



# Evolution of periodicity in insect mate-seeking behaviour: a male–female coevolutionary game model

MICHIO KONDOH\* & JUN-YA IDE†

\*Center for Ecological Research, Kyoto University

†Department of Zoology, Graduate School of Science, Kyoto University

(Received 29 April 2002; initial acceptance 6 June 2002;  
final acceptance 22 September 2002; MS. number: 7309)

It is widely observed that mate-seeking behaviour in insects starts suddenly at a species-specific time and lasts at most for a few hours (i.e. periodic). Although several hypotheses have been proposed to explain why periodicity occurs, none has incorporated a game-theoretical situation within and between the sexes at the same time. Using a theoretical model, we show that the coevolution of mating strategies can result in the emergence of two distinct population level phases: with and without mate seeking. In the mate-seeking phase, all individuals (male or female) search for mates, whereas no individuals seek mates in the phase without mate seeking. If there are individuals that do not seek mates in the mate-seeking phase, the model predicts that these should be of the sex with (1) lower survivorship during mate-seeking behaviour; (2) higher survivorship during nonmate-seeking behaviour; (3) higher expected future reproductive potential or (4) the sex towards which the sex ratio is biased. Furthermore, the model predicts that the mate-seeking phase is favoured when individuals have (1) high searching efficiency, (2) high survivorship during mate-seeking behaviour of either males or females, (3) low survivorship during nonmate-seeking behaviour of either males or females, or (4) low future reproductive potential for either males or females. In addition, the model suggests the existence of a critical environmental condition that divides these two phases, predicting that gradual changes in this condition trigger a sudden transition between the mate-seeking and nonmate-seeking phases.

© 2003 Published by Elsevier Science Ltd on behalf of The Association for the Study of Animal Behaviour.

Periodic mate-seeking behaviour is widespread among insect species. For example, swarming is a frequent mate-seeking tactic amongst Diptera, Ephemeroptera, Heteroptera, Hymenoptera, Neuroptera and Trichoptera (Sivinski & Petersson 1997). Generally, swarms form suddenly at species-specific times and last at most for a few hours. All copulation that takes place during that day occurs in this short period, and neither males nor females show mating behaviour for the rest of the day (Kon 1984; Allan & Flecker 1989; Gaugler & Schutz 1989). This type of daily rise in mate-seeking activity and the sudden transition between seeking and nonseeking phases are also observed in species with other kinds of mate-locating behaviour, such as territory holding, searching flight and sex pheromone releasing (Bitzer & Shaw 1995; Cardé et al. 1996; Koshio 1996; Harari et al. 2000; Kawamura

et al. 2001). Hereafter we refer to this type of mate-seeking activity pattern as 'periodic mate-seeking behaviour'.

Some authors have suggested that periodic mate-seeking behaviour takes place when there are periodic changes in environmental conditions, for example predation pressure (Yuval & Bouskila 1993) or air temperature (Bitzer & Shaw 1995), that determine the cost or efficiency of mate seeking. Periodicity of mating behaviour has been explained by considering mating strategies from the male perspective. In some situations, the periodic mate-seeking behaviour of males has been attributed to a corresponding periodic mate-seeking behaviour by females (Iwasa & Obara 1989; Rutowski et al. 1996). In some insect species, females tend to be sexually receptive for only a brief period (Cardé et al. 1996; Harari et al. 2000). For example, females of the almond moth, *Ephestia cautella*, release sex pheromones only during the first half of the night (Quartey & Coaker 1996). In such species, it would be adaptive for males to synchronize their mate-seeking behaviour with the release of the sex pheromones by the females, as independent mate-seeking behaviour

Correspondence and present address: J.-Y. Ide, Department of Environmental Science, Graduate School of Science and Technology, Kumamoto University, 2-39-1 Kurokami, Kumamoto 860-8555, Japan (email: ide@sci.kumamoto-u.ac.jp). M. Kondoh is now at the Cardiff School of Biosciences, Cardiff University, P.O. Box 915, Cardiff CF10 3TL, U.K.

would be costly and inefficient. This type of synchronization occurs in *E. cautella*, where male attraction to synthetic female sex pheromones peaks when the release of pheromones by the females is greatest (Quartey & Coaker 1996).

However, there are problems with these explanations of the periodicity of mating behaviour. First, most hypotheses (Iwasa & Obara 1989; Yuval & Bouskila 1993; Bitzer & Shaw 1995; Rutowski et al. 1996) have considered the interest of the males alone. In reality, however, the different interests of both sexes would simultaneously determine the mating system. Females should be regarded as an active sex, with the potential to alter the mating period and mating behaviour. Second, previous models have either overlooked a game-theoretical situation within each sex (Bitzer & Shaw 1995; Rutowski et al. 1996), or have assumed a fixed strategy for either sex (Iwasa & Obara 1989; Quartey & Coaker 1996; Rutowski et al. 1996), and therefore have not incorporated a game-theoretical situation between males and females. Individuals of one sex can be considered a resource for the other sex. Therefore, the reproductive success of an individual often increases with an increase in available mates, and decreases as the number of competing individuals increases. This is true not only for males but also for females in situations where male numbers limit the reproductive success of females (Arnqvist & Nilsson 2000). An increased number of potential mates can increase the females' opportunity to choose a mate and ensure mating with a high-quality male (Thornhill & Alcock 1983), increase the nuptial gift provided to the female (Thornhill 1976), or decrease the mate-searching time, thereby increasing the period spent on oviposition (Wickman & Jansson 1997). In such cases, the female's mate-seeking behaviour would be subject to natural selection, and therefore male–female mate-seeking behaviour would coevolve. A change in the strategy of one sex would drive further changes in the adaptive behaviour of the other sex. To incorporate these interactions between population members, it is essential to consider a game-theoretical situation within each sex as well as between the sexes (Székely et al. 1996; Ide & Kondoh 2000).

We present a theoretical hypothesis to understand how a species-specific mating period is determined and explain why the mating behaviour of some insects is periodic. We show that the male–female coevolutionary game can be a key to population-level transition between mating and nonmating phases. We compare two simple models (with and without a male–female game) of the evolution of mate-seeking behaviour. One model (a model without male–female coevolution) considers a game-theoretical situation of mate-seeking behaviour within either sex alone, and the other model (a model with male–female coevolution) incorporates a game-theoretical situation both within each sex and between the sexes. In the model without male–female coevolution, the fraction of mate-seeking individuals gradually changes with gradual changes in environmental conditions. This implies that previous hypotheses that attribute population-level phase transition to environmental change are not applicable to the cases without

sudden changes in environmental conditions (e.g. Allan & Flecker 1989). In contrast, in the model with a male–female game, two population-level phases of reproductive behaviour, a mate-seeking phase (where all individuals search for mates) and a nonmate-seeking phase (no individual search for mates) emerge and a sudden transition between them is triggered by gradual changes in environmental conditions. This is explained by a positive feedback mechanism operating between mate availability and the strategies of both sexes. These distinct strategies determine the number of mate-seeking and nonmate-seeking individuals of each sex. This determines the potential number of mates and competitors for each sex and drives further male–female coevolution.

In the present model we do not explicitly consider dynamic changes in sexually active or nonactive individual abundances that result from mate-seeking behaviour, although such dynamics can influence the adaptive timing of mate-seeking behaviour (Iwasa & Obara 1989). Instead, we assume that an individual's strategy has little influence on the abundance of sexually active or nonactive individuals. This assumption may be too simplified, but has two advantages. First, reproductive dynamics have a potential to generate switching between mate-seeking and nonmate-seeking phases under some assumptions. By excluding this effect, we focus on the effect of a game-theoretical situation on mate-seeking behaviour. Second, reproductive dynamics usually make system behaviour very complex, especially when considering a game-theoretical situation. Keeping the model analytically tractable allows clear insight into the mechanism operating in the present model.

## THE MODEL AND RESULTS

Consider an insect population composed of males and females with densities of  $M$  and  $F$ , respectively. In this model the time period is divided into a number of intervals (i.e. bouts). In each bout, an individual of each sex chooses a mate-seeking behaviour from two alternatives: mate-seeking or nonmate-seeking. Mate-seeking behaviour includes any behaviours that promote copulation, such as wandering to find a mate, sitting-and-waiting for a mate-seeking individual, holding a mating territory, visiting a mating territory, releasing sex pheromones, attraction to sex pheromones, and so on. A mate-seeking male and a mate-seeking female will then meet and mate. Assume that male and female individuals seek to locate mates with probability  $p$  ( $0 \leq p \leq 1$ ) and  $q$  ( $0 \leq q \leq 1$ ), respectively. Also assume that if there are  $\bar{M}$  males and  $\bar{F}$  females searching for mates,  $e\bar{M}\bar{F}$  copulations occur in the present bout, where  $e$  ( $\leq 1$ ) represents searching efficiency. A small value of  $e$  implies difficulty in finding a mate because of environmental factors other than population density or sex ratio.

If most males and females adopt the strategies  $p^*$  and  $q^*$ , respectively, the fractions of mate-seeking males and females are also represented by  $p^*$  and  $q^*$ , respectively. In this paper we investigate the evolutionary dynamics of these values. If we assume that the survivorships of mate-seeking males and females before mating are given

by  $\phi_m$  ( $0 < \phi_m \leq 1$ ) and  $\phi_f$  ( $0 < \phi_f \leq 1$ ), respectively, the densities of males and females joining the present bout are given by  $(\phi_m p^* M)$  and  $(\phi_f q^* F)$ , respectively. The expected number of mates for a mutant male ( $N_m$ ) with a slightly different strategy  $p'$  is then given by the product of 'probability of surviving in the present bout ( $p' \phi_m$ )' and 'expected number of available mates for a mate-seeking male ( $\phi_f q^* F / \phi_m p^* M$ )', that is:

$$N_m = p' \phi_m \frac{e \phi_f q^* F}{\phi_m p^* M}. \quad (1a)$$

This equation implies that the number of available females increases with increasing numbers of females joining the bout and decreases with increasing numbers of males joining the bout, representing intrasexual competition over mates. Similarly, the expected number of mates for a mutant female with strategy  $q'$  ( $N_f$ ) is given by

$$N_f = q' \phi_f \frac{e \phi_m p^* M}{\phi_f q^* F}. \quad (1b)$$

In general, a male's reproductive success is limited by the number of females with which he mates and tends to increase with the number of available mates (Bateman 1948; Trivers 1972; Thornhill & Alcock 1983). The latter relation holds true for females where high mate availability increases the opportunity to mate with a high-quality mate and decreases time spent searching (Thornhill & Alcock 1983), although the female's fitness might saturate at lower levels of mate availability. Individuals that do not survive the present bout of reproduction are assumed to lose all future reproduction. If we assume that the survivorships of mate-seeking males and females after mating are given by  $\phi'_m$  ( $0 \leq \phi'_m \leq 1$ ) and  $\phi'_f$  ( $0 \leq \phi'_f \leq 1$ ), respectively, and that the survivorships of nonmate-seeking males and females are given by  $\hat{\phi}_m$  ( $0 < \hat{\phi}_m \leq 1$ ) and  $\hat{\phi}_f$  ( $0 < \hat{\phi}_f \leq 1$ ), respectively, the fitness of the mutant males,  $W_m$ , is then given by an increasing function of the total number of mates located in present and future bouts, that is,

$$W_m = w_m(N_m + \{(1 - p')\hat{\phi}_m + p'\phi_m\phi'_m\}Q_m), \quad (2a)$$

where  $w_m(N_m^{\text{total}})$  represents the fitness gain as an increasing function of the number of mates located by a male (note that  $w_m(N_m^{\text{total}})$  can be any increasing function of expected mate number,  $N_m^{\text{total}}$ , including linear, saturated or exponential);  $Q_m$  is the value of the expected numbers of future mates for males; and  $\{(1 - p')\hat{\phi}_m + p'\phi_m\phi'_m\}$  is the probability that a male survives the present reproductive event. Similarly, the fitness of the mutant females is given by

$$W_f = w_f(N_f + \{(1 - q')\hat{\phi}_f + q'\phi_f\phi'_f\}Q_f). \quad (2b)$$

In the present form we assumed that expected future reproduction values ( $Q_m$  and  $Q_f$ ) are independent of other parameters. An alternative and likely assumption is that future reproductive gain decreases with increasing effort allocated to the present bout for gametic or energetic

limitation or other trade-offs (i.e.  $Q_m$  and  $Q_f$  decrease, with increasing  $p'$  and  $q'$ , respectively). Analysis for this alternative case is provided in Appendix 1.

In the following analysis we consider cases where  $\hat{\phi}_m > \phi_m \phi'_m$  and  $\hat{\phi}_f > \phi_f \phi'_f$ , as it is unlikely that survivorship of mate-seeking individuals is higher than that of nonmate-seeking individuals.

## Evolutionary Equilibrium without Male–Female Coevolution

We can obtain the adaptive behaviour of a male (or female) by examining the evolutionary dynamics of the fraction of mate-seeking males,  $p$  (or  $q$ ), assuming that a constant fraction,  $q^*$  ( $p^*$ ), of females (or males) is seeking mates. In such a case, the evolutionary dynamics of  $p^*$  is given by  $dp^*/dt = G(d \ln W_m / dp^*)|_{p'=p^*}$ , where  $G$  is a constant value and represents additive genetic variances (Iwasa et al. 1991). The evolutionarily stable fraction  $\bar{p}$  of mate-seeking males, which is obtained by solving  $dp^*/dt = 0$ , is given by

$$\bar{p} = e \phi_f [F q^* / M \{Q_m (\hat{\phi}_m - \phi_m \phi'_m)\}] \quad (3a)$$

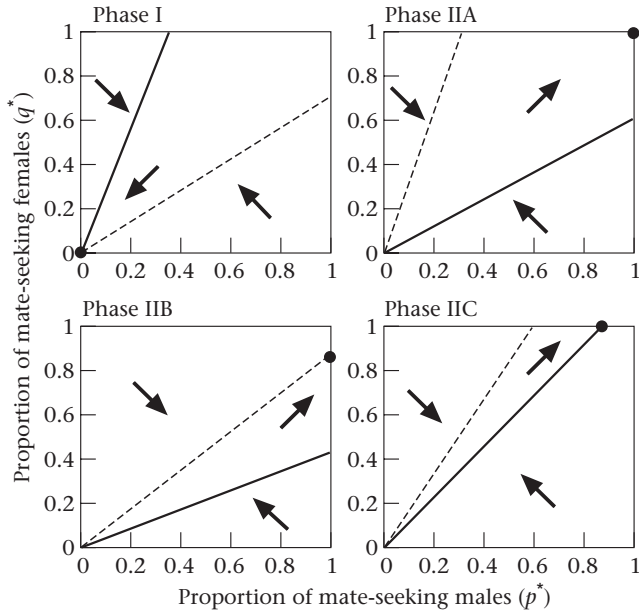
(see Appendix 2 for a more detailed analysis). Similarly, the evolutionarily stable fraction,  $\bar{q}$ , of mate-seeking females for a given fraction,  $p^*$ , of mate-seeking males is obtained by solving  $dq^*/dt = G(d \ln W_f / dq^*)|_{q'=q^*} = 0$ , and given by

$$\bar{q} = e \phi_m [M p^* / F \{Q_f (\hat{\phi}_f - \phi_f \phi'_f)\}]. \quad (3b)$$

Equations (3a) and (3b) suggest that the equilibrium fraction of mate-seeking males,  $\bar{p}$  (or females,  $\bar{q}$ ) gradually increases with: (1) increasing searching efficiency,  $e$ ; (2) increasing survivorship of mate-seeking individuals,  $\phi_m \phi'_m$  (females,  $\phi_f \phi'_f$ ); (3) decreasing survivorship of nonmate-seeking individuals,  $\hat{\phi}_m$  (females,  $\hat{\phi}_f$ ); (4) increasing survivorship of the other sex before mating,  $\phi_f$  (females,  $\phi_m$ ); (5) sex ratio biased to female (male); (6) decreasing future reproduction of males,  $Q_m$  (females,  $Q_f$ ); and (7) increasing the fraction of mate-seeking females,  $q^*$  (males,  $p^*$ ). Where each individual joins only one bout ( $\phi'_m = 0$  or  $\phi'_f = 0$ ), the outcome does not depend on the survivorship of mate-seeking individuals before mating ( $\phi_m$  or  $\phi_f$ ). These results imply that without male–female coevolution, gradual changes in environmental conditions ( $e$ ,  $\phi_m$ ,  $\phi_f$ ,  $\phi'_m$ ,  $\phi'_f$ ,  $\hat{\phi}_m$ ,  $\hat{\phi}_f$ ,  $Q_m$ ,  $Q_f$ ,  $M$ ,  $F$ ) should result in gradual changes in the fraction of mate-seeking individuals, and so a sudden transition between mate-seeking and nonmate-seeking phases is not observed in the absence of sudden changes in environmental conditions.

## Male–Female Coevolutionary Game and Its Outcome

Next, consider that the behaviours of males and females ( $p^*$  and  $q^*$ ) both evolve, that is, male–female coevolution takes place. The coevolutionary dynamics of



**Figure 1.** Equilibrium of the dynamic system (indicated by a filled circle) is obtained by a vector field of  $(p^*, q^*)$ . The zero isoclines for  $p^*$  and  $q^*$  are given as  $\partial \ln W_m / \partial p' |_{p'=p^*} = (dw_m / dN_i^{\text{total}}) \{e\phi_i(Fq^*/Mp^*) - Q_m(\hat{\phi}_m - \phi_m\hat{\phi}_m)\} / W_m = 0$  (solid line) and  $\partial \ln W_f / \partial q' |_{q'=q^*} = (dw_f / dN_m^{\text{total}}) \{e\phi_m(Mp^*/Fq^*) - Q_f(\hat{\phi}_f - \phi_f\hat{\phi}_f)\} / W_f = 0$  (broken line), respectively. (The zero isoclines suggest that if there is an equilibrium, it is always locally stable.) No mating occurs  $((p^{\text{cs}}, q^{\text{cs}}) = (0, 0))$  at the evolutionary equilibrium (Phase I) if the survivorship of a mate-seeking individual is sufficiently low for males ( $\phi_m$  or  $\hat{\phi}_m$ ) and females ( $\phi_f$  or  $\hat{\phi}_f$ ); if the survivorship of a nonmate-seeking individual is sufficiently high for males ( $\hat{\phi}_m$ ) and females ( $\hat{\phi}_f$ ); if the expected future reproduction of males ( $Q_m$ ) and females ( $Q_f$ ) is sufficiently high; if the searching efficiency ( $e$ ) is sufficiently low ( $Q_m Q_f \{(\hat{\phi}_m/\phi_m) - \hat{\phi}_m\} \{(\hat{\phi}_f/\phi_f) - \hat{\phi}_f\} > e^2$ ). If it holds that  $Q_m Q_f \{(\hat{\phi}_m/\phi_m) - \hat{\phi}_m\} \{(\hat{\phi}_f/\phi_f) - \hat{\phi}_f\} < e^2$ , mating occurs ( $p^{\text{cs}} > 0, q^{\text{cs}} > 0$ ); mate-seeking phase; Phase II). The proportion of mate-seeking individuals depends on environmental conditions: all males and females seek mates ( $p^{\text{cs}} = 1$  and  $q^{\text{cs}} = 1$ ) if it holds that  $Q_f(\hat{\phi}_f - \phi_f\hat{\phi}_f) / e\phi_m < M/F < e\phi_f / Q_m(\hat{\phi}_m - \phi_m\hat{\phi}_m)$  (Phase IIA); all males ( $p^{\text{cs}} = 1$ ) and a fraction ( $q^{\text{cs}} = Me\phi_m / FQ_f(\hat{\phi}_f - \phi_f\hat{\phi}_f) < 1$ ) of females seek mates if  $M/F < Q_f(\hat{\phi}_f - \phi_f\hat{\phi}_f) / e\phi_m$  (Phase IIB); a fraction ( $p^{\text{cs}} = Fe\phi_f / MQ_m(\hat{\phi}_m - \phi_m\hat{\phi}_m) < 1$ ) of males and all females ( $q^{\text{cs}} = 1$ ) seek mates if  $e\phi_f / Q_m(\hat{\phi}_m - \phi_m\hat{\phi}_m) < M/F$  (Phase IIC). For Fig. 1 parameters ( $M, F, e, \phi'_m, \phi'_f, \hat{\phi}_m, \hat{\phi}_f$ ) = (1, 1, 0.7, 1, 1, 1, 1, 1), (0.7, 0.7, 1, 0.5), (0.6, 0.4, 0.3, 0.8) and (0.6, 0.5, 1, 0.5) for Phases I, IIA, B and C, respectively.

the mate-seeking strategy of males,  $p^*$ , and females,  $q^*$ , is given by

$$\frac{d}{dt} \begin{pmatrix} p^* \\ q^* \end{pmatrix} = \begin{pmatrix} G_p & B \\ B & G_q \end{pmatrix} \begin{pmatrix} \partial \ln W_m / \partial p' \\ \partial \ln W_f / \partial q' \end{pmatrix} \Big|_{p'=p^*, q'=q^*} \quad (4)$$

where  $G_p$  and  $G_q$  are additive genetic variances for  $p$  and  $q$ , respectively, and  $B$  is the additive genetic covariance between them (Iwasa et al. 1991). We assume that  $B=0$  for simplicity. Our analysis suggests that this assumption does not change the equilibrium if  $B$  is sufficiently small.

The model analysis (Fig. 1) reveals that the male–female coevolutionary dynamics determine an evolutionarily equilibrium state  $(p^*, q^*) = (p^{\text{cs}}, q^{\text{cs}})$ , and generates two

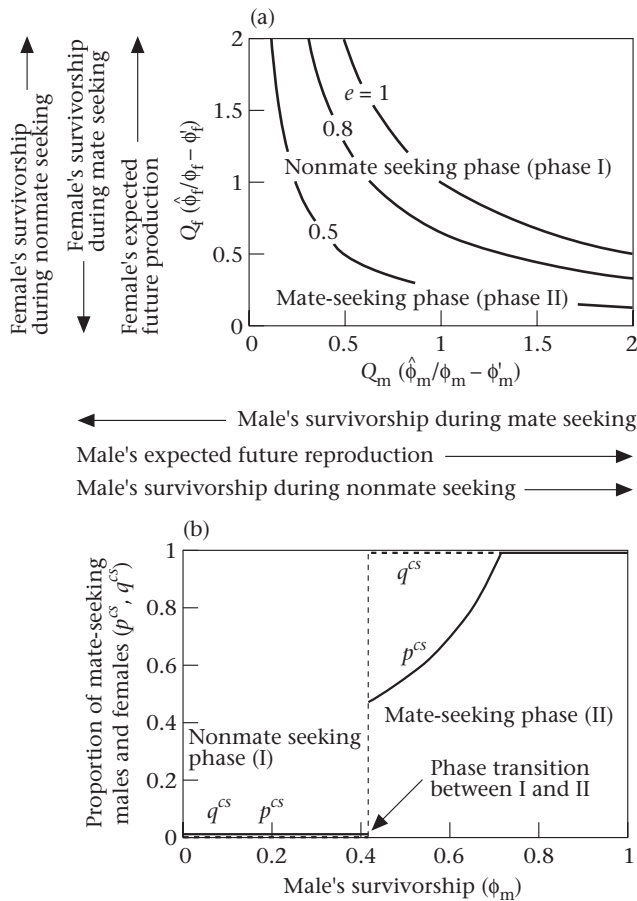
distinct population-level outcomes. In one outcome no individuals seek mates ( $p^{\text{cs}} = 0, q^{\text{cs}} = 0$ ), and in the other all males or all females seek mates  $((p^{\text{cs}}, q^{\text{cs}}) = (1, 1), (1, Me\hat{\phi}_m / FQ_f(\hat{\phi}_f - \phi_f\hat{\phi}_f))$ , or  $(Fe\hat{\phi}_f / MQ_m(\hat{\phi}_m - \phi_m\hat{\phi}_m), 1)$ ). We refer the former and latter outcomes to a nonmate-seeking phase (Phase I) and a mate-seeking phase (Phases IIA, B, C), respectively. The realized equilibrium is always evolutionarily stable, and is uniquely determined by mate-searching efficiency ( $e$ ), expected future reproduction ( $Q_m, Q_f$ ), survivorship of the mate-seeking or nonmate-seeking individuals ( $\phi_m, \phi_f, \hat{\phi}_m, \hat{\phi}_f$ ) and the sex ratio ( $M/F$ ). In general, the mate-seeking phase is favoured under the following conditions: (1) high searching efficiency ( $e$ ); (2) high survivorship during mate-seeking behaviour for males ( $\phi_m\hat{\phi}_m$ ) or females ( $\phi_f\hat{\phi}_f$ ); (3) low survivorship during nonmate-seeking behaviour for males ( $\hat{\phi}_m$ ) or females ( $\hat{\phi}_f$ ); and (4) low future reproduction of males ( $Q_m$ ) or females ( $Q_f$ ) (Fig. 2a). If individuals of either sex are constrained not to join more than one bout ( $\hat{\phi}_m = 0$  or  $\hat{\phi}_f = 0$ ), the outcome does not depend on after-mating survivorship of that sex ( $\phi_m, \phi_f$ ). These results are qualitatively the same irrespective of the form of  $W_i$  ( $i = m$  or  $f$ ).

In the mate-seeking phase, all males (Phases IIA, B) and females (Phases IIA, C) seek mates. Which sex has non-seeking individuals and the proportion of nonmate-seeking members depend on the relative importance of present reproduction to the future reproductive success of each sex (Fig. 1). If the present sex ratio is male biased (female biased), if the mate-seeking male’s (female’s) survivorship is low, if the nonmate-seeking male’s (female’s) survivorship is high, or if the male’s (female’s) future reproduction is high, the relative importance of future reproduction increases for males (females). Then the male (female) tends to be the sex with nonmate-seeking individuals. Similarly, the fraction of nonmate-seeking males (females) increases with male-biased (female-biased) sex ratio, decreasing male (female) survivorship during mate-seeking behaviour, increasing male (female) survivorship during nonmate-seeking behaviour, and increasing future reproduction of males (females). The form of  $W_i$  ( $i = m$  or  $f$ ) does not alter this result qualitatively.

If we assume that there is a trade-off between present and future mate-seeking efforts, the model system can generate more complex properties such as multiple stable states and hysteresis effects (i.e. the present states depend not only on environmental parameters but also on previous states of the system). However, it does not change the major result that mate-seeking and nonmate-seeking phases emerge and transition between these phases should be abrupt (Appendix 1).

## DISCUSSION

We have shown that a male–female coevolutionary game leads to two population-level phases of reproductive behaviour, a mate-seeking phase and a nonmate-seeking phase. In the mate-seeking phase, most members seek mates, and in the nonmate-seeking phase no individuals seek mates.



**Figure 2.** Phase transition between mate-seeking and nonmate-seeking phases caused by gradual changes in environmental conditions. (a) Parameter space of  $Q_m\{(\hat{\phi}_m/\hat{\phi}_m) - \hat{\phi}_m'\}$  and  $Q_f\{(\hat{\phi}_f/\hat{\phi}_f) - \hat{\phi}_f'\}$  divided into mate-seeking and nonmate-seeking phases. Phase transition should be observed as it crosses the threshold line dividing Phase I and Phase II. Parameters  $(M, F)=(1, 1)$ . (b) An example of the phase transition (indicated by an arrow) caused by the change in environmental conditions. This figure shows a case where the male's survivorship ( $\hat{\phi}_m$ ) is changed. Solid and broken lines represent the equilibrium proportions of mate-seeking males and females, respectively. The parameters  $(e, M, F, \hat{\phi}_f, \hat{\phi}_m', \hat{\phi}_f', \hat{\phi}_m, \hat{\phi}_f, Q_{m'}, Q_f)=(0.7, 1, 1, 0.4, 1, 1, 1, 1, 1, 0.5)$ .

One important determinant of the realized phase is an environmental (i.e. extrinsic) condition that affects mate-searching efficiency or the survivorship of mate-seeking individuals. For example, temperature would have the potential to alter which phase is realized, because it would influence the flight activity of searching individuals and therefore affect searching efficiency and survivorship. Males of the cabbage white butterfly, *Pieris rapae crucivora*, search for virgin females in the morning, adjusting their searching time to female eclosion (Iwasa & Obara 1989; Hirota & Obara 2000a). However, the male's activity peak (0900 hours) is 3 h later than the female's eclosion peak (0600 hours; Hirota & Obara 2000b). Virgin females hide behind the leaves of host plants for 30 min after eclosion, during which time the female's wings become fully expanded and hardened (Obara 1987). Females do not move to the surface of the leaves, where

they would be easily seen, until about 2 h after eclosion (Hirota et al. 2001). This discrepancy between the female's sexually acceptable time (30 min after eclosion) and accepting time (2 h after eclosion) may imply that the female's behaviour is influenced by the reproductive behaviour of males, who need intense sunlight to raise their body temperatures for flight (Hirota & Obara 2000b).

The expected future reproductive success of both sexes (i.e. intrinsic condition) can also be a determinant of the realized phase. Because a low potential for future reproduction (a small  $Q_m$  or  $Q_f$ ) favours the mate-seeking phase, the mate-searching period would be longer in a population with little potential for future reproduction. In contrast, when expected future reproductive success is large, the mate-searching period would become shorter and restricted to periods when searching efficiency, or survivorship during mating behaviour, is high. This hypothesis can be tested by examining how a realized phase is determined by the average age of members of either sex. In general, future reproductive success decreases with age, so the average age of either sex should influence sexual activities of the whole population, not only the sex whose age changes.

Our model suggests that there is a critical environmental condition that determines the transition point between the mate-seeking and nonmate-seeking phases (Fig. 2). Suppose that an environmental condition that first occurs in Phase I gradually moves towards Phase II (Fig. 2b). Within Phase I no individuals seek mates. However, as the environmental condition crosses the threshold to enter Phase II, all males or females begin to seek mates. This implies that the phase transition takes place abruptly even if the environmental conditions change gradually with time. This result is completely different from that obtained by the model without male-female coevolution. In this model the equilibrium fraction of mate-seeking individuals increases (or decreases) gradually with changing parameters, and such distinct phases do not occur unless environmental conditions suddenly change (Yuval & Bouskila 1993). This discrepancy between the models implies that a male-female game can be a driving force for the evolution of the observed phase transition in mate-seeking behaviour (e.g. Caspers 1984; Watson et al. 2000). This, however, does not mean that a male-female game is always required for the phase transition; other hypotheses may explain this phenomenon, including one based on positive interaction (i.e. cooperation) within a sex (Houston & McNamara 1987).

A phase transition, combined with a periodic change in environmental conditions, can lead to periodic mating behaviour. Environmental factors that have the potential to influence the mating behaviour of both males and females change periodically. For example, predator activity, which could affect survivorship during the mating period, often has a circadian rhythm (Ashe & Timm 1987). Moonlight, which determines searching efficiency in certain species, periodically changes with the lunar cycle (Schwanck 1987). Periodic changes in these environmental conditions would result in periodic phase

transition, and would facilitate temporally concentrated mating behaviours such as the swarming behaviour observed in midges (Kon 1984; Yuval & Bouskila 1993).

We have attempted to explain why insect species show periodic mating behaviour by considering a male–female coevolutionary game. The model predicts that this game results in one of two reproductive phases, a mate-seeking phase or a nonmate-seeking phase. The model also predicts that a sudden phase transition should take place in response to a critical environmental condition, which suggests that male–female coevolution has the potential to generate population-level periodicity in mating behaviour. However, some simple assumptions may limit the application range of the model, as is the case for any model. For example, one could include reproductive dynamics of sexually active and nonactive individuals, because such population-level dynamics can be important in determining individual sexual activity. Such an extension would be a useful check of the robustness of the present theory to those situations. An important extension would be to examine the effects of heterogeneity of age, body size, diet and physical condition within the population. These heterogeneities would generate a heterogeneity in searching efficiency, future reproduction or survivorship within a population (Yuval et al. 1993; Droney 1996; Papadopoulos et al. 1998; Kaspi & Yuval 2000), and would therefore explain the common observation that only a proportion of both sexes participate in mating behaviour, even when in the mate-seeking phase (Courtney & Parker 1985; Kon et al. 1986; Alcock 1996).

### Acknowledgments

We thank C. Koshio, R. Bennett and two anonymous referees for helpful suggestions that greatly improved the manuscript. M.K. is supported by JSPS Research Fellowship for Young Scientists.

### References

- Alcock, J. 1996. Timing of mate-locating by males in relation to female activity in the carpenter bee *Xylocopa varipuncta* (Hymenoptera: Apidae). *Journal of Insect Behavior*, **9**, 321–328.
- Allan, J. D. & Flecker, A. S. 1989. The mating biology of a mass-swarming mayfly. *Animal Behaviour*, **37**, 361–371.
- Arnqvist, G. & Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour*, **60**, 145–164.
- Ashe, J. S. & Timm, R. M. 1987. Predation by and activity patterns of ‘parasitic’ beetles of the genus *Amblyopinus* (Coleoptera: Staphylinidae). *Journal of Zoology*, **212**, 429–437.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349–368.
- Bitzer, R. J. & Shaw, K. C. 1995. Territorial behavior of the red admiral, *Vanessa atalanta* (Lepidoptera: Nymphalidae) I. The role of climatic factors and early interaction frequency on territorial start time. *Journal of Insect Behavior*, **8**, 47–66.
- Cardé, R. T., Charlton, R. E., Wallner, W. E. & Baranchikov, Y. N. 1996. Pheromone-mediated diel activity rhythms of male Asian gypsy moths (Lepidoptera: Lymantriidae) in relation to female eclosion and temperature. *Annals of the Entomological Society of America*, **89**, 745–753.
- Caspers, H. 1984. Spawning periodicity and habitat of the palolo worm *Eunuce viridis* (Polychaeta: Eunicidae) in the Samoan Islands. *Marine Biology*, **79**, 229–236.
- Courtney, S. P. & Parker, G. A. 1985. Mating behaviour of the tiger blue butterfly (*Tarucus theophrastus*): competitive mate-searching when not all females are captured. *Behavioral Ecology and Sociobiology*, **17**, 213–222.
- Droney, D. C. 1996. Environmental influences on male courtship and implications for female choice in a lekking Hawaiian *Drosophila*. *Animal Behaviour*, **51**, 821–830.
- Gaugler, R. & Schutz, S. 1989. Environmental influences on hovering behavior of *Tabanus nigrovittatus* and *T. conterminus* (Diptera: Tabanidae). *Journal of Insect Behavior*, **2**, 775–786.
- Harari, A. R., Ben-Yakir, D. & Rosen, D. 2000. Male pioneering as a mating strategy: the case of the beetle *Maladera matrida*. *Ecological Entomology*, **25**, 387–394.
- Hirota, T. & Obara, Y. 2000a. Time allocation to reproductive and feeding behaviors in the male cabbage butterfly. *Zoological Science*, **17**, 323–327.
- Hirota, T. & Obara, Y. 2000b. The influence of air temperature and sunlight intensity on mate-locating behavior of *Pieris rapae crucivora*. *Zoological Science*, **17**, 1081–1087.
- Hirota, T., Hamano, K. & Obara, Y. 2001. The influence of female post-emergence behavior on the time schedule of male mate-locating in *Pieris rapae crucivora*. *Zoological Science*, **18**, 475–482.
- Houston, A. I. & McNamara, J. M. 1987. Singing to attract a mate: a stochastic dynamic game. *Journal of Theoretical Biology*, **129**, 57–68.
- Ide, J.-Y. & Kondoh, M. 2000. Male–female evolutionary game on mate-locating behaviour and evolution of mating systems in insects. *Ecology Letters*, **3**, 433–440.
- Iwasa, Y. & Obara, Y. 1989. A game model for the daily activity schedule of the male butterfly. *Journal of Insect Behavior*, **2**, 589–608.
- Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences II. The ‘handicap’ principle. *Evolution*, **45**, 1431–1442.
- Kaspi, R. & Yuval, B. 2000. Post-teneral protein feeding improves sexual competitiveness but reduces longevity of mass-reared sterile male Mediterranean fruit flies (Diptera: Tephritidae). *Annals of the Entomological Society of America*, **93**, 949–955.
- Kawamura, F., Arakaki, N., Kishita, M. & Sadoyama, Y. 2001. Mating behavior of the black chafer, *Holotrichia loochooana loochooana* (Coleoptera: Scarabaeidae). *Entomological Science*, **4**, 223–227.
- Kon, M. 1984. Swarming and mating of *Chironomus yoshimatsui* (Diptera: Chironomidae): seasonal change in the timing of swarming and mating. *Journal of Ethology*, **2**, 37–45.
- Kon, M., Otsuka, K. & Hidaka, T. 1986. Mating system of *Tokunagayusurika akamusi* (Diptera: Chironomidae): I. Copulation in the air by swarming and on the ground by searching. *Journal of Ethology*, **4**, 49–58.
- Koshio, C. 1996. Reproductive behaviour of the white-tailed zygænid moth, *Elcysma westwoodii* (Lepidoptera, Zygaenidae). II. Female mating strategy. *Journal of Ethology*, **14**, 21–25.
- Obara, Y. 1987. Avoidance of maladaptive, precocious copulation in the cabbage white butterfly, *Pieris rapae crucivora*. *Journal of Insect Physiology*, **33**, 403–406.
- Papadopoulos, N. T., Katsoyannos, B. I., Kouloussis, N. A., Economopoulos, A. P. & Carrey, J. R. 1998. Effect of adult age, food, and time of day on sexual calling incidence of wild and mass-reared *Ceratitis capitata* males. *Entomologia Experimentalis et Applicata*, **89**, 175–182.

Quartey, G. K. & Coaker, T. H. 1996. Periodicity of activity and sexual response of adult *Ephestia cautella* (Walk.) (Lep., Phycitidae). *Journal of Applied Entomology*, **120**, 335–339.

Rutowski, R. L., Demlong, M. J. & Terkanian, B. 1996. Seasonal variation in mate-locating activity in the desert hackberry butterfly (*Asterocampa leilia*; Lepidoptera: Nymphalidae). *Journal of Insect Behavior*, **9**, 921–931.

Schwanck, E. 1987. Lunar periodicity in the spawning of *Tilapia mariae* in the Ethiop River, Nigeria. *Journal of Fish Biology*, **30**, 533–537.

Sivinski, J. M. & Petersson, E. 1997. Mate choice and species isolation in swarming insects. In: *The Evolution of Mating Systems in Insects and Arachnids* (Ed. by J. C. Choe & B. J. Crespi), pp. 294–309. Cambridge: Cambridge University Press.

Székely, T., Webb, J. N. & Cuthill, I. C. 1996. Mating patterns, sexual selection and parental care: an integrative approach. In: *Vertebrate Mating Systems* (Ed. by M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 159–183. London: World Science Press.

Thornhill, R. 1976. Sexual selection and paternal investment in insects. *American Naturalist*, **110**, 153–163.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.

Trivers, R. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. New York: Aldine.

Watson, G. J., Williams, M. E. & Bentley, M. G. 2000. Can synchronous spawning be predicted from environmental parameters? A case study of the lugworm *Arenicola marina*. *Marine Biology*, **136**, 1003–1017.

Wickman, P.-O. & Jansson, P. 1997. An estimate of female mate searching costs in the lekking butterfly *Coenonympha pamphilus*. *Behavioral Ecology and Sociobiology*, **40**, 321–328.

Yuval, B. & Bouskila, A. 1993. Temporal dynamics of mating and predation in mosquito swarms. *Oecologia*, **95**, 65–69.

Yuval, B. J., Wekesa, W. & Washino, R. K. 1993. Effect of body size on swarming behavior and mating success of male *Anopheles freeborni* (Diptera: Culicidae). *Journal of Insect Behavior*, **3**, 333–342.

### Appendix 1

*Analysis of the evolutionary dynamics when there is a trade-off between present and future mate-seeking efforts*

Suppose that there is a trade-off between the present and future mate-seeking efforts,  $p$  and  $p_f$ . If present effort is provided at the expense of future effort, the future effort,  $p_i$ , may be given by  $(1 - c_i p)$ , where  $c_i$  ( $0 \leq c_i \leq 1$ ,  $i=m$  and  $f$  for male and female, respectively) is the degree of trade-off. Expected gain in the future ( $Q_i$ ) can be represented as an increasing function of future effort in a similar way to the present bout, that is,  $Q_i = p_i R_i$ , where  $R_i$  is influenced by the operational sex ratio, seeking efficiency and so on. Then, the fitness functions for male and female are given by

$$W_m = w_m(N_m + \{(1 - p')\hat{\phi}_m + p'\phi_m\phi'_m\}R_m(1 - c_m p')) \quad (A1a)$$

and

$$W_f = w_f(N_f + \{(1 - q')\hat{\phi}_f + q'\phi_f\phi'_f\}R_f(1 - c_f q')), \quad (A1b)$$

respectively. The zero isoclines for  $p^*$  and  $q^*$  should hold that  $\partial \ln W_m / \partial p' |_{p'=p^*} = 0$  and,  $\partial \ln W_f / \partial q' |_{q'=q^*} = 0$ , and are given by:

$$e\phi_f(Fq^*/Mp^*) + R_m\{2p^*c_m(\hat{\phi}_m - \phi_m\phi'_m) + \phi_m\phi'_m - \hat{\phi}_m(1 + c_m)\} = 0 \quad (A2a)$$

and

$$e\phi_m(Mp^*/Fq^*) + R_f\{2q^*c_f(\hat{\phi}_f - \phi_f\phi'_f) + \phi_f\phi'_f - \hat{\phi}_f(1 + c_f)\} = 0 \quad (A2b)$$

for  $p^*$  and  $q^*$ , respectively. Zero-isocline analysis suggests that there are four possible stable points: (1) (0, 0), (2) (1, 1), (3) (1,  $q_3^*$ ), (4) ( $p_4^*$ , 1), where

$$q_3^* = \frac{(1 + c_f - \phi_f) - \sqrt{(1 + c_f - \phi_f)^2 - 8e\phi_m M c_f (1 - \phi_f)/R_f F}}{4c_f(1 - \phi_f)},$$

and

$$p_4^* = \frac{(1 + c_m - \phi_m) - \sqrt{(1 + c_m - \phi_m)^2 - 8e\phi_f F c_m (1 - \phi_m)/R_m M}}{4c_m(1 - \phi_m)}.$$

The condition for the respective stable points 1–4 to occur is as follows:

$$R_m R_f \left\{ \frac{(1 + c_m)\hat{\phi}_m - \phi'_m}{\phi_m} \right\} \left\{ \frac{(1 + c_f)\hat{\phi}_f - \phi'_f}{\phi_f} \right\} > e^2, \quad (A3a)$$

$$X_1 < 1 \text{ and } X_2 < 1, \quad (A3b)$$

$$X_1 < q_3^* < 1, \quad (A3c)$$

$$X_2 < p_4^* < 1, \quad (A3d)$$

for stable points 1, 2, 3 and 4, respectively, where

$$(X_1, X_2) = \left( \frac{R_m M \{(1 - c_m)\hat{\phi}_m + (2c_m - 1)\phi_m\phi'_m\}}{e\phi_f F}, \frac{R_f F \{(1 - c_f)\hat{\phi}_f + (2c_f - 1)\phi_f\phi'_f\}}{e\phi_m M} \right).$$

This system may have one to four stable points for a given parameter set. Among 15 possible combinations of the four stable points, 12 combinations are topologically possible, while three are impossible: (3 and 4), (2, 3 and 4) and (1, 3 and 4).

This result suggests that there are only mate-seeking (2, 3, 4) and nonmate-seeking (1) phases, although these two phases can occur at the same time. Inequality (A3a) suggests that the nonmate-seeking phase is favoured by (1) small  $e$ ; (2) small  $\phi_m$  or  $\phi_f$ ; (3) small  $\hat{\phi}_m$  or  $\hat{\phi}_f$ ; (4) large  $\hat{\phi}_m$  or  $\hat{\phi}_f$ ; and (5) high  $R_m$  or  $R_f$  (which represent the values of future bouts and therefore correspond to  $Q_m$  and  $Q_f$  in the original model) in agreement with the result of the model with no trade-off between present and future mate-seeking efforts. However, the relation between conditions and the realized phase becomes less clear, because the system can have multiple stable states and allows both phases to occur under the same condition. For the same reason, this model does not make a clear prediction about population characteristics and the

nonmate-seeking sex or frequency of nonmate-seeking individuals.

## Appendix 2

### *Stability analysis of the evolutionary dynamics*

The equilibrium point of the evolutionary dynamics governed by equation  $dp^*/dt = G(d \ln W_m / dp^*)|_{p^*=p^*}$  is given by setting the right-hand side of this equation to zero. Noting that  $G(d \ln W_m / dp^*)|_{p^*=p^*} = G\{(dW_m / dN_m^{\text{total}})$

$(dN_m^{\text{total}} / dp^*) / W_m\}|_{p^*=p^*}$ ,  $G > 0$ ,  $[W_m]_{p^*=p^*} > 0$  and  $[dW_m / dN_m^{\text{total}}]_{p^*=p^*} > 0$ , the equilibrium should be a solution of  $[dN_m^{\text{total}} / dp^*]_{p^*=p^*} = (e\phi_f q^* F / p^* M) - (\hat{\phi}_m - \phi_m \phi'_m) Q_m = 0$ . By solving this equation, the equilibrium point is given by  $e\phi_f [F q^* / M \{Q_m (\hat{\phi}_m - \phi_m \phi'_m)\}]$ . This equilibrium should be an evolutionarily stable point  $p^* = \hat{p}$ , because  $[dN_m^{\text{total}} / dp^*]_{p^*=p^*}$  is a decreasing function of  $p^*$  (i.e.  $d\{[dN_m^{\text{total}} / dp^*]_{p^*=p^*} / dp^* = d\{(e\phi_f q^* F / p^* M) - (\hat{\phi}_m - \phi_m \phi'_m) Q_m\} / dp^* < 0$ ). By the same token, the evolutionarily stable fraction of mate-seeking females,  $\hat{q}$ , for a given fraction,  $p^*$ , of mate-seeking males is given by  $\hat{q} = e\phi_m [M p^* / F \{Q_f (\hat{\phi}_f - \phi_f \phi'_f)\}]$ .