

## GHAOS IN SOCIOBIOLOGY

J.R. CHRISTIE, K. GOPALSAMY AND JIBIN LI

It is shown that the dynamical game theoretic mating behaviour of males and females can be modelled by a planar system of autonomous ordinary differential equations. This system occurs in modelling “the battle of the sexes” in evolutionary biology. The existence of a heteroclinic cycle and a continuous family of periodic orbits of the system is established; then the dynamical characteristics of a time-periodic perturbation of the system are investigated. By using the well-known Melnikov’s method, a sufficient condition is obtained for the perturbed system to have a transverse heteroclinic cycle and hence to possess chaotic behaviour in the sense of Smale. Finally, subharmonic Melnikov theory is used to obtain a criterion for the existence of subharmonic periodic orbits of the perturbed system.

### 1. INTRODUCTION

It is common for individuals of the same species to behave differently when conflicts arise. One of the important aspects of sociobiology deals with the choice of mates and mating behaviour. In this article, we consider the dynamics of mating behaviour, commonly known as “the battle of the sexes” [8]. We consider a single species population of males and females divided into distinct groups according to their behaviour patterns. We assume that the behavioural patterns of individuals do not change during their lifetime and the patterns are inherited by their offspring. Let us suppose that there are  $n$  distinct behavioural patterns known as “pure strategies”, say  $E_1, E_2, \dots, E_n$ , corresponding to some conflict. The state of the population concerned with this conflict is described by a vector  $x = (x_1, x_2, \dots, x_n) \in \mathbb{R}_+^n$  in which  $x_i$  denotes the frequency of individuals with strategy  $E_i$ ,  $i = 1, 2, \dots, n$ . Thus,  $x_i \geq 0$ ,  $i = 1, 2, \dots, n$ , and  $\sum_{i=1}^n x_i = 1$ . We let

$$(1.1) \quad S_n = \{x = (x_1, x_2, \dots, x_n) \in \mathbb{R}^n : \sum_{i=1}^n x_i = 1, x_i \geq 0, i = 1, 2, \dots, n\}$$

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be the simplex of all possible strategies.

Using game theoretical ideas, we derive a dynamical system described by a set of differential equations modelling the temporal evolution of the frequencies of individuals with distinct strategies [9]. We assume that individuals encounter others at random and a confrontation results, and depending on the behaviour patterns, each receives a pay-off. If an individual with strategy  $E_i$  confronts an individual with strategy  $E_j$ , then we assume that the Darwinian fitness of the former is altered by the “pay-off”, say  $a_{ij}$ ,  $i, j = 1, 2, \dots, n$ . Let the matrix  $A = (a_{ij})$  denote the matrix of pay-offs. Under the assumption of random encounters, the average pay-off for an individual of strategy  $E_i$  in a population distribution  $x_1, x_2, \dots, x_n$  is given by  $p_i$  and the average pay-off for the whole population itself is  $p$ , where

$$(1.2) \quad p_i = \sum_{j=1}^n a_{ij}x_j, \quad i = 1, 2, \dots, n,$$

and

$$(1.3) \quad p = \sum_{i=1}^n p_i x_i = \sum_{i=1}^n \left( \sum_{j=1}^n a_{ij}x_j \right) x_i.$$

It is not unreasonable to assume [10] that the average rate of change of the frequency  $x_i$ ,  $i = 1, 2, \dots, n$ , is equal to the difference between the pay-off of the  $E_i$ -individuals and that of the whole population. Thus, we arrive at the coupled system of ordinary differential equations

$$\frac{1}{x_i} \frac{dx_i}{dt} = \left( \sum_{j=1}^n a_{ij}x_j \right) - \sum_{k=1}^n \left( \sum_{j=1}^n a_{kj}x_j \right) x_k$$

which simplifies to

$$(1.4) \quad \frac{dx_i}{dt} = x_i \left( \sum_{j=1}^n a_{ij}x_j - \sum_{k=1}^n \sum_{j=1}^n a_{kj}x_kx_j \right), \quad t > 0, i = 1, 2, \dots, n.$$

The system (1.4) governs the dynamical evolution of groups of individuals with various strategies.

The plan of the paper is as follows. In Section 2, we consider the dynamics of a population with a conflict of evolutionary significance, concerned with mating behaviour, and known as “the battle of the sexes”. We derive a system of differential equations modelling the population dynamics of the problem and we examine the phase

space structure of the system. In Section 3, we perturb the system and use Melnikov's method [7, 11] to establish a sufficient condition for the existence of chaotic behaviour in the sense of Smale. Then, in Section 4, we consider a special case of the perturbed system. We first simplify the Melnikov condition derived in Section 3 and we then use subharmonic Melnikov theory [7, 11] to deduce a criterion for the existence of subharmonic periodic solutions of the perturbed system. Finally, in Section 5, we briefly comment on the biological relevance of the perturbations and their implications.

## 2. THE BATTLE OF THE SEXES

In this section, we briefly describe a model known as "the battle of the sexes" introduced by Dawkins [4] dealing with the dynamical characteristics of a two sex population of males and females which use different strategies in their choice of partners. Suppose that the males use strategies  $E_1, E_2$  and the females use strategies  $F_1, F_2$ . Let  $a_{ij}$  denote the pay-off for males using strategy  $E_i$  against a female using strategy  $F_j$ ; similarly, let  $b_{ij}$  denote the pay-off for a female using strategy  $F_i$  against a male using strategy  $E_j$ . Let  $x_i$ ,  $i = 1, 2$ , denote the proportion of males using strategy  $E_i$  and let  $y_i$  denote the proportion of females using strategy  $F_i$ ; thus

$$(2.1) \quad x_1 + x_2 = 1, \quad y_1 + y_2 = 1.$$

The pay-off for a male using strategy  $E_i$  against a female population  $(y_1, y_2)$  is

$$(2.2) \quad a_{i1}y_1 + a_{i2}y_2$$

and the average pay-off for the male population is

$$(2.3) \quad (a_{11}y_1 + a_{12}y_2)x_1 + (a_{21}y_1 + a_{22}y_2)x_2.$$

The other pay-offs are similar. The dynamical equations governing the population of males and females can be obtained from (1.4) as follows:

$$(2.4) \quad \begin{aligned} \frac{1}{x_1} \frac{dx_1}{dt} &= (a_{11}y_1 + a_{12}y_2) - [(a_{11}y_1 + a_{12}y_2)x_1 + (a_{21}y_1 + a_{22}y_2)x_2] \\ \frac{1}{x_2} \frac{dx_2}{dt} &= (a_{21}y_1 + a_{22}y_2) - [(a_{11}y_1 + a_{12}y_2)x_1 + (a_{21}y_1 + a_{22}y_2)x_2] \\ \frac{1}{y_1} \frac{dy_1}{dt} &= (b_{11}x_1 + b_{12}x_2) - [(b_{11}x_1 + b_{12}x_2)y_1 + (b_{21}x_1 + b_{22}x_2)y_2] \\ \frac{1}{y_2} \frac{dy_2}{dt} &= (b_{21}x_1 + b_{22}x_2) - [(b_{11}x_1 + b_{12}x_2)y_1 + (b_{21}x_1 + b_{22}x_2)y_2]. \end{aligned}$$

Since we have

$$(2.5) \quad \frac{d}{dt}(x_1 + x_2) = \frac{d}{dt}(y_1 + y_2) = 0,$$

then the product of the simplexes  $S_2 \times S_2$ , that is, the set of all possible strategies, is invariant, so we consider the restriction of (2.4) to  $S_2 \times S_2$ . Furthermore, if  $c_1$  and  $c_2$  are arbitrary constants, then

$$\begin{aligned}
 & [(a_{11} - c_1)y_1 + (a_{12} - c_2)y_2] - [(a_{11} - c_1)y_1 + (a_{12} - c_2)y_2]x_1 \\
 & \quad - [(a_{21} - c_1)y_1 + (a_{22} - c_2)y_2]x_2 \\
 (2.6) \quad & = a_{11}y_1 + a_{12}y_2 - [(a_{11}y_1 + a_{12}y_2)x_1 + (a_{21}y_1 + a_{22}y_2)x_2] \\
 & \quad - (c_1y_1 + c_2y_2) + (c_1y_1 + c_2y_2)(x_1 + x_2) \\
 & = a_{11}y_1 + a_{12}y_2 - [(a_{11}y_1 + a_{12}y_2)x_1 + (a_{21}y_1 + a_{22}y_2)x_2] \\
 & = \frac{1}{x_1} \frac{dx_1}{dt}.
 \end{aligned}$$

A similar subtraction of constants from the respective coefficients and subsequent simplification, as in the derivation of (2.6), can be performed for the other equations in (2.4). Thus, arbitrary constants can be subtracted from the columns of the two pay-off matrices  $A = (a_{ij})$  and  $B = (b_{ij})$  without affecting the dynamics described by (2.4). In view of this, we can assume that the pay-off matrices are of the form

$$(2.7) \quad A = \begin{pmatrix} 0 & a_{12} \\ a_{21} & 0 \end{pmatrix}, \quad B = \begin{pmatrix} 0 & b_{12} \\ b_{21} & 0 \end{pmatrix}.$$

The first equation of (2.4) becomes

$$\begin{aligned}
 \frac{1}{x_1} \frac{dx_1}{dt} & = a_{12}y_2 - [a_{12}x_1y_2 + a_{21}x_2y_1] \\
 & = a_{12}(1 - y_1) - a_{12}x_1(1 - y_1) - a_{21}y_1(1 - x_1) \\
 & = a_{12}(1 - y_1)(1 - x_1) - a_{21}y_1(1 - x_1) \\
 & = (1 - x_1)[a_{12} - y_1(a_{12} + a_{21})];
 \end{aligned}$$

thus, we obtain

$$(2.8) \quad \frac{dx_1}{dt} = x_1(1 - x_1)[a_{12} - (a_{12} + a_{21})y_1].$$

Similarly,

$$\begin{aligned}
 (2.9) \quad \frac{dy_1}{dt} & = y_1[b_{12}(1 - x_1) - b_{12}y_1(1 - x_1) - b_{21}x_1(1 - y_1)] \\
 & = y_1[b_{12}(1 - x_1)(1 - y_1) - b_{21}x_1(1 - y_1)] \\
 & = y_1(1 - y_1)[b_{12} - (b_{12} + b_{21})x_1].
 \end{aligned}$$

For subsequent analysis, it is convenient to let  $x_1 = x$ ,  $y_1 = y$ ,  $a_{12} = \alpha$ ,  $a_{12} + a_{21} = \beta$ ,  $b_{12} = \gamma$  and  $b_{12} + b_{21} = \delta$ . Then, we have the system

$$(2.10) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x)(\alpha - \beta y) \\ \frac{dy}{dt} &= y(1-y)(\gamma - \delta x). \end{aligned}$$

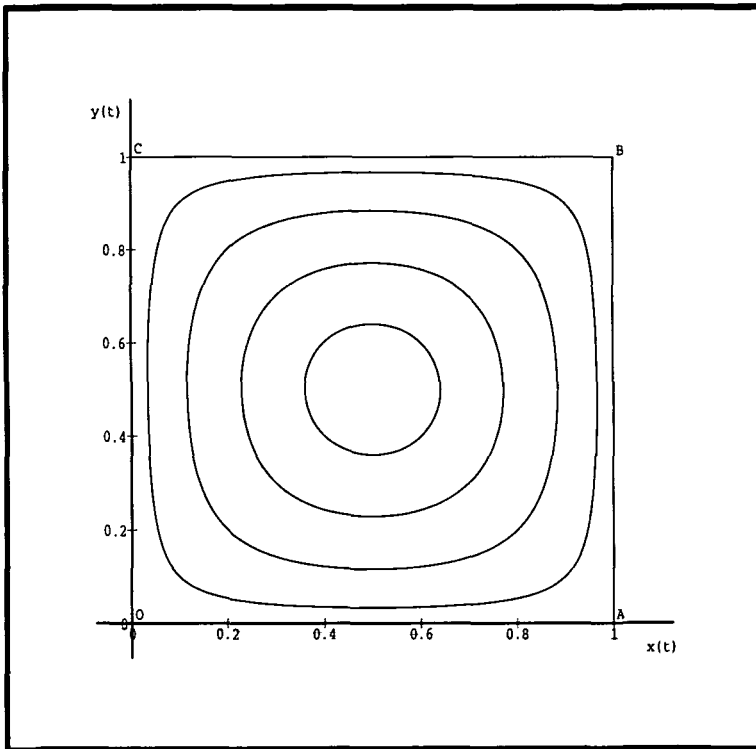


Figure 1. The phase space of (2.10) restricted to the unit square for  $\alpha = 1$ ,  $\beta = 2$ ,  $\gamma = -1$  and  $\delta = -2$ .

In general, this system is non-Hamiltonian, but the system is integrable with first integral given by

$$(2.11) \quad V(x, y) = x^{-\gamma} y^{\alpha} (1-x)^{\gamma-\delta} (1-y)^{\beta-\alpha} = h,$$

for  $0 < x < 1$ ,  $0 < y < 1$ , where  $h$  is the integral constant. Assume that  $0 < \alpha/\beta < 1$ ,  $0 < \gamma/\delta < 1$  and  $\alpha\gamma < 0$ . Then, the fixed point  $(\gamma/\delta, \alpha/\beta)$  of (2.10) is a

centre, and the other fixed points of (2.10) at  $O(0,0)$ ,  $A(1,0)$ ,  $B(1,1)$  and  $C(0,1)$  are all saddles. The centre at  $(\gamma/\delta, \alpha/\beta)$  is surrounded by a continuous family of periodic orbits given by (2.11) for  $h \in (0, \alpha^\alpha \beta^{-\beta} \gamma^{-\gamma} \delta^\delta (\beta - \alpha)^{\beta-\alpha} (\delta - \gamma)^{\gamma-\delta})$ , and there are four heteroclinic orbits consisting of four straight line segments connecting the four saddles, as shown in Figure 1. The existence of this heteroclinic cycle enables us to consider an application of Melnikov’s method in the next section.

### 3. CHAOTIC DYNAMICS

The parameters  $a_i$  in (1.4) are constants in a first approximation. In reality, the system (1.4) is susceptible to small perturbations arising through mutations and other random events which affect the pay-off values [5]. Thus, it is reasonable to consider the system (1.4) and hence the system (2.10) subjected to perturbations; in particular, we consider the following perturbed version of (2.10):

$$(3.1)_\varepsilon \quad \begin{aligned} \frac{dx}{dt} &= x(1-x)(\alpha - \beta y) + \varepsilon(\lambda_1 x + \lambda_2 \sin \omega t) \\ \frac{dy}{dt} &= y(1-y)(\gamma - \delta x) + \varepsilon(\lambda_1 y + \lambda_2 \sin \omega t), \end{aligned}$$

in which  $0 \leq \varepsilon \ll 1$  denotes the perturbation parameter,  $\omega > 0$  is the frequency of the perturbation, and  $\lambda_1$  and  $\lambda_2$  are real parameters. When  $\varepsilon = 0$ , by integrating the unperturbed system  $(3.1)_{\varepsilon=0}$ , we easily find the parametric representations of the four heteroclinic orbits as follows:

$$(3.2) \quad \begin{aligned} \text{OA: } y_0(t) &= 0, \quad x_0(t) = \frac{1}{1 + \exp(-\alpha t)} = \frac{\exp(\alpha t/2)}{2 \cosh(\alpha t/2)}, \\ \text{AB: } x_0(t) &= 1, \quad y_0(t) = \frac{1}{1 + \exp[-(\gamma - \delta)t]} = \frac{\exp((\gamma - \delta)t/2)}{2 \cosh((\gamma - \delta)t/2)}, \\ \text{BC: } y_0(t) &= 1, \quad x_0(t) = \frac{1}{1 + \exp[-(\alpha - \beta)t]} = \frac{\exp((\alpha - \beta)t/2)}{2 \cosh((\alpha - \beta)t/2)}, \\ \text{CO: } x_0(t) &= 0, \quad y_0(t) = \frac{1}{1 + \exp(-\gamma t)} = \frac{\exp(\gamma t/2)}{2 \cosh(\gamma t/2)}. \end{aligned}$$

The system  $(3.1)_\varepsilon$  is of the form

$$\begin{aligned} \frac{dx}{dt} &= f_1(x, y) + \varepsilon g_1(x, y, t) \\ \frac{dy}{dt} &= f_2(x, y) + \varepsilon g_2(x, y, t) \end{aligned}$$

and we write

$$f(x, y) = \begin{pmatrix} f_1(x, y) \\ f_2(x, y) \end{pmatrix} \quad \text{and} \quad g(x, y, t) = \begin{pmatrix} g_1(x, y, t) \\ g_2(x, y, t) \end{pmatrix}.$$

We now investigate the conditions for the existence of transverse heteroclinic cycles for the system (3.1)<sub>ε</sub>. We have noted that, in general, the unperturbed system (3.1)<sub>ε=0</sub> is non-Hamiltonian. Let  $q_0(t) = (x_0(t), y_0(t))$  be one of the heteroclinic solutions given by (3.2). By using Melnikov's method, the Melnikov function corresponding to the perturbed system (3.1)<sub>ε</sub> is defined as [1, 2]

(3.3)

$$\begin{aligned} M(t_0) &= \int_{-\infty}^{\infty} f(q_0(t)) \wedge g(q_0(t), t + t_0) \exp\left(-\int_0^t \text{trace } Df(q_0(s)) ds\right) dt \\ &= \int_{-\infty}^{\infty} \left[ x_0(t)(1 - x_0(t))(\alpha - \beta y_0(t))(\lambda_1 y_0(t) + \lambda_2 \sin(\omega(t + t_0))) \right. \\ &\quad \left. - y_0(t)(1 - y_0(t))(\gamma - \delta x_0(t))(\lambda_1 x_0(t) + \lambda_2 \sin(\omega(t + t_0))) \right] \\ &\quad \times \exp\left(-\int_0^t [(1 - 2x_0(s))(\alpha - \beta y_0(s)) + (1 - 2y_0(s))(\gamma - \delta x_0(s))] ds\right) dt. \end{aligned}$$

For convenience, we denote by

$$A(t) = \exp\left(-\int_0^t [(1 - 2x_0(s))(\alpha - \beta y_0(s)) + (1 - 2y_0(s))(\gamma - \delta x_0(s))] ds\right),$$

and we write a three-parameter integral and two four-parameter integrals as follows:

$$\begin{aligned} I_0(p, q, \mu) &= \int_{-\infty}^{\infty} \frac{\exp(qt)}{\cosh^\mu(pt)} dt, \\ I_1(p, q, \mu, \omega) &= \int_{-\infty}^{\infty} \frac{\exp(qt) \sin \omega t}{\cosh^\mu(pt)} dt, \quad I_2(p, q, \mu, \omega) = \int_{-\infty}^{\infty} \frac{\exp(qt) \cos \omega t}{\cosh^\mu(pt)} dt. \end{aligned}$$

To calculate (3.3) along the four heteroclinic orbits, we have, after some simplification, the following results:

(3.4)

$$\begin{aligned} M(t_0) \Big|_{OA} &= \alpha \lambda_2 \left[ \cos \omega t_0 \int_{-\infty}^{\infty} x_0(t)(1 - x_0(t))A(t) \sin \omega t dt \right. \\ &\quad \left. + \sin \omega t_0 \int_{-\infty}^{\infty} x_0(t)(1 - x_0(t))A(t) \cos \omega t dt \right] \\ &= 2^{\delta/\alpha} \alpha \lambda_2 \left[ I_1\left(\frac{\alpha}{2}, \frac{\delta}{2} - \gamma, -\frac{\delta}{\alpha}, \omega\right) \cos \omega t_0 + I_2\left(\frac{\alpha}{2}, \frac{\delta}{2} - \gamma, -\frac{\delta}{\alpha}, \omega\right) \sin \omega t_0 \right], \end{aligned}$$

(3.5)

$$\begin{aligned}
M(t_0) \Big|_{AB} &= (\delta - \gamma) \left\{ \lambda_1 \int_{-\infty}^{\infty} y_0(t)(1 - y_0(t))A(t) dt \right. \\
&\quad + \lambda_2 \left[ \cos \omega t_0 \int_{-\infty}^{\infty} y_0(t)(1 - y_0(t))A(t) \sin \omega t dt \right. \\
&\quad \left. \left. + \sin \omega t_0 \int_{-\infty}^{\infty} y_0(t)(1 - y_0(t))A(t) \cos \omega t dt \right] \right\} \\
&= 2^{\beta/(\delta-\gamma)}(\delta - \gamma) \left\{ \lambda_1 I_0 \left( \frac{\gamma - \delta}{2}, \alpha - \frac{\beta}{2}, \frac{\beta}{\gamma - \delta} \right) \right. \\
&\quad + \lambda_2 I_1 \left( \frac{\gamma - \delta}{2}, \alpha - \frac{\beta}{2}, \frac{\beta}{\gamma - \delta}, \omega \right) \cos \omega t_0 \\
&\quad \left. + \lambda_2 I_2 \left( \frac{\gamma - \delta}{2}, \alpha - \frac{\beta}{2}, \frac{\beta}{\gamma - \delta}, \omega \right) \sin \omega t_0 \right\},
\end{aligned}$$

(3.6)

$$\begin{aligned}
M(t_0) \Big|_{BC} &= (\alpha - \beta) \left\{ \lambda_1 \int_{-\infty}^{\infty} x_0(t)(1 - x_0(t))A(t) dt \right. \\
&\quad + \lambda_2 \left[ \cos \omega t_0 \int_{-\infty}^{\infty} x_0(t)(1 - x_0(t))A(t) \sin \omega t dt \right. \\
&\quad \left. \left. + \sin \omega t_0 \int_{-\infty}^{\infty} x_0(t)(1 - x_0(t))A(t) \cos \omega t dt \right] \right\} \\
&= 2^{\delta/(\beta-\alpha)}(\alpha - \beta) \left\{ \lambda_1 I_0 \left( \frac{\alpha - \beta}{2}, \gamma - \frac{\delta}{2}, \frac{\delta}{\alpha - \beta} \right) \right. \\
&\quad + \lambda_2 I_1 \left( \frac{\alpha - \beta}{2}, \gamma - \frac{\delta}{2}, \frac{\delta}{\alpha - \beta}, \omega \right) \cos \omega t_0 \\
&\quad \left. + \lambda_2 I_2 \left( \frac{\alpha - \beta}{2}, \gamma - \frac{\delta}{2}, \frac{\delta}{\alpha - \beta}, \omega \right) \sin \omega t_0 \right\},
\end{aligned}$$

(3.7)

$$\begin{aligned}
M(t_0) \Big|_{CO} &= -\gamma \lambda_2 \left[ \cos \omega t_0 \int_{-\infty}^{\infty} y_0(t)(1 - y_0(t))A(t) \sin \omega t dt \right. \\
&\quad \left. + \sin \omega t_0 \int_{-\infty}^{\infty} y_0(t)(1 - y_0(t))A(t) \cos \omega t dt \right] \\
&= 2^{\beta/\gamma} \gamma \lambda_2 \left[ I_1 \left( \frac{\gamma}{2}, \frac{\beta}{2} - \alpha, -\frac{\beta}{\gamma}, \omega \right) \cos \omega t_0 + I_2 \left( \frac{\gamma}{2}, \frac{\beta}{2} - \alpha, -\frac{\beta}{\gamma}, \omega \right) \sin \omega t_0 \right].
\end{aligned}$$

Denote by  $I_{12} = (I_1^2 + I_2^2)^{1/2}$ , and define  $\phi$  by  $\sin \phi = I_1/I_{12}$  and  $\cos \phi = I_2/I_{12}$ .



Then, (3.4)-(3.7) can be rewritten as:

$$(3.8) \quad M(t_0) \Big|_{OA} = 2^{\delta/\alpha} \alpha \lambda_2 I_{12}^{OA} \sin(\omega t_0 + \phi_{OA}),$$

$$(3.9) \quad M(t_0) \Big|_{AB} = 2^{\beta/(\delta-\gamma)} (\delta - \gamma) [\lambda_1 I_0^{AB} + \lambda_2 I_{12}^{AB} \sin(\omega t_0 + \phi_{AB})],$$

$$(3.10) \quad M(t_0) \Big|_{BC} = 2^{\delta/(\beta-\alpha)} (\alpha - \beta) [\lambda_1 I_0^{BC} + \lambda_2 I_{12}^{BC} \sin(\omega t_0 + \phi_{BC})],$$

$$(3.11) \quad M(t_0) \Big|_{CO} = 2^{\beta/\gamma} \gamma \lambda_2 I_{12}^{CO} \sin(\omega t_0 + \phi_{CO}).$$

From (3.8)-(3.11), we see that if

$$(3.12) \quad \left| \frac{\lambda_1}{\lambda_2} \right| < \min \left( \frac{I_{12}^{AB}}{I_0^{AB}}, \frac{I_{12}^{BC}}{I_0^{BC}} \right),$$

then each Melnikov function has simple zeros and hence the system (3.1) <sub>$\epsilon$</sub>  has a transverse heteroclinic cycle; it follows that the Poincaré map of (3.1) <sub>$\epsilon$</sub>  has transverse homoclinic points, so that chaotic behaviour in the sense of Smale exists in the system (3.1) <sub>$\epsilon$</sub>  for sufficiently small  $\epsilon$  by the Smale-Birkhoff homoclinic theorem [12], that is, we have:

**THEOREM 3.1.** *Suppose that  $0 < \alpha/\beta < 1$ ,  $0 < \gamma/\delta < 1$ ,  $\alpha\gamma < 0$  and  $\omega > 0$ . If the condition (3.12) holds, then chaotic behaviour in the sense of Smale exists in the system (3.1) <sub>$\epsilon$</sub>  for sufficiently small  $\epsilon$ .*

#### 4. A SPECIAL CASE OF SUBHARMONIC SOLUTIONS

In this section, we take  $\alpha = 1$ ,  $\beta = 2$ ,  $\gamma = -1$  and  $\delta = -2$ , that is, we consider the perturbed system

$$(4.1)_{\epsilon} \quad \begin{aligned} dx/dt &= x(1-x)(1-2y) + \epsilon(\lambda_1 x + \lambda_2 \sin \omega t) \\ dy/dt &= y(1-y)(-1+2x) + \epsilon(\lambda_1 y + \lambda_2 \sin \omega t). \end{aligned}$$

In this case, the unperturbed system (4.1) <sub>$\epsilon=0$</sub>  has the Hamiltonian

$$(4.2) \quad H(x, y) = xy(1-x)(1-y) = h.$$

First of all, we can simplify the condition (3.12) because the integrals can be analytically

evaluated [6]. We have

$$\begin{aligned}
 I_0^{AB} &= I_0 \left( \frac{1}{2}, 0, 2 \right) = \int_{-\infty}^{\infty} \frac{1}{\cosh^2(t/2)} dt = 2 \int_0^{\infty} \frac{1}{\cosh^2(t/2)} dt = 2 \left[ 2 \tanh \left( \frac{t}{2} \right) \right]_0^{\infty} = 4, \\
 I_1^{AB} &= I_1 \left( \frac{1}{2}, 0, 2, \omega \right) = \int_{-\infty}^{\infty} \frac{\sin \omega t}{\cosh^2(t/2)} dt = 0, \\
 I_2^{AB} &= I_2 \left( \frac{1}{2}, 0, 2, \omega \right) = \int_{-\infty}^{\infty} \frac{\cos \omega t}{\cosh^2(t/2)} dt = 2 \int_0^{\infty} \frac{\cos \omega t}{\cosh^2(t/2)} dt = \frac{4\pi\omega}{\sinh(\pi\omega)}, \\
 I_0^{BC} &= I_0 \left( -\frac{1}{2}, 0, 2 \right) = \int_{-\infty}^{\infty} \frac{1}{\cosh^2(-t/2)} dt = \int_{-\infty}^{\infty} \frac{1}{\cosh^2(t/2)} dt = I_0^{AB} = 4, \\
 I_1^{BC} &= I_1 \left( -\frac{1}{2}, 0, 2, \omega \right) = \int_{-\infty}^{\infty} \frac{\sin \omega t}{\cosh^2(-t/2)} dt = \int_{-\infty}^{\infty} \frac{\sin \omega t}{\cosh^2(t/2)} dt = I_1^{AB} = 0, \\
 I_2^{BC} &= I_2 \left( -\frac{1}{2}, 0, 2, \omega \right) = \int_{-\infty}^{\infty} \frac{\cos \omega t}{\cosh^2(-t/2)} dt = \int_{-\infty}^{\infty} \frac{\cos \omega t}{\cosh^2(t/2)} dt = I_2^{AB} = \frac{4\pi\omega}{\sinh(\pi\omega)}.
 \end{aligned}$$

Hence, the Melnikov condition (3.12) for the existence of chaotic behaviour becomes

$$\left| \frac{\lambda_1}{\lambda_2} \right| < \frac{\pi\omega}{\sinh(\pi\omega)}.$$

We now consider the existence of subharmonic periodic solutions of (4.1)<sub>ε</sub>. When  $h \in (0, 1/16)$ , (4.2) defines a continuous family of periodic orbits surrounding the centre (1/2, 1/2). We can show that the parametric representation of this family of periodic solutions of (4.1)<sub>ε=0</sub> is as follows:

$$(4.3) \quad x_k(t) = \frac{1}{2} - \frac{k}{2} \operatorname{sn} \left( \frac{t}{2}, k \right), \quad y_k(t) = \frac{1}{2} + \frac{k}{2} \frac{\operatorname{cn}(t/2, k)}{\operatorname{dn}(t/2, k)},$$

where  $k = \sqrt{1 - 16h}$ , and  $\operatorname{sn}(u, k)$ ,  $\operatorname{cn}(u, k)$  and  $\operatorname{dn}(u, k)$  are Jacobi elliptic functions with modulus  $k$  [3]. The orbit  $(x_k(t), y_k(t))$  has period  $T(k) = 8K(k)$ , where  $k \in (0, 1)$ , in which  $K(k)$  is the complete elliptic integral of the first kind [3]. We next use subharmonic Melnikov theory [7, 11] to examine the existence of subharmonic periodic solutions of (4.1)<sub>ε</sub>. For relatively prime positive integers  $m$  and  $n$ , the subharmonic Melnikov function (for a Hamiltonian unperturbed system) is defined as [7, 11]

$$M^{m/n}(t_0) = \int_{-mT/2}^{mT/2} f(q_k(t)) \wedge g(q_k(t), t + t_0) dt,$$

where  $q_k(t) = (x_k(t), y_k(t))$ , and the resonance condition is  $T(k) = (mT/n)$ , in which  $T > 0$  is the period of the perturbation. For  $n = 1$ , the resonance condition is

$$(4.4) \quad T(k) = 8K(k) = \frac{2\pi m}{\omega} = mT.$$

For a given  $m$ , it defines a relationship  $k = k(m)$ . Corresponding to the periodic orbit  $q_k(t) = (x_k(t), y_k(t))$  with  $k = k(m)$ , the subharmonic Melnikov function is:

(4.5)

$$\begin{aligned}
 M^{m/1}(t_0) &= \int_{-mT/2}^{mT/2} \left[ x_k(t)(1 - x_k(t))(1 - 2y_k(t))(\lambda_1 y_k(t) + \lambda_2 \sin(\omega(t + t_0))) \right. \\
 &\quad \left. - y_k(t)(1 - y_k(t))(-1 + 2x_k(t))(\lambda_1 x_k(t) + \lambda_2 \sin(\omega(t + t_0))) \right] dt \\
 &= \int_{-mT/2}^{mT/2} \left[ \frac{dx_k}{dt}(t)(\lambda_1 y_k(t) + \lambda_2 \sin(\omega(t + t_0))) \right. \\
 &\quad \left. - \frac{dy_k}{dt}(t)(\lambda_1 x_k(t) + \lambda_2 \sin(\omega(t + t_0))) \right] dt \\
 &= \lambda_1 \int_{-mT/2}^{mT/2} \left( y_k(t) \frac{dx_k}{dt}(t) - x_k(t) \frac{dy_k}{dt}(t) \right) dt \\
 &\quad + \lambda_2 \omega \sin \omega t_0 \int_{-mT/2}^{mT/2} x_k(t) \sin \omega t \, dt \\
 &\quad + \lambda_2 \omega \cos \omega t_0 \int_{-mT/2}^{mT/2} y_k(t) \cos \omega t \, dt \\
 &= -2 \left\{ \lambda_1 \left[ \frac{1 - k^2}{8} \int_{-2K}^{2K} \left( \frac{1}{\operatorname{dn}^2(u, k)} - 1 \right) du + \frac{k^2}{8} \int_{-2K}^{2K} \operatorname{cn}^2(u, k) du \right] \right. \\
 &\quad - \lambda_2 \omega \left[ k \sin \omega t_0 \int_{-2K}^{2K} \operatorname{sn}(u, k) \sin \left( \frac{m\pi u}{2K} \right) du \right. \\
 &\quad \left. \left. - k \cos \omega t_0 \int_{-2K}^{2K} \frac{\operatorname{cn}(u, k)}{\operatorname{dn}(u, k)} \cos \left( \frac{m\pi u}{2K} \right) du \right] \right\}.
 \end{aligned}$$

The first two integrals of (4.5) can be found from [3]. The last two integrals require the Fourier series expansion of  $\operatorname{sn}(u, k)$  and  $\operatorname{cn}(u, k)/\operatorname{dn}(u, k) \equiv \operatorname{cd}(u, k)$  respectively; both of these can be obtained using contour integration and are listed in [3]. By calculating the integrals of (4.5), we have

$$\begin{aligned}
 M^{2m+1/1}(t_0) &= -2 \left\{ \lambda_1 [E(k) - (1 - k^2)K(k)] \right. \\
 (4.6) \quad &\quad \left. + \lambda_2 \pi \omega \operatorname{cosech} \left( \frac{(2m + 1)\pi K'(k)}{2K(k)} \right) [-\sin \omega t_0 + (-1)^m \cos \omega t_0] \right\}
 \end{aligned}$$

where  $E(k)$  is the complete elliptic integral of the second kind, and  $K'(k) = K(k')$ , in which  $k' = \sqrt{1 - k^2}$  is the complementary modulus [3]. From (4.6), we see that if

$$(4.7) \quad \left| \frac{\lambda_1}{\lambda_2} \right| < \frac{\pi \omega \operatorname{cosech}((2m + 1)\pi K'(k)/(2K(k)))}{E(k) - (1 - k^2)K(k)},$$

then  $M^{2m+1/1}(t_0)$  has simple zeros. In order to deduce that the system (4.1) $_{\epsilon}$  has subharmonic periodic solutions of order  $2m + 1$  [7, Theorem 4.6.2], we need to show that  $\frac{dT(k)}{dh(k)} \neq 0$ . Using (4.3) and (4.4), we obtain

$$(4.8) \quad \frac{dT}{dh} = \frac{dT}{dk} \frac{dk}{dh} = -\frac{64}{\sqrt{1-16h}} \frac{dK}{dk} < 0,$$

since  $K$  is an increasing function of  $k$ . In summary, we have the following conclusion:

**THEOREM 4.1.** *For  $\omega > 0$ , if the condition (4.7) holds where  $K(k) = \pi(2m + 1)/4\omega$ , then the system (4.1) $_{\epsilon}$  has a subharmonic periodic orbit of period  $(2m + 1)T$  for sufficiently small  $\epsilon$ .*

## 5. CONCLUSION

Most population systems are susceptible to time-periodic perturbations due to periodic fluctuations of the environment like food availability, mating habits and other resources. There are also evolutionary perturbations in the fitness parameters arising due to mutations and other fluctuations influencing the phenotypic behaviour resulting in the variation of strategies. We have considered a class of perturbations in (3.1) $_{\epsilon}$ , and we have established that the densities of males and females adopting different strategies in their mating behaviour can vary in a complex way without converging to any limiting form. Such a variability is necessary for the evolutionary forces to be in action since one of the essential ingredients of evolutionary modifications is variety. Our analysis is complementary to the analysis of Foster and Young [5].

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School of Information Science and Technology  
The Flinders University of South Australia  
GPO Box 2100  
Adelaide SA 5001  
Australia

School of Information Science and Technology  
The Flinders University of South Australia  
GPO Box 2100  
Adelaide SA 5001  
Australia

Institute of Applied Mathematics  
of Yunnan Province  
Department of Mathematics  
Kunming Institute of Technology  
Yunnan 650093  
People's Republic of China