Co-evolution of nuptial gift and female multiple mating resulting in diverse breeding systems

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ABSTRACT

To show how diverse breeding systems, including polyandry, evolve in insects, I present a model of co-evolution between nuptial gift size and female multiple mating. I assume that males and females determine their strategy (amount of nuptial gift and frequency of mating, respectively) according to the strategy adopted by the other sex. The model demonstrates that co-evolution leads to diverse breeding systems: systems with both nuptial gift and female multiple mating, systems with nuptial gift only and systems with neither nuptial gift nor female multiple mating. The equilibrium breeding system is determined based on the sex ratio, efficiency of nuptial gift on the improvement of offspring survivorship, cost of nuptial gift production and cost of additional mating.

Keywords: breeding system, co-evolution, conflict resolution, nuptial gift, polyandry.

INTRODUCTION

The classical view (Bateman, 1948; Trivers, 1972; Emlen and Oring, 1977; Clutton-Brock and Vincent, 1991) is that a male's reproductive success is limited by the number of mates it copulates with, while a female's reproductive success is limited by ovule size. Thus, males can be seen as the competing sex and females as the choosing sex. If this is the case, then multiple mating will only be profitable for males (e.g. Bateman, 1948). There is, however, evidence to suggest that female multiple mating – that is, matings with more than one partner (Walker, 1980; Thornhill and Alcock, 1983; Smith, 1984; Reynolds, 1996; Yasui, 1998) – is widespread in many animal taxa, including insects, mammals, birds and fish (Thornhill and Alcock, 1983; Smith, 1984; Yamamura, 1986; Clutton-Brock, 1989; Eberhard, 1991; Birkhead and Møller, 1992; Turner, 1993).

Of the several hypothesized benefits of female multiple mating, 'direct benefits' are the most readily understood. The provision of nutrients, protection against predators and parental care are male investments that can increase female reproductive success by offsetting remating costs (Walker, 1980; Davies, 1992; Davies *et al.*, 1996; Reynolds, 1996; Yasui, 1998). Nutritious items provided by males at copulation (Thornhill, 1976;

Zeh and Smith, 1985) are consumed during or after insemination, enhancing the fecundity of females and/or offspring fitness (Gwynne, 1984a, 1988a,b, 1993; Simmons, 1990; Wedell, 1994; but see Wedell and Arak, 1989; Reinhold and Heller, 1993). This may facilitate female multiple mating in some insect species (Sakaluk and Cade, 1980; Burpee and Sakaluk, 1993).

This 'direct benefit' hypothesis states that both the females engaging in multiple mating and males providing the direct benefit play essential roles in the evolution of polyandry. Previous studies (Whittingham *et al.*, 1992; Westneat and Sherman, 1993; Sozou and Houston, 1994; Harada and Iwasa, 1996; Iwasa and Harada, 1998) have shown how the magnitude of paternal investment may depend on the frequency of multiple mating among females. There are two mechanisms by which the frequency of female multiple mating has an effect on the magnitude of paternal investment: first, it alters the paternity of the males (Whittingham *et al.*, 1992; Westneat and Sherman, 1993); second, it provides a game-theoretical situation about the amount of investment between the males sharing the same mate (Sozou and Houston, 1994; Harada and Iwasa, 1996; Iwasa and Harada, 1998). Although some models (Whittingham *et al.*, 1992; Westneat and Sherman, 1993; Sozou and Houston, 1994; Harada and Iwasa, 1996; Iwasa and Harada, 1998) have demonstrated how female multiple mating influences the optimal amount of paternal investment, they have not addressed the role of the female performing the multiple mating (but see Harada and Iwasa, 1996; Iwasa and Harada, 1998). In addition, these models (Harada and Iwasa, 1996; Iwasa and Harada, 1998), incorporating the interests of both sexes, assume perfect information about paternity to males. This makes it difficult to apply them to insect species where nuptial gifts are provided pre-zygotically or males do not discriminate between females engaging in many matings (Lynam *et al.*, 1992; but see Simmons *et al.*, 1993, 1994, where males discriminate against older females).

To predict how this interaction between female multiple mating and nuptial gift shapes a breeding system, it is necessary to take into consideration simultaneously the interests of both the investing sex (male) and the invested-in sex (female). However, such an interaction can be very complicated. Suppose that males provide nuptial gifts to females during courtship. In this case, multiple mating may also be favourable to females as they receive more gifts, so polyandry evolves. However, once evolved, the value of female multiple mating decreases, because the male's return from providing gifts will diminish as the share of paternity is reduced. Males will be selected to reduce their nuptial gifts, resulting in the recurrence of monogamy. If, on the other hand, environmental productivity is sufficiently high, females will not need nuptial gifts to rear their offspring. In this case, polyandry and nuptial gifts may not be selected. Such complicated interactions between male interests, female interests and environmental constraints require more than verbal argument.

Here, I present an analytically tractable model of male–female co-evolution for a breeding system. For the purpose of applying this model to an insect species for which a nuptial gift plays the role of enhancing female multiple mating, I restrict the model to the case where males do not know their paternity or where they cannot flexibly adjust the size of the nuptial gift to meet the share of paternity in each copulation. Furthermore, the population dynamics of receptive and unreceptive individuals, which is considered an important factor in shaping a breeding system (Yamamura, 1986; Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992; Parker and Simmons, 1996; Kvarnemo and Ahnesjö, 1996), is incorporated explicitly.

THE MODEL

Reproductive cycles of the sexes

Consider a population of animals that mate at a particular mating site. During a breeding season, M males mate repeatedly. Receptive females enter the mating site at constant rate, f, to mate and then lay eggs. The frequency of female matings in the mating site is x^* (≥ 1).

When a receptive male and a receptive female encounter one another, the male provides the female with sperm and an amount y^* (≥ 0) of a nuptial gift that increases offspring survivorship. The probability of the male fathering the offspring is given by $p(x, j)$ (≤ 1), independent of the size of the nuptial gift, where x is the number of males with which the female mates in the site and j ($\leq x$) is the order in which the male is accepted by the female.

After mating, the male spends time, yr_m, producing a gift for the next mating, where r_m is the time cost for a unit gift production. It takes longer to produce a larger gift. On finishing gift production, a male then searches for another mate. To acquire a receptive female takes time, s_m, which is determined by the density of receptive females. These assumptions capture a trade-off between the amount of the nuptial gift and mating frequency: a male with a smaller nuptial gift can mate with more females.

On completing x matings the female lays her eggs. The number of offspring surviving, w, increases with the amount r ($= xy$) of gift provided through matings by $w(r)$, where $w(r)$ is a smooth and monotonous increasing function of r with a convex curve converging to a constant (normalized to 1 in the model); that is, $w'(r) > 0$, $w''(r) < 0$ and $\lim_{r \to \infty} w(r) = 1$.
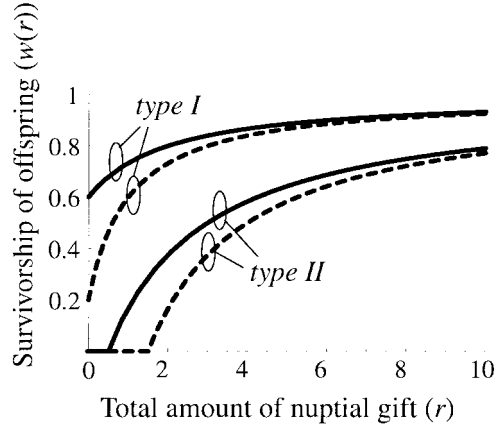
Two types of functions are assumed for $w(r)$ (Fig. 1). Type I is for the case where some offspring can survive without the nuptial gift; that is, $w(r) > 0$; $w'(r) > 0$; $w''(r) < 0$; $w(0) = w_0 > 0$. In this case, $r/Q(r)$ increases with r at $r = 0$, where $Q(r) = w(r)/w'(r)$. $r/Q(r)$ is also assumed to quickly become a decreasing function of r as r increases, implying a quick saturation of $w(r)$ with increasing r. Assume that $r/Q(r) \to 0$ as $r \to \infty$, implying that $w'(r)/w(r)$ goes to 0 as $r \to \infty$ in an order greater than r. Thus, $w'(r)$ goes to 0; that is, $w(r)$ saturates as $r \to \infty$.

With a Type II function, the nuptial gift is essential for offspring survivorship. That is, no offspring can survive without the nuptial gift: $w(r) = 0$ for $r \leq 0$; $w(r) = 0$ for $r < r_0$; $w(r) > 0$; $w'(r) > 0$; $w''(r) < 0$. Here, it is assumed that $r/Q(r)$ decreases with r, where $Q(r) = w'(r)/w(r)$, for $w(r) > 0$, implying that $w(r)$ saturates quickly as r increases.

The physical condition of the female is also assumed to influence the shape of the survivorship function: the nuptial gift increases offspring survivorship more when the female's physical condition is poor; that is, $w'(r)$ and $w(r)$ are set to a higher and lower value, respectively, for a poorer physical condition (Fig. 1). Furthermore, it is assumed that female multiple mating brings about a cost to the female's lifetime reproductive success because of the increased risk of predation, sexual disease or energy cost. For simplicity, for the cost function $C(x)$ I used an exponential function, $\exp(-cx)$, where c represents the extent of this mating cost.

Population dynamics

Assume that the frequency of a female's matings and the size of the nuptial gift are strongly concentrated around x^* and y^*, respectively. At equilibrium, the density of females mated

Fig. 1. Two types of the offspring-survivorship function $w(r)$. In Type I, the nuptial gift is not essential for offspring survivorship. The survivorship of offspring with no nuptial gift is set to a constant, w_0. Type II is for where the amount r_0 of nuptial gift is essential for offspring survivorship. Solid and dotted lines represent good and poor physical condition of females, respectively. To construct the figure, the following functions are used: $w(r) = (r + aw_0)/(r + a)$, where $(a, w_0) = (2, 0.6)$ (for good condition) or $(1, 0.2)$ (for poor condition) for Type I; $w(r) = (r - r_0)/(r + a)$, where $(a, r_0) = (2, 0.5)$ (for good condition) or $(1.5, 1)$ (for poor condition) for Type II.

n times, $f_s^*(n)$, should be the same value f_s^* for all n, since all receptive females mate with males at the same rate ($aM_s f_s(n)$). The total density of receptive females, F_s^*, at equilibrium is the sum of receptive females with n matings for all n, that is,

$$F_s^* = x^* f_s^* \tag{1}$$

The ratio of the number of receptive males, M_s^*, to that of non-receptive males, $(M - M_s^*)$, is equal to the inverted ratio of the non-receptive period, yr_m, to the receptive period (searching time, $s_m^* = 1/(aF_s^*)$). Then, it must hold that

$$\frac{M_s^*}{M - M_s^*} = \frac{(1/aF_s^*)}{y^* r_m} \tag{2}$$

As receptive female recruits and those becoming non-receptive should balance at equilibrium, it follows that

$$f_s^*(x) = \frac{f}{aM_s^*} \tag{3}$$

Taking equations (1), (2) and (3) together, the number of receptive females, F_s^*, and males, M_s^*, at equilibrium are given by

$$F_s^* = x^* f_s^* = \frac{1}{a\{(M/fx^*) - y^* r_m\}} \tag{4a}$$

and

$$M_s^* = M - fr_m x^* y^* \tag{4b}$$

respectively. The searching time for a male to acquire one receptive female, s_m^* $(= 1/(aF_s^*))$, and that for a female to find one receptive male, s_f^* $(= 1/(aM_s^*))$, can also be determined.

Evolutionary dynamics

Let us now examine the evolutionary dynamics of x^* and y^*. Suppose that most females engage in x^* matings and that most males provide y^* of nuptial gift. The fitness of a mutant female engaging in multiple mating with a slightly different frequency x is given by

$$W_f = w(xy^*)C(x) \tag{5}$$

where xy^* is the total amount of nuptial gift provided to the mutant female, w is the number of the surviving offspring and $C(x)$ is the cost of an additional mating.

On the other hand, the fitness of a rare male with a slightly different amount y of nuptial gift is given by its rate of reproduction:

$$W_m = \frac{w((x^* - 1)y^* + y)Q_{x*}}{s_m^* + yr_m} \tag{6}$$

where the numerator on the right-hand side represents the expected number of surviving offspring fathered by the male (given by the product of the surviving-offspring number, w, and the probability with which one offspring is fathered by the male, Q_{x*}) and the denominator is the time required for one breeding cycle. Since the eggs of a female are all fertilized by the males accepted in the mating site and the expected paternity should be the same for all males, it follows that Q_{x*} must be equivalent to the average paternity $1/x^*$.

Assuming that the population dynamics time-scale is much faster than that of evolutionary dynamics, the co-evolutionary dynamics of x^* and y^* can be approximated by examining the gradient of (ln W_f) and (ln W_m) at population equilibrium. For simplicity, I treat the female mating frequency as a continuous trait, although, in reality, it is a discrete trait. (By conducting numerical calculations for a discrete version of this model, I confirmed that this approximation does not change the qualitative aspects of the main results.) Assuming that the genetic covariance of x^* and y^* is negligibly small, the co-evolutionary dynamics is given by

$$\frac{dx^*}{dt} = g_x \left(\frac{\partial \ln W_f}{\partial x} \bigg|_{x=x^*} \right) \tag{7a}$$

and

$$\frac{dy^*}{dt} = g_y \left(\frac{\partial \ln[W_m]_{S_m = S_m^*(x^* \cdot y^*)}}{\partial y} \bigg|_{y=y^*} \right) \tag{7b}$$

where g_x and g_y are constant values representing the intensity of selection (Abrams *et al.*, 1993; for its derivation as an approximation of a simple quantitative genetic model, see Iwasa *et al.*, 1991; Taper and Case, 1992).

RESULTS

The co-evolutionary dynamics of a female's mating frequency, x^*, and the size of the nuptial gift, y^*, can be obtained by combining the evolutionary dynamics of female mating frequency with that of nuptial gift.

Type I function

The evolutionary (Maynard-Smith, 1982) – and also convergent-stable (CS; Christiansen, 1991) – frequency x^{CS} of female mating and the CS size of nuptial gift y^{CS} are given as solutions of

$$y^* w'/w - c = 0 \qquad (8a)$$

and

$$(w'/w) - (fr_m x^*/M) = 0 \qquad (8b)$$

respectively. These are derived from $\partial \ln W_f/\partial x|_{x=x^*} = 0$ and $\partial \ln W_m/\partial y|_{y=y^*} = 0$, respectively; note that $\partial^2 \ln W_f/\partial x^2|_{x=x^*} < 0$ and $\partial(\partial \ln W_f/\partial y|_{x=x^*})/\partial x^* < 0$ for x^{CS}, and that $\partial^2 \ln W_m/\partial y^2|_{y=y^*} < 0$ and $\partial(\partial \ln W_m/\partial y|_{y=y^*})/\partial y^* < 0$ for y^{CS}. Equation (8a) suggests that x^{CS} is a unimodal function of y^*, implying the existence of a value of y^* that maximizes the CS frequency of female mating. Equation (8b) suggests that the CS nuptial gift size decreases monotonously with increasing frequency x^* of female mating, and is zero when x^* is large enough (Fig. 2b).

By taking the dynamics of x^* and y^* together, the six possible co-evolutionary dynamics shown in Fig. 2b are obtained. This system always converges to a unique equilibrium breeding system, $(\hat{x}, \hat{y})$, which is given as follows (see Appendix for dynamical stability).

If it holds that $(M/fr_m)\{w'(r^*)/w(r^*)\} > 1$, then

$$(\hat{x}, \hat{y}) = ((M/fr_m)\{w'(r^*)/w(r^*)\},\ c\{w(r^*)/w'(r^*)\}) \qquad (9a)$$

where

$$r^* = cM/fr_m \qquad (9b)$$

If it holds that $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} \leq 1$ and that $w'(0)/w(0) > fr_m/M$, then

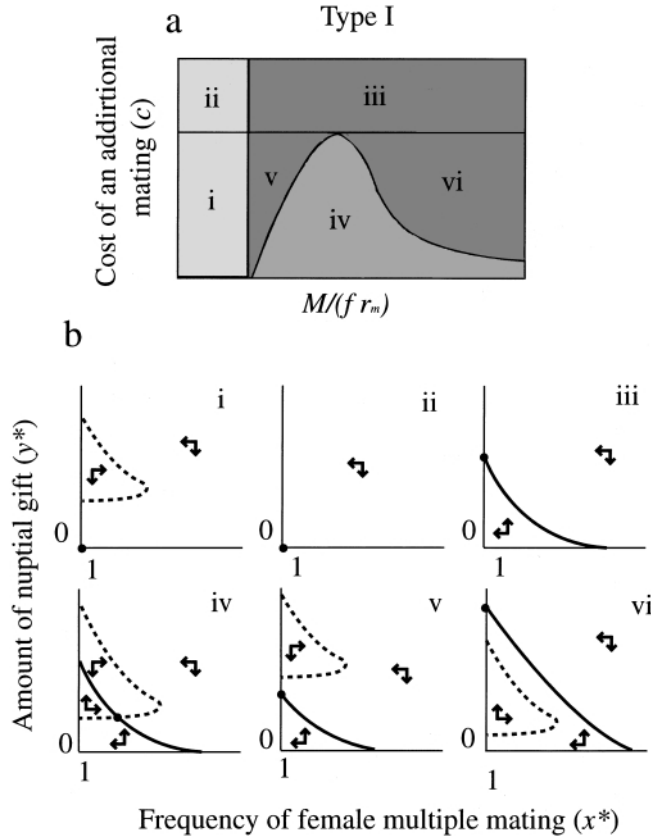$$(\hat{x}, \hat{y}) = (1, \tilde{y}) \qquad (10a)$$

and

$$r^* = \tilde{y} \qquad (10b)$$

where $\tilde{y}$ is a solution of equation (8b) for $x^* = 1$.

If it holds that $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} \leq 1$ and that $w'(0)/w(0) \leq fr_m/M$, then

$$(\hat{x}, \hat{y}) = (1, 0) \qquad (11a)$$

Fig. 2. (a) Six regions (regions i–vi) in the parameter space of (M/fr_m, c) that represent the conditions under which different evolutionary dynamics develop for the Type I function; (b) the corresponding six evolutionary dynamics (i–vi) of frequency of female multiple mating and nuptial gift size. The function $w(r) = (r + aw_0)/(r + a)$ (where $a > 0$) is used to construct this figure. In (a) the light grey, grey and dark grey regions represent the conditions under which breeding systems I-A, I-B and I-C (defined in the text) develop, respectively. In (b) an arrow represents the vector indicating the direction of evolutionary dynamics in each region surrounded by zero-isoclines (represented by solid lines for female multiple mating and by dotted lines for nuptial gift) of the dynamic system. Solid circles represent the stable steady states of the system.

and

$$r^* = 0 \qquad (11b)$$

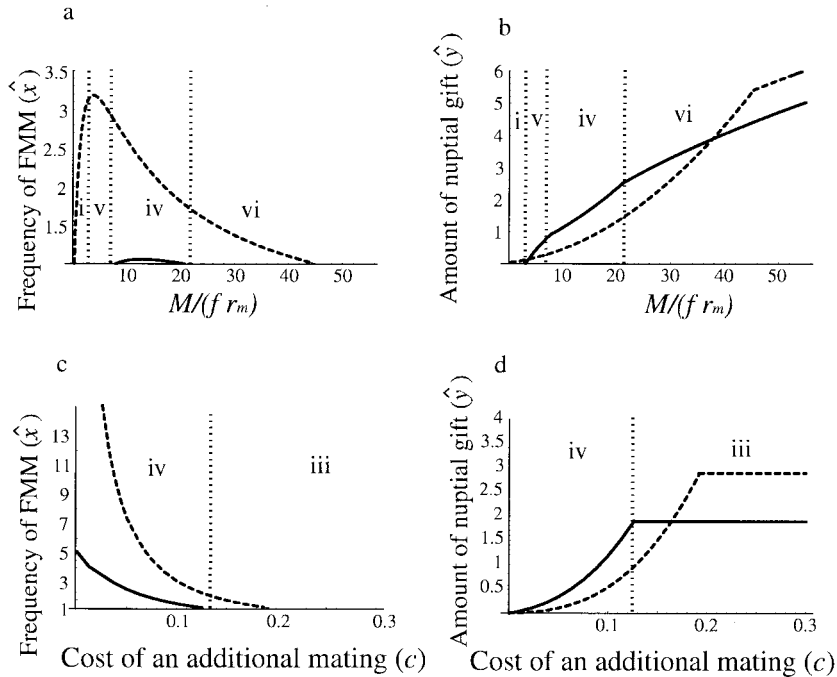The equilibrium breeding systems can be classified into the following three types:

- *Type I-A*, where the amount of nuptial gift is zero, and hence females engage in no multiple matings ($\hat{x} = 1$ and $\hat{y} = 0$).
- *Type I-B*, where female multiple mating and a nuptial gift both evolve ($\hat{x} > 1$ and $\hat{y} > 0$).
- *Type I-C*, where a nuptial gift evolves but female multiple mating does not ($\hat{x} = 1$ and $\hat{y} > 0$).

The environmental conditions under which each breeding system evolves can be represented in the parameter space of $M/(fr_m)$ and c (Fig. 2a). When $M/(fr_m)$ is smaller than a threshold value (to hold that $M/(fr_m) \leq w(0)/w'(0)$; to fall in region i or ii in Fig. 2a), a Type I-A system develops. A Type I-B system develops when $M/(fr_m)$ is moderate and c is small ($M/(fr_m) > w(0)/w'(0)$ and $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} > 1$; region iv in Fig. 2a). When $M/(fr_m)$ is either small or high and c is large ($M/(fr_m) > w(0)/w'(0)$ and $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} < 1$; region iii, v or vi in Fig. 2a), a Type I-C system develops.

The equilibrium frequency $\hat{x}$ of female mating peaks when $M/(fr_m)$ is intermediate (Fig. 3a,b). The equilibrium size $\hat{y}$ of the nuptial gift increases monotonously with increasing $M/(fr_m)$. With increasing cost of additional mating c, $\hat{x}$ decreases, while $\hat{y}$ increases (Fig. 3c,d). When the improvement efficiency of the nuptial gift on offspring survivorship is high, $\hat{y}$ is high when female multiple mating does not occur (i.e. $\hat{x} = 1$), whereas $\hat{x}$ is higher and $\hat{y}$ is lower if female multiple mating does occur (Fig. 3).

Type II function

For a Type II function, the CS frequency, x^{CS}, of female mating and the CS size of nuptial gift, y^{CS}, are given as solutions to equations (8a) and (8b), respectively. The CS size of nuptial gift, y^{CS}, decreases monotonously with increasing frequency, x^*, of female mating

Fig. 3. The typical pattern of the dependence of frequency of female multiple mating, $\hat{x}$, and nuptial gift size, $\hat{y}$, at the evolutionary equilibrium on $\{M/(fr_m)\}$ (a, b) and c (c, d) for a Type I function. The parameters are $c = 0.12$ for the former and $\{M/(fr_m)\} = 15$ for the latter. To construct this figure, the functions given in Fig. 2 were used. The set of $(\hat{x}, \hat{y})$ at the equilibrium is classified into phases i–vi in Fig. 2.
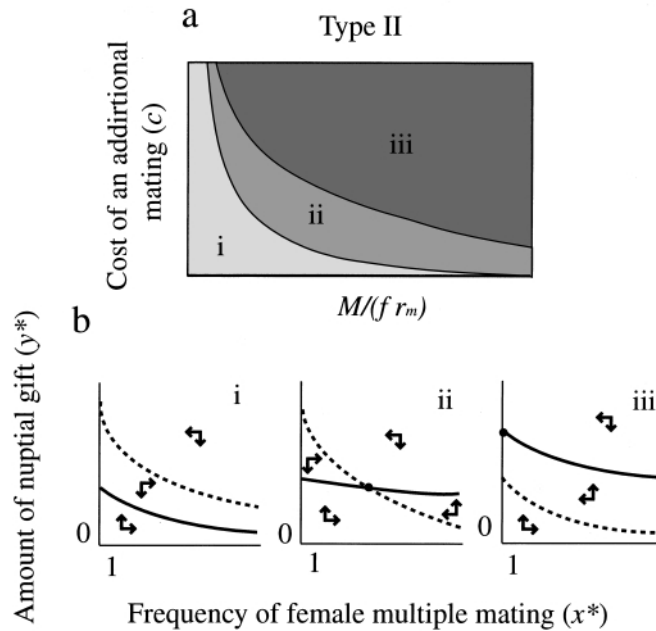
(as indicated by the zero-isocline for y^* in Fig. 4b). In this case, a nuptial gift size less than r_0 makes offspring survivorship zero, and the CS amount, y^{CS}, of the nuptial gift never reaches 0 even if x^* is very large. The CS frequency, x^{CS}, of female mating increases with decreasing nuptial gift (as indicated by the zero-isocline for x^* in Fig. 4b).

The equilibrium breeding systems can be classified into the following three types (Fig. 4b):

- *Type II-A*, where a nuptial gift evolves but female multiple mating does not ($\hat{x} = 1$ and $\hat{y} > 0$; the equilibrium is given by equations 10a and 10b).
- *Type II-B*, where the system reaches the unique evolutionarily stable point where female multiple mating and a nuptial gift both evolve ($\hat{x} > 1$ and $\hat{y} > 0$; the equilibrium is given by equations 9a and 9b).
- *Type II-C*, where an arms race develops, where the size of the nuptial gift converges to zero as female mating frequency goes to infinity ($\hat{x} \to \infty$ and $\hat{y} \to 0$).

The environmental conditions necessary for each breeding system are as follows. When $M/(fr_m)$ and c are large (to hold that $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} \leq 1$; region iii in Fig. 4a), the Type II-A system develops. When either $M/(fr_m)$ or c decrease (to hold that $(M/fr_m)\{w'(cM/fr_m)/w(cM/fr_m)\} > 1$; region ii), the equilibrium system is that of Type II-B. For smaller $M/(fr_m)$ or decreased c ($r_0 \geq cM/(fr_m)$; region ii), the Type II-C system develops.
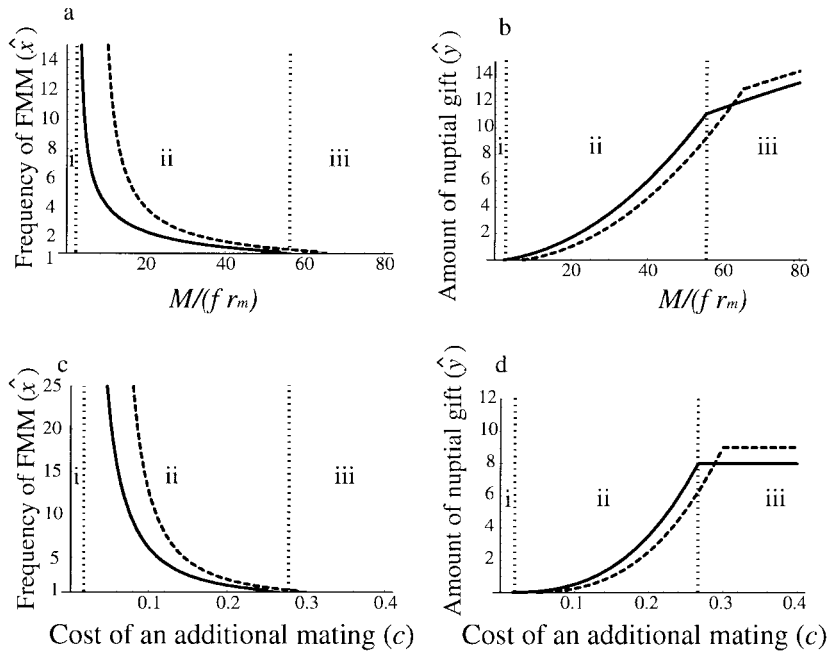

Fig. 4. (a) Three regions (i, ii and iii) in the parameter space (M/fr_m, c) that represent the conditions under which different evolutionary dynamics develop for a Type II function; (b) the three corresponding evolutionary dynamics (i, ii and iii) of female multiple mating and nuptial gift. Function $w(r) = (r - r_0)/(r + a)$ (where $a > 0$) is used to construct this figure. In panel (a) the dark grey, grey and light grey regions represent the conditions under which breeding systems II-A, II-B and II-C develop, respectively. The symbols used are the same as those in Fig. 2.

With increasing $M/(fr_m)$, the equilibrium female mating frequency, $\hat{x}$, decreases, while the equilibrium size of nuptial gift, $\hat{y}$, increases (Fig. 5a,b). As c increases, $\hat{x}$ decreases and $\hat{y}$ increases (Fig. 5c,d). A greater improvement efficiency enhances $\hat{x}$ and decreases $\hat{y}$ if female multiple mating occurs, whereas it increases $\hat{y}$ if it does not (Fig. 5).

DISCUSSION

First, I summarize the potential interactions between the evolution of nuptial gift size and frequency of female multiple mating. The female mating frequency always decreases with increasing size of the paternal nuptial gift. There are two reasons for this negative effect. First, the benefit of giving a nuptial gift to a female engaging in more multiple mating and, therefore, who receives additional nuptial gifts from other males, is lowered (Sozou and Houston, 1994; Harada and Iwasa, 1996). Second, the number of receptive females, f_s, increases with female mating frequency (see Parker and Simmons, 1996). This increases mate availability for males (i.e. searching time, s_m, is lowered) and thus favours males with smaller nuptial gifts whose reproductive success is achieved by mating with more females rather than by donating more nuptial gifts.

The model clearly illustrates that larger nuptial gifts do not always facilitate female multiple mating. Rather, the effect of the size of nuptial gift on female mating frequency is strongly dependent on the importance of the nuptial gift for offspring survivorship. When

Fig. 5. The typical pattern of the dependence of frequency of female multiple mating, $\hat{x}$, and nuptial gift size, $\hat{y}$, at the evolutionary equilibrium on $\{M/(fr_m)\}$ (a, b) and c (c, d) for a Type II function. The parameters are $c = 0.2$ for the former and $\{M/(fr_m)\} = 30$ for the latter. To construct this figure, the functions given in Fig. 1 were used. The set of $(\hat{x}, \hat{y})$ at the equilibrium can be classified into phases i–iii in Fig. 4.

the nuptial gift is not essential for offspring survivorship (i.e. Type I survivorship function), peak female mating frequency occurs when the size of that gift is intermediate. This is because either a larger nuptial gift from one male, which is sufficient for the survivorship of offspring, or a smaller gift, which does not meet the cost of additional matings, does not favour the evolution of female multiple mating. In contrast, when a certain amount of nuptial gift is essential for offspring survivorship (i.e. Type II survivorship function where an amount r_0 of nuptial gift is always required), the favoured female mating frequency increases with decreasing size of nuptial gift.

Co-evolution can result in diverse breeding systems, including systems with female multiple mating and nuptial gifts, systems with nuptial gifts but no female multiple mating and systems with neither nuptial gifts nor female multiple mating. What breeding system evolves is determined by a combination of environmental constraints: the sex ratio, the time cost per unit of nuptial gift, the cost of an additional mating and the shape of the offspring-survivorship function (including the improvement efficiency and the importance of a nuptial gift). In addition, the model suggests that the pattern of sperm precedence (expressed by the shape of the function $p(n, j)$) does not affect the evolving breeding system as long as males cannot discriminate females that have already mated.

The predicted effects of these environmental constraints on the behaviour of the sexes can be summarized as follows:

Nuptial gift. The size of the nuptial gift increases with a male-biased sex ratio, decreased cost of nuptial gift or increased cost of additional mating. The effect of the improvement efficiency can act in opposite directions depending on whether or not female multiple mating occurs (i.e. phase iv for Type I and all phases for Type II). When females do not engage in multiple matings, the higher efficiency of the nuptial gift in improving offspring survivorship, which increases the benefit of a nuptial gift, enhances that gift. In contrast, when female multiple mating does occur, the more improved efficiency leads to increased female mating frequency, resulting in a reduction in the nuptial gift.

Female multiple mating. The effects of sex ratio and cost of nuptial gift on female multiple mating equilibrium strongly depends on the type of survivorship function. If the function is Type I and if either (M/f) is small or r_m is large (falling on $M/(fr_m)$, which gives x^* on the left-hand side of the peak of the convex curve in Fig. 2a), either the female-biased sex ratio or the higher cost of nuptial gift will prevent female multiple mating from occurring. A female-biased sex ratio and a higher cost of nuptial gift favours female multiple mating under the following conditions: (1) the function is Type I and either (M/f) is large or r_m is small (to fall on $M/(fr_m)$, which gives x^* on the right-hand side of the peak of the convex curve in Fig. 2a); (2) the function is Type II. The higher efficiency of the nuptial gift and lower cost of additional mating always enhance female mating frequency.

The model predicts that the diet condition (or habitat productivity), influencing either the time cost per unit of nuptial gift, r_m, or the improvement efficiency of the nuptial gift on survivorship function, have the potential to alter the breeding system. Studies on crickets (Gwynne, 1984b, 1990, 1993; Gwynne and Simmons, 1990; Simmons and Bailey, 1990), in which diet condition (or population density affecting the food availability) altered the size of nutritional spermatophore or female mating frequency, support this prediction. All of the above studies showed that diet condition is negatively correlated with the size of nuptial gift. These findings do not contradict the predictions of the present model that, when

female multiple mating occurs, the increased cost of the nuptial gift and the alteration of the survivorship function from a non-efficient to an efficient one, lower the size of the nuptial gift in all cases.

Furthermore, the model predicts that the effect of reduced diet on the frequency of female mating varies, depending on the relative intensity and direction of the two effects of the alteration in the survivorship function and the increased cost of the nuptial gift. Indeed, when diet is reduced, female mating frequency sometimes increases (Gwynne, 1990; Gwynne and Simmons, 1990; Simmons and Bailey, 1990), but sometimes does not (Gwynne, 1984b, 1993).

The model demonstrates that, if the survivorship function is of Type II and if either $Ml(fr_m)$ or c is small to fall on region i, an apparent endless arms race of nuptial gift size and frequency of female multiple mating can take place. The amount of nuptial gift converges to zero, while female mating frequency goes to infinity. This can be explained as follows. Under the Type II function, female multiple mating is facilitated by a lowered amount of nuptial gift. Once females become engaged in frequent multiple mating, mutant males with a smaller nuptial gift always invade the population, since the loss of fitness by giving less nuptial gift is small because a larger nuptial gift is provided by other males. Thus, the increase in female mating frequency, which is caused by the decreased size of nuptial gift, enhances a further reduction in the amount of nuptial gift, resulting in the endless arms race.

In the present paper, I have considered a case where the pre-zygotic nuptial gift provides benefits to offspring. In fact, the spermatophore of crickets is supposed to enhance offspring survivorship in some species (Wedell, 1994). However, it is also known that the spermatophore of some species has no effect on longevity, fecundity or egg weight (Wedell and Arak, 1989; Reinhold and Heller, 1993; Will and Sakaluk, 1994; Vahed and Gilbert, 1997; Kasuya and Sato, 1998) and is supposed to function as a mating effort of males to increase paternity (Sakaluk, 1984; Wedell, 1991, 1993, 1994; Reinhold and Heller, 1993). This role of the nuptial gift is not considered in the present paper, but it may generate another co-evolutionary process of nuptial gift and female multiple mating, and hence another relationship between environmental conditions and breeding systems.

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APPENDIX: STABILITY ANALYSIS OF THE EQUILIBRIUM POINT $(\hat{x}, \hat{y})$

The vector field of i, ii, iii, v and vi in Fig. 2b and the vector field of iii in Fig. 4b show that these equilibria are evolutionarily and convergent stable. The other equilibrium, $(\hat{x}, \hat{y})$, is also evolutionarily and convergent stable. A proof follows. The criteria are $F_{xx} + G_{yy} < 0$ and $F_{xx}G_{yy} - F_{xy}G_{yx} > 0$, where:

$$F_{xx} = (d/dx^*)(\partial \ln W_f/\partial x|_{x=x^*, y=y^*}) \qquad G_{yy} = (d/dy^*)(\partial \ln W_m/\partial y|_{x=x^*, y=y^*})$$

$$F_{xy} = (d/dy^*)(\partial \ln W_f/\partial x|_{x-=x^*, y=y^*}) \qquad G_{yx} = (d/dx^*)(\partial \ln W_m/\partial y|_{x=x^*, y=y^*})$$

(Abrams *et al.*, 1993). In our model, F_{xx}, G_{yy}, F_{xy} and G_{yx} are given as $y^2\phi$, $x\phi$, $(w'/w) + xy\phi$ and $y\phi - (r_m f/M)$, respectively, where $\phi = d(w'/w)/dr$. F_{xx} and G_{yy} are negative because $\phi = (w''w - w'^2)/w^2 < 0$, suggesting that $F_{xx} + G_{yy} < 0$. Noting $dy^*/dt = (w'/w) - (fr_m x^*/M) = 0$ at the equilibrium, it follows that $F_{xx}G_{yy} - F_{xy}G_{yx} = y\phi\{(fr_m x^*/M) - (w'/w)\} + (w'/w)(r_m f/M) = (w'/w)(r_m f/M) > 0$. Thus, this proves that the equilibrium point is stable.