of female-biased sex ratios in local mate competition.

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Keywords: Local mate competition; Schedule; Lethal male combat; Evolutionary game theory; Pontrjagin's maximum principle

1. Introduction

Primary sex ratio has been widely studied in evolutionary biology. According to Fisher's theory (Fisher, 1958), the investments by parents to male and female offsprings will evolve to be equal. This explains why primary sex ratio (defined as the proportion of males) in many creatures is 1/2. However, there are some exceptional cases. Hamilton (1967) first explained female-biased sex ratios in local mate competition (LMC). LMC occurs when matings among related individuals are often. For many gregarious parasitoid wasps, matings often take place among offsprings

produced by one or a few foundresses that parasitize a host. Only mated females disperse to new patches as new foundresses. Under such LMC, female-biased sex ratio is favored because it reduces competition for mates among brothers and increases the number of daughters as potential foundresses. Through their haplo-diploid sex determination system, an ovipositing female wasp can change her primary sex ratio and female-biased sex ratios are actually observed (Werren, 1980; Herre, 1985, 1987). A primary sex ratio of 1/4 in haplo-diploid social insects is then explained by assuming that workers are in control of the sex ratio (for review, see Trivers, 1985).

Many authors proposed evolutionary game models for the optimal sex ratio under LMC (Hamilton, 1967; Suzuki and Iwasa, 1980; Wilson and Colwell, 1981; Bulmer and Taylor, 1980; Taylor and Bulmer, 1980;

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Herre, 1985; Frank, 1985, 1986, 1987; van Tienderen and de Jong, 1986). Recently, Courteau and Lessard (2000) proposed a generalized model that involves many previous results as special cases. They considered (1) haplo-diploid, haplo or diploid populations, (2) maternal or paternal control of sex ratio, (3) the limitation of host resources, (4) partial dispersal before mating resulting in partial outbreeding, and (5) partial dispersal after mating. They derived ESS and CSS sex ratios for various combinations of the assumptions (1)–(4). Neglecting unrealistic cases (paternal control in haplo-diploid population), the optimal sex ratio in superparasitism is at least $3/14$ (this occurs when two haplo-diploid foundresses parasitize a host and control sex ratio with no limitation of host resources and no dispersal before mating) and increases to approach $1/2$ as the number of foundresses or the degree of outbreeding increase. In completely inbred populations (for example, when superparasitism is quite rare), the optimal sex ratio for a two foundresses case is slightly smaller than $3/14$ (Herre, 1985). The stochastic effect (stochastic brood size per foundress, stochastic number of foundress per host, finite population, extinction of a colony due to the absence of one sex, etc.) also changes the optimal sex ratio slightly (Frank, 1985; Nishimura, 1993; Courteau and Lessard, 1999). Despite all these theoretical predictions, extraordinarily small sex ratios (less than 5%) are observed in LMC in *Melittobia* wasps even when multiple foundresses parasitize a host (Abe et al., 2003a; Cooperband et al., 2003). When the group size (the number of foundresses) is variable, the sex ratio is predicted to be very female-biased when the average group size is close to one (Nunney and Luck, 1988). However, the sex ratio of this species can neither be explained by this model because more than one foundress often attack a host in nature (Cooperband et al., 2003; Abe et al., 2005). In this study, we consider the following two points that may explain the extraordinary small sex ratios.

The first is the effect of lethal male combat. In many creatures, competition for mates among males is observed. Actually, severe male–male combat is observed in *Melittobia* wasps and this has been proposed as a possible cause of the extraordinary female-biased sex ratio (Abe et al., 2003a, b). When the competition is lethal (lethal male combat), the mortality of males depends on the intensity of the combat. Thus, we assume male mortality is an increasing function of the number of males. This assumption is justified in a *Melittobia* case (Abe, personal communication) although some studies show different patterns (West et al., 2001; Reinhold, 2003). In random mixing populations, the sexual difference in mortality does not change the optimal sex ratio because the loss of fitness due to the death of a male is exactly cancelled by the increase in the value of a male that survived. However, in LMC, the

problem is more complicated because we need to consider the reduction of competition for mates caused by increased male mortality.

The second is the problem of the schedule of sex ratio. Although primary sex ratios are $1/2$ in many creatures, they are not always constant during a reproduction period. For example, some sea mammals bear more males in the first half of a reproduction period and then bear more females in the second half (reviewed by Trivers, 1985). Haplo-diploid wasps might also be able to control their primary sex ratio at each stage of their reproduction period. In *Melittobia* wasps, a foundress continues to lay eggs in the same host for long reproduction period and thus the scheduled game (when to lay male eggs) may play an important role in superparasitism (Abe et al., 2005). Female wasps disperse soon after copulation while males stay at a host and are able to mate many females until they die. Thus, it might be adaptive to produce males first. On the other hand, in order to avoid competition for mates, it might be adaptive to produce more males when there exist fewer males. The latter effect might be stronger when male–male combat is more severe and lethal. Actually, *Melittobia* wasps lay male eggs intermittently rather than intensively (Abe et al., 2005). There are some theoretical studies on the schedule of sex ratio (e.g. Iwasa and Odendaal, 1984; West and Godfray, 1997) but few models focus on sex ratio control in LMC (but see Frank (1987) for a model of inter-generational change of sex ratio).

In this paper, we construct mathematical models to study these effects. First, we study the effect of lethal male combat alone by using a static model. Then, we construct a dynamical model describing the number of males on a host during a reproduction period. For simplicity, we only consider the symmetric case in which foundresses keep laying eggs on the same host for the same reproduction period. The optimal schedule of sex ratio is obtained as a Nash equilibrium of the scheduled game, which is derived using Pontrjagin's maximum principle. Then, the effect of lethal male combat is incorporated into this scheduled game model by setting the mortality of males as an increasing function of the number of males. The dependence of the optimal schedule on this mortality function is studied.

2. Model and result

2.1. Assumptions

Since there had been many theoretical studies on sex ratios in LMC, we first summarize the assumptions of our model to avoid confusion. According to Frank (1985), there are two effects that favor female-biased sex ratio. One is the effect of asymmetric inheritance (in

haplo-diploid species) and the other is Wright’s index of panmixia. Due to the former, the relatedness to daughters becomes slightly larger than that to sons in LMC. The latter is the effect of assortative mating, i.e. frequent sib-mating that is essential to LMC. In this study, we neglect the former for simplicity and focus only on the latter. In other words, we assume diploid populations. This assumption justifies us to adopt a simple and intuitive method for calculating fitness. We consider a situation where N foundresses parasitize the same host with N being constant. Only daughters disperse after mating. Sons contribute to their mother’s fitness by mating these dispersing daughters. We assume that every daughter achieves a constant amount of reproductive success, i.e., the resource is not limited. We assume no dispersal of males, no dispersal of females before mating, no inbreeding depression and no generation overlap. We assume the symmetric game, i.e., foundresses are equal in all traits such as fertility, mortality, fighting ability of her son and so on. Mating occurs randomly among offsprings (no kin recognition, no mechanism to avoid incest). In scheduled models, all foundresses start and stop producing offsprings simultaneously.

2.2. Non-scheduled model with lethal male combat

Consider a non-scheduled game played by two foundresses ($N = 2$). Let x and y be their primary sex ratios. Fitness functions are

$$F_x(x, y) = s_d\beta(1 - x) + \frac{s_s\beta x}{s_s\beta x + s_s\beta y} \times s_d\{\beta(1 - x) + \beta(1 - y)\},$$

$$F_y(x, y) = s_d\beta(1 - y) + \frac{s_s\beta y}{s_s\beta x + s_s\beta y} \times s_d\{\beta(1 - x) + \beta(1 - y)\},$$

where s_d and s_s are the survival rates of a daughter and a son, respectively. $s_s = s_s(x, y)$ is a decreasing function of x and y , which represents lethal male combat. β is the number of eggs per foundress. The first term represents the gain of fitness through daughters while the second term through sons. Dividing by $s_d\beta$, we can normalize the fitness functions as

$$F_x(x, y) = (1 - x) + \frac{x}{x + y}(2 - x - y),$$

$$F_y(x, y) = (1 - y) + \frac{y}{x + y}(2 - x - y).$$

The Nash equilibrium of the game is the pair of the strategies (x^*, y^*) such that x^* maximizes $F_x(x, y^*)$ and that y^* maximizes $F_y(x^*, y)$. As Hamilton (1967) showed, the solution is $(x^*, y^*) = (1/4, 1/4)$.

It is worth noticing that the sexual difference in survival rates of offsprings do not influence the optimal

sex ratio. This is true even if the survival rate of males is any function of sex ratio. Here, we conclude that lethal male combat does not influence the optimal sex ratio in a non-scheduled LMC model (but see Abe et al. (2003b) for asymmetric cases).

2.3. Scheduled model without lethal male combat

Here we explicitly consider a time axis. Assume two foundresses, namely X and Y, produce offsprings during a reproduction period $0 \leq t \leq T$. Without loss of generality, we rescale time so that each foundress produces unit offspring per unit time. Let $x(t)$ and $y(t)$ be the schedule of their primary sex ratios. Thus, during a time interval $[t, t + dt]$, a foundress X produces $x(t) dt$ males and $(1 - x(t)) dt$ females. A foundress X tries to maximize her fitness F_x by changing $x(t)$, i.e. $x(t)$ is a strategy of a foundress X. Similarly, $y(t)$ is a strategy of a foundress Y. Fitness functions are

$$F_x = \int_0^T (1 - x) + \frac{m_x}{m_x + m_y}(2 - x - y) dt,$$

$$F_y = \int_0^T (1 - y) + \frac{m_y}{m_x + m_y}(2 - x - y) dt, \tag{1}$$

where m_x and m_y denote the numbers of sons on a host, the dynamics of which are

$$\frac{d}{dt}m_x = -\gamma m_x + x,$$

$$\frac{d}{dt}m_y = -\gamma m_y + y, \tag{2}$$

where γ represents a natural mortality. Note that time is rescaled and thus $\gamma = \Gamma/B$, where Γ and B are a natural death rate of sons and a fecundity rate of foundresses measured in non-rescaled (original) time, respectively. At this stage, we do not consider lethal male combat and thus γ is a constant.

The fitness of a foundress Y depends on the opponent’s strategy $x(t)$ as well as her own strategy $y(t)$. For the sake of explanation, we first seek the optimal $y(t)$ that maximizes F_y when $x(t)$ is fixed. This type of dynamic optimization problem can be solved by using Pontrjagin’s maximum principle (for an application of the principle to problems in social evolution, see Day and Taylor (1997)). The principle assures that the optimal $y(t)$ maximizes Hamiltonian H at every moment (a necessary condition for optimality). In our case, H is denoted by

$$H = (1 - y) + \frac{m_y}{m_x + m_y}(2 - x - y) + \lambda(-\gamma m_y + y)$$

$$= 1 + \frac{m_y}{m_x + m_y}(2 - x) - \lambda\gamma m_y$$

$$+ \left\{ \lambda - 1 - \frac{m_y}{m_x + m_y} \right\} y, \tag{3}$$

where λ is a co-state variable which obeys the following equations:

$$\frac{d}{dt}\lambda = -\frac{\partial H}{\partial m_y} = -\frac{m_x}{(m_x + m_y)^2}(2 - x - y) + \gamma\lambda, \tag{4}$$

$$\lambda(T) = 0. \tag{5}$$

Biologically, the co-state variable $\lambda(t)$ can be interpreted as the value of a son at time t . As H is a linear function of y ,

$$\lambda = 1 + \frac{m_y}{m_x + m_y} \tag{6}$$

must hold when intermediate sex ratios ($0 < y(t) < 1$) are optimal. The right-hand side represents a net increase in fitness by producing a daughter while λ represents that by producing a son. Only when the two values are equal, the optimal sex ratio takes an interior value in $[0,1]$. Hereafter, for simpler notation, we define $z \equiv m_y, a \equiv m_x$. Putting

$$y = \gamma z + z' \tag{2'}$$

(the prime symbol denotes the derivative with respect to time) and

$$\lambda = 1 + \frac{z}{a + z} \tag{6'}$$

into Eq. (4) yields

$$\begin{aligned} & \frac{z'(a + z) - z(a' + z')}{(a + z)^2} \\ &= \frac{-a(2 - x - \gamma z - z') + \gamma(a + z)^2 + \gamma z(a + z)}{(a + z)^2} \end{aligned}$$

or

$$2\gamma z^2 + (4a\gamma + a')z - a(2 - x) + \gamma a^2 = 0 \tag{7}$$

which is a quadratic equation of $z(t)$ (note that $a(t)$ and $x(t)$ are fixed here). This equation gives the optimal control when $0 < y(t) < 1$.

An ESS of a scheduled game is the strategy $x^*(t)$ such that $x^*(t)$ is the best response (optimal control) to itself. Thus, $x^*(t)$ must satisfy Eq. (7) when $x(t) = y(t)$ and $a(t) = z(t)$. Putting these into Eqs. (2') and (7) yields

$$2\gamma z^2 + (4\gamma z + z')z - z(2 - \gamma z - z') + \gamma z^2 = 0$$

or

$$8\gamma z^2 - 2z + 2zz' = 0. \tag{8}$$

The solution is $z = 0$ or

$$z = \frac{1}{4\gamma}(1 - e^{-4\gamma t}), \tag{9}$$

where an integral constant is determined by the initial condition $z(0) = 0$. Putting Eq. (9) into Eq. (2'), an ESS

is denoted by

$$x = y = \frac{1 + 3e^{-4\gamma t}}{4} \tag{10}$$

which monotonically decreases from $x(0) = 1$ to $x(\infty) = 1/4$. As γ is larger, the decrease is quicker, while the sex ratio approaches $1/4$ regardless of γ .

Note that this is the condition that an ESS must satisfy when $0 < x(t) < 1$. At the end of the period, the control is expected to be on its edge ($x = 0$). Mathematically, this is required by the terminal condition Eq. (5). As long as the sex ratio is symmetric and intermediate, $\lambda = 3/2$ (see Eq. (6)). When it is switched from Eq. (10) to $x = 0$ at $t = T_c$, λ begins to decrease and reaches zero at $t = T$. This condition determines T_c . When $x = 0$, Eqs. (2) and (4) become

$$\begin{aligned} \frac{d}{dt}z &= -\gamma z, \\ \frac{d}{dt}\lambda &= -\frac{1}{2z} + \gamma\lambda \end{aligned}$$

or

$$\begin{aligned} z &= z(T_c)e^{-\gamma(t-T_c)}, \\ \frac{d}{dt}\lambda &= -\frac{e^{\gamma(t-T_c)}}{2z(T_c)} + \gamma\lambda. \end{aligned}$$

The solution is

$$\lambda(t) = \left(\frac{3}{2} - \frac{t - T_c}{2z(T_c)}\right)e^{\gamma(t-T_c)}.$$

T_c is determined by $\lambda(T) = 0$. Finally, we obtain a complete notation of an ESS,

$$x(t) = \begin{cases} \frac{1 + 3e^{-4\gamma t}}{4} & (0 \leq t < T_c), \\ 0 & (T_c \leq t < T), \end{cases} \tag{11}$$

where T_c is a solution of $T_c = T - 3z(T_c)$. The ES sex ratio and the number of males as functions of time are plotted in Fig. 1. When $\gamma = 0$, Eq. (11) reduces to

$$x(t) = \begin{cases} 1 & (0 \leq t < 1/4), \\ 0 & (1/4 \leq t < T), \end{cases}$$

which means that producing female offspring earlier than the opponent has no advantage when males never die. Notice that the total sex ratio of all offsprings during the reproduction period is always equal to $1/4$ because

$$\begin{aligned} & \frac{1}{T} \int_0^T x(t) dt \\ &= \frac{1}{T} \int_0^{T_c} \frac{1 + 3e^{-4\gamma t}}{4} dt = \frac{T_c}{4T} + \frac{3}{4T} \left[-\frac{e^{-4\gamma t}}{4\gamma}\right]_0^{T_c} \\ &= \frac{T_c}{4T} + \frac{3}{4T} z(T_c) = \frac{1}{4} \end{aligned}$$

holds.

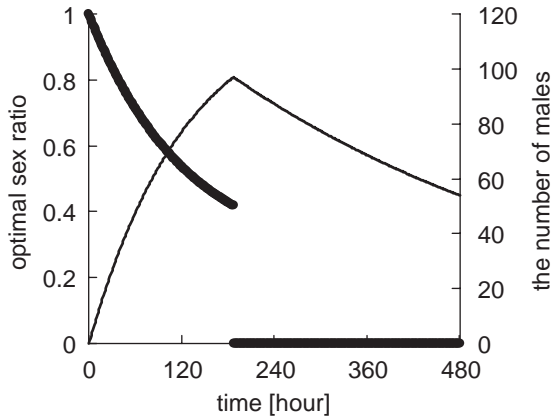


Fig. 1. Scheduled model without lethal male combat. Optimal primary sex ratio (bold filled circles) and the number of males on a host (solid curve) are plotted against time. Parameter values are $T = 480$ and $\gamma = 0.002$ which are consistent with the experimental data of *Melittobia wasps* (Abe et al., 2003a).

As a conclusion of this subsection, the ESS schedule of sex ratio is not constant but a decreasing function of time. However, the total sex ratio is independent of a natural mortality of males and fecundity of foundresses. Even when mortality of a son is very large, the sex ratio is controlled toward 1/4, which means the operational sex ratio becomes strongly female-biased (Eq. (9)).

2.4. Scheduled model with lethal male combat (simple case)

Here we consider the effect of lethal combat among males. We use the same fitness functions,

$$F_x = \int_0^T (1 - x) + \frac{m_x}{m_x + m_y} (2 - x - y) dt,$$

$$F_y = \int_0^T (1 - y) + \frac{m_y}{m_x + m_y} (2 - x - y) dt,$$

while the dynamics of the number of sons includes the effect of the combat,

$$\frac{d}{dt} m_x = -c(m_x + m_y)m_x + x,$$

$$\frac{d}{dt} m_y = -c(m_x + m_y)m_y + y.$$

Here we assume that the frequency of combat per male is proportional to an encounter rate that is proportional to the number of males. Therefore, due to the lethal male combat, every male suffers the mortality $c(m_x + m_y)$ where c represents the intensity of the combat. For simplicity, we ignore a natural mortality.

In this case, an ESS becomes

$$x(t) = \begin{cases} \frac{2}{11}\theta(t) & (0 \leq t < T_c), \\ 0 & (T_c \leq t < T), \end{cases} \quad (12)$$

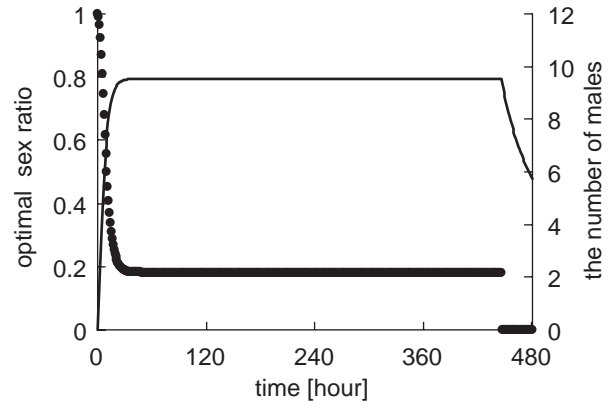


Fig. 2. Optimal sex ratio (bold filled circles) and the number of males on a host (solid line) are plotted against time (see text for details $T = 480$, $c = 0.001$).

where $\theta(t) \equiv (\alpha^2 + 20\alpha + 1)/(\alpha + 1)^2$ with $\alpha \equiv \exp(2\sqrt{11}ct)$ (for details, see the following subsection and Appendix A). Therefore, the ESS sex ratio is $x(0) = 1$ and decreases to approach 2/11. It is difficult to derive the analytical expression of T_c and hence the total sex ratio. In fact, it depends on both the intensity of combat (c) and a reproduction period (T). We numerically derived ESSs and the total sex ratios for some parameter values (Figs. 2 and 3). In general, the total sex ratio decreases from 1/4 to 2/11 as T or c increases.

The major difference from the previous model is that the ESS sex ratio is controlled toward 2/11. Notice the intensity of combat (c) does not change this value. The existence of lethal male combat alone changes the result.

2.5. Scheduled model with lethal male combat (general case)

We here relax the assumption about the number foundresses (N). For arbitrary $N (\geq 2)$, fitness functions are

$$F_i = \int_0^T \left[(1 - x_i) + \frac{m_i}{\sum_{j=1}^N m_j} \sum_{j=1}^N (1 - x_j) \right] dt,$$

where i is an index for each foundress. We also consider more general classes of mortality functions. The first is a class of power functions denoted by

$$\frac{d}{dt} m_i = -c \left(\sum_{j=1}^N m_j \right)^n m_i + x_i.$$

Both c and n represent the intensity of combat. For example, assume there are M males on a host. The mortality per time per individual is cM^n and thus the probability with which a focal individual survives combat among these M males for t time is $\exp(-cM^n t)$ (Fig. 4). As n becomes larger, the probability becomes a more rapidly decreasing function of M . When n is very large, it becomes like a Heaviside function,

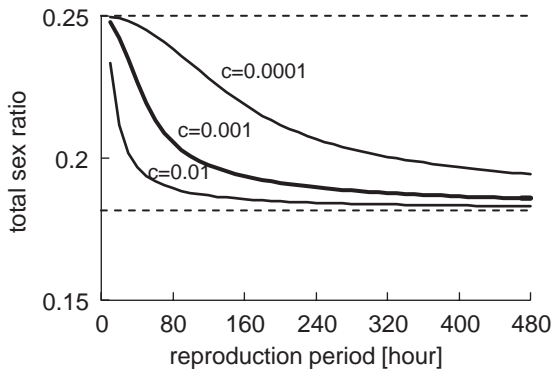


Fig. 3. Total sex ratios are plotted as a function of reproduction period T (solid curves). Two dashed lines indicate $x = 1/4$ and $2/11$ (see text for detail).

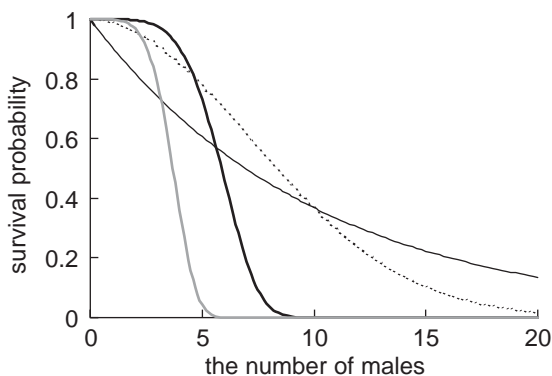


Fig. 4. The probability with which a focal male survives the combat after 1 h is plotted against the number of males on a host. Parameters for each line are: solid line ($c = 0.1, n = 1$), dotted line ($c = 0.01, n = 2$), thick line ($c = 0.0001, n = 5$), and grey line ($c = 0.001, n = 5$).

corresponding to the situation in which there is the maximum number of males that can coexist on a host. Such a situation is biologically expected when the area that each male can patrol is limited. Detailed analysis (see Appendix A) shows that there exists a unique ESS that satisfies $x^*(0) = 1$ and monotonically decreases with time to approach

$$X = \frac{N(N - 1)}{N(N - 1) + (N + 1)(N + n)}$$

It is also proved that $x^* = 0$ only for the last some period. As $N \rightarrow \infty, X \rightarrow \frac{1}{2}$ which is Fisher's equal investment result. When $n = 0$ (no lethal male combat), $X = (N - 1)/2N$ that is equivalent to the former result (Hamilton, 1967). When $N = 2, X = 2/(3n + 8)$ that apparently involves the two preceding results as special cases.

The second is a class of exponential functions denoted by

$$\frac{d}{dt} m_i = -\gamma \exp\left(k \sum_{j=1}^N m_j\right) m_i + x_i,$$

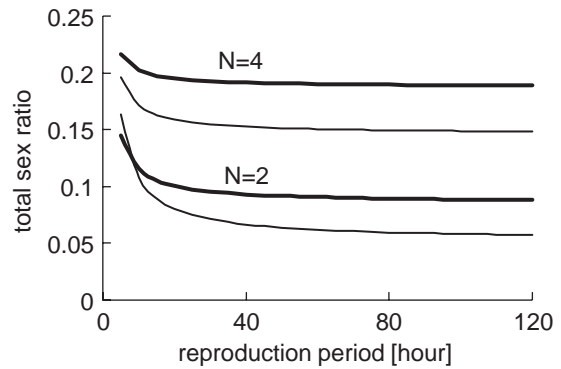


Fig. 5. Total sex ratios are plotted as a function of reproduction period (T). Solid curves are of power function mortality models ($c = 0.001, n = 10$) and bold curves are of exponential mortality models ($\gamma = 0.001, k = 5$). Upper two curves are for $N = 4$ and lower two curves are for $N = 2$ (see text for detail).

where γ denotes a natural mortality (mortality when males are absent) and k represents the intensity of the combat. Detailed analysis (see Appendix B) shows that an ESS satisfies $x^*(0) = 1$ and monotonically decreases to approach an equilibrium value that decreases as k increases or γ decreases. We expect that $x^* = 0$ for the last some period.

In both cases, we numerically confirmed that total sex ratio is lower when lethal male combat is more severe (Table 1), the number of foundresses is smaller, or a reproduction period is longer (Fig. 5).

3. Discussion

We have studied the optimal primary sex ratio in local mate competition. In the non-scheduled game model, the sexual difference in mortality does not change the optimal sex ratio even when the difference is a function of sex ratio itself. In biological words, the existence or strength of lethal male combat does not matter when foundresses lay eggs only once and leave. On the other hand, in the scheduled game model without lethal male combat, the optimal sex ratio is a decreasing function of time. The foundress first produces only males and then gradually increases the proportion of females so that her primary sex ratio approaches to an equilibrium value. Finally, she abruptly changes her behavior to produce only females. Despite such a complex schedule, the total sex ratio averaged over whole the reproduction period remains unchanged, independent of the mortality of males or the fecundity of foundresses. We have also constructed the integrated model including lethal male combat and schedule. The analytical treatment of the model shows that the optimal schedule behaves qualitatively similar. However, both the equilibrium sex ratio and total sex ratio are smaller than the former value. The total sex ratio is a decreasing function of both a reproduction period and the intensity of combat.

Finally, we have constructed more generalized models that can deal with arbitrary number of foundresses. The mortality function of males (the way lethal male combat works) has also been generalized. We have confirmed that the result remains true in the generalized models.

Most of our results are consistent with experimental data in *Melittobia* wasps (Abe et al., 2003a, 2005). Observed emergence patterns show that males emerge earlier than females on average. Observed sex ratio of newly emerging wasps is around 3% when two foundresses parasitized a host, which corresponds to very severe male–male combat in our model. In a male–male combat experiment in which two males are introduced into a small chamber, either male killed his opponent within 2 days in 49 pairs out of 53. These qualitative agreements suggest that the integrated effect of lethal male combat and schedule contributes to the extraordinary female-biased sex ratio in *Melittobia* wasps. Our model might also be applied to other species where lethal male combat and LMC occurs, such as fig wasps (West et al., 2001), *Cardiocondyla* ants (Cremer and Heinze, 2002) and *Ozopemon* beetles (Jordal et al., 2002).

It might be useful to describe how the present study is related to previous theoretical studies most of which use a kin-selection approach. Since we assume complete dispersal of female (and thus foundresses competing in the same host are not related), we did not need to consider inclusive fitness. This reduces the complexity of the problem and we could focus only on the effect of dynamic structure (sequential decision making). However, complete mixing of females is impossible (dispersal must be local to some extent) and foundresses sharing a host are generally related. Many previous studies had focused the effect of such a geographical structure. The integration of the two different approaches might be possible. Day and Taylor (1997) provide a generalized Hamilton’s rule that can be applicable in a dynamic game model. The expansion of the present study in this direction might be an interesting subject.

Throughout the paper, we have implicitly assumed that the optimal strategy is symmetric Nash equilibrium. In our model, such a solution is always an evolutionarily stable strategy (ESS). When we consider the evolution of the schedule of primary sex ratio, however, several analyses are necessary in order to show that a certain ESS is evolutionarily reached. In this paper, we have derived analytical expression of an ESS that is a prime candidate of the evolutionary outcomes. The uniqueness proof assures that there exists only one symmetric (monomorphic) ESS. Detailed evolutionary simulation might reveal if asymmetric (polymorphic) ESSs or non-convergent evolutionary dynamics are possible, which is left for future work.

Our model assumes complete symmetry between foundresses and also between males. However, in

superparasitism in the field, there must be asymmetry in the order by which a foundress finds a host and starts laying eggs. Moreover, an experiment on male–male combat in the *Melittobia* wasp shows that the order of emergence plays an important role for males, i.e., preexisting males almost always kill a newly emerged male (Abe et al., 2003a). In such an asymmetric game, the optimal behavior could be different from our result, which would be studied in future.

Acknowledgments

I greatly thank J. Abe for many valuable comments, carefully reading the draft, and fruitful discussions. I also thank the anonymous reviewers for helpful comments.

Appendix A

The dynamics of the number of sons are denoted by

$$\frac{d}{dt}m_i = -c \left(\sum_{j=1}^N m_j \right)^n m_i + x_i.$$

We seek the optimal control for a foundress with $i = 1$ when the other foundresses take the same wild-type strategy. Let $y = x_1$ and $x = x_2 = x_3 = \dots = x_N$.

$$\begin{aligned} H &= (1 - y) + \frac{m_1}{\sum_{j=1}^N m_j} (N - y - (N - 1)x) \\ &\quad + \lambda \left[-c \left(\sum_{j=1}^N m_j \right)^n m_1 + y \right] \\ &= 1 + \frac{m_1}{\sum_{j=1}^N m_j} (N - (N - 1)x) + \lambda \left[-c \left(\sum_{j=1}^N m_j \right)^n m_1 \right] \\ &\quad + y \left(\lambda - 1 - \frac{m_1}{\sum_{j=1}^N m_j} \right), \end{aligned}$$

$$\begin{aligned} \frac{d\lambda}{dt} &= -\frac{\partial H}{\partial m_1} = -\sum_{j=2}^N m_j \left(\sum_{j=1}^N m_j \right)^{-2} (N - y - (N - 1)x) \\ &\quad + c\lambda \left(\sum_{j=1}^N m_j + nm_1 \right) \left(\sum_{j=1}^N m_j \right)^{n-1}, \end{aligned}$$

$$\lambda(T) = 0.$$

These are generalized equations for Eqs. (3)–(5). Here we only consider a symmetric solution (ESS) and denote $z \equiv m_i$. For the internal y to be optimal,

$$\lambda = \frac{N + 1}{N}$$

and

$$x = y = z' + c(Nz)^n z = z' + cN^n z^{n+1}$$

hold. Putting these into

$$\begin{aligned} \frac{d}{dt}\lambda &= -\frac{(N-1)z}{(Nz)^2}(N-Nx) + c\lambda(Nz+nz)(Nz)^{n-1} \\ &= -\frac{N-1}{Nz}(1-x) + c\lambda(N+n)z(Nz)^{n-1}, \end{aligned}$$

we obtain (after some algebra)

$$z' = f(z), \tag{A.1}$$

$$f(z) = 1 - \frac{N(N-1) + (N+1)(N+n)}{N-1} cN^{n-1} z^{n+1}. \tag{A.2}$$

These are generalized form of Eq. (7). In a simple case ($n = 1$ and $N = 2$), we can directly solve Eqs. (A.1)–(A.2) to obtain Eq. (12). In general, $f(0) = 1$ and

$$f'(z) = -\frac{N(N-1) + (N+1)(N+n)}{N-1} cN^{n-1} (n+1)z^n < 0$$

for $z > 0$. For sufficiently large z , $f(z) < 0$. Thus, $f(z) = 0$ has a unique solution

$$Z = \left(cN^{n-1} \frac{N(N-1) + (N+1)(N+n)}{N-1} \right)^{-1/(n+1)}.$$

The solution of $z' = f(z)$ with the initial condition $z(0) = 0$ is the monotonic increase of z to converge to stable equilibrium $z = Z$. The sex ratio is

$$\begin{aligned} x &= 1 - \frac{N(N-1) + (N+1)(N+n)}{N-1} cN^{n-1} z^{n+1} + cN^n z^{n+1}, \\ &= 1 - cN^{n-1} \frac{(N+1)(N+n)}{N-1} z^{n+1}, \end{aligned}$$

which is a monotonically decreasing function of z . When $z = 0$, $x = 1$. When $z = Z$,

$$\begin{aligned} x &= 1 - \frac{(N-1)}{N(N-1) + (N+1)(N+n)} \cdot \frac{(N+1)(N+n)}{N-1} \\ &= \frac{N(N-1)}{N(N-1) + (N+1)(N+n)}. \end{aligned}$$

Therefore, $x(t)$ monotonically decreases from $x(0) = 1$ to approach the above expression.

We have obtained how the ESS sex ratio changes when it takes an intermediate value ($0 < x < 1$). Next we check the terminal condition. λ must decrease from $(N+1)/N$ to 0. When $x = 0$,

$$z' = -cN^n z^{n+1}$$

or

$$1 = (cN^n nt + C)z^n.$$

As long as $z > 0$, $z(t)$ monotonically decreases to converge to zero but $z = 0$ is impossible. As

$$\frac{d}{dt}\lambda = -\frac{N-1}{Nz} + c\lambda(N+n)N^{n-1}z^n \tag{A.3}$$

holds, $d\lambda/dt \rightarrow -\infty$ when $z \rightarrow +0$. This shows the terminal condition $\lambda(T) = 0$ can be satisfied by setting $x = 0$ for a finite period.

We have now found a solution satisfying the conditions Pontrjagin’s maximum principle requires. Next, we prove the uniqueness of the solution. The optimal control is

$$x = \begin{cases} 0 & \left(\lambda < \frac{N+1}{N} \right), \\ 1 & \left(\lambda > \frac{N+1}{N} \right). \end{cases}$$

Using this and

$$\begin{aligned} \frac{d\lambda}{dt} &= \frac{N-1}{Nz}(x-1) + c(N+n)N^{n-1}z^n\lambda, \\ \frac{dz}{dt} &= x - cN^n z^{n+1} \end{aligned}$$

we can perform phase plane analysis on (z, λ) space (Fig. 6). $z = (cN^n)^{-1/(n+1)}$ is an isocline for z when $x = 1$. $\lambda = (N-1)/c(N+n)N^n z^{n+1}$ is an isocline for λ when $x = 0$. Note that on a line $\lambda = (N+1)/N$, the vector field is not uniquely determined. In order to remain on the line, the control must take a special function $0 < x^*(t) < 1$, which we have obtained in the preceding analysis. The initial and terminal conditions are $z(0) = 0$ and $\lambda(T) = 0$, respectively. Thus, the solution must start from any point on λ -axis and reach any point on z -axis at $T = 0$. Looking into Fig. 6, it is apparent that such a solution must start from P , move right on a $\lambda = (N+1)/N$ line to reach Q , and then reach R by setting $x = 0$ (see Fig. 6).

Define $T = T_{P \rightarrow Q} + T_{Q \rightarrow R}$. Note that staying at point P is impossible because setting $x > 0$ causes increase in z and because setting $x = 0$ causes decrease in λ . Staying at point Q is also impossible because $z^*(t)$ is a monotonically increasing function of t . The point R is

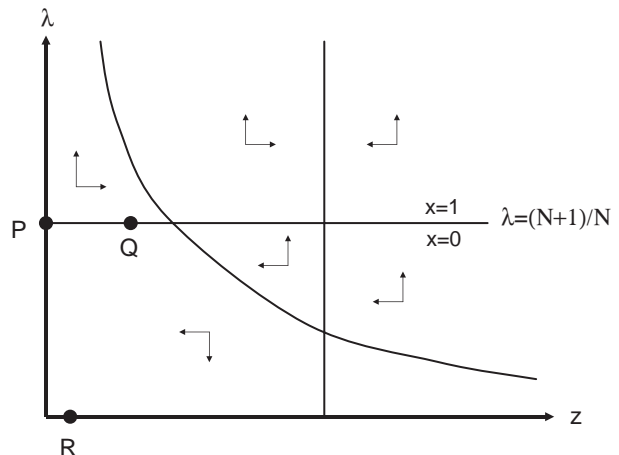


Fig. 6. Phase plane analysis (see text for detail).

uniquely determined by the point Q . Let z -coordinate of Q be z_Q . We prove both $T_{P \rightarrow Q}$ and $T_{Q \rightarrow R}$ are strictly increasing functions of z_Q , which proves the uniqueness of the point Q . The first part is obvious because we have already shown that z (strictly) monotonically increases when $0 < x < 1$. When $x = 0$, Eq. (A.3) shows that $d\lambda/dt$ is a strictly monotonically increasing function of z . Thus, it takes more time for λ to decrease from $(N + 1)/N$ to zero as z_Q is larger. This proves the second part.

As $z \rightarrow 0$, $d\lambda/dt \rightarrow -\infty$ and thus $T \rightarrow 0$ as $z_Q \rightarrow 0$. Therefore, there always exist a unique solution $P \rightarrow Q \rightarrow R$ for any $T > 0$.

Appendix B

In this case, we obtain

$$\frac{d}{dt} m_i = -\gamma \exp\left(k \sum_{j=1}^N m_j\right) m_i + x_i,$$

$$\begin{aligned} H &= (1 - y) + \frac{m_1}{\sum_{j=1}^N m_j} (N - y - (N - 1)x) \\ &\quad + \lambda \left[-\gamma \exp\left(k \sum_{j=1}^N m_j\right) m_1 + y \right] \\ &= 1 + \frac{m_1}{\sum_{j=1}^N m_j} (N - (N - 1)x) \\ &\quad + \lambda \left[-\gamma \exp\left(k \sum_{j=1}^N m_j\right) m_1 \right] + y \left(\lambda - 1 - \frac{m_1}{\sum_{j=1}^N m_j} \right), \end{aligned}$$

$$\begin{aligned} \frac{d\lambda}{dt} &= -\frac{\partial H}{\partial m_1} = -\sum_{j=2}^N m_j \left(\sum_{j=1}^N m_j \right)^{-2} (N - y - (N - 1)x) \\ &\quad + k\gamma\lambda \exp\left(k \sum_{j=1}^N m_j\right) m_1 + \gamma\lambda \exp\left(k \sum_{j=1}^N m_j\right), \end{aligned}$$

$$\lambda(T) = 0.$$

We denote $z \equiv m_i$ again. For the internal y to be optimal,

$$\lambda = \frac{N + 1}{N}$$

and

$$x = y = z' + \gamma Az$$

hold where $A \equiv \exp(kNz)$. Putting these into

$$\frac{d}{dt} \lambda = -\frac{N - 1}{Nz} (1 - x) + \gamma\lambda A (1 + kz)$$

we obtain

$$z' = g(z),$$

$$g(z) = 1 - \gamma Az \left\{ 1 + \frac{N + 1}{N - 1} (1 + kz) \right\}.$$

As $g(0) = 1$ and $g'(z) < 0$, $z(t)$ monotonically increases to converge to the equilibrium $z = Z$ where $g(Z) = 0$. The sex ratio

$$x = 1 - \gamma Az \frac{N + 1}{N - 1} (1 + kz)$$

monotonically decreases from $x(0) = 1$ to

$$X = \frac{N - 1}{2N + (N + 1)\alpha},$$

where $\alpha = kZ$ and it satisfies

$$\left\{ 1 + \frac{N + 1}{N - 1} (1 + \alpha) \right\} \alpha \exp(2\alpha) = \frac{k}{\gamma}.$$

The left-hand side is monotonically increasing function of α , while the right-hand side is a constant. Therefore, as k increases or λ decreases, α increases, i.e. X decreases.

Next we check the terminal condition. λ must decrease from $(N + 1)/N$ to 0. When $x = 0$,

$$z' = -\gamma z \exp(kNz)$$

hold. As long as $z > 0$, $z(t)$ monotonically decreases to converge to zero

$$\frac{d}{dt} \lambda = -\frac{N - 1}{Nz} + \gamma\lambda \exp(kNz) (1 + kz).$$

When z is infinitesimally small positive, $d\lambda/dt$ is infinitely small negative. This shows the terminal condition $\lambda(T) = 0$ can be satisfied by setting $x = 0$ for a finite period of time.

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