Hawks and Doves in Heterogeneous Environments

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Abstract—Two environments, each possessing populations described by the homogeneous hawk-dove game, are linked via migration. Aggregation techniques are used to simplify the dynamics and solve the system analytically. Contrary to the homogeneous hawk-dove model, for certain physically realistic parameter values, the final populations structure is found to depend critically upon the initial population structure.

Keywords—Aggregation, Hawk-dove game theory, Migration, Heterogeneous environment.

1. INTRODUCTION

Hawk-dove game theory applied to a population in a homogeneous environment is well known [1]. The population is composed of individuals which can have two differing "life strategies", and the success or failure of these strategies has a direct consequence upon the continued reproductive success of the individuals. These ideas have also been extended to populations possessing more than two strategies [2]. For example, there may be an undecided strategy that spends half its time being a hawk and the other half being a dove. On the whole, the homogeneous case allows analytical progress, and consequently, a good understanding of the dynamical system.

Real environments are not homogeneous. Climate alters, food sources move and change, available territory expands and contracts, etc. All these changes will have an effect upon the behavioural strategy of inhabiting populations. The problem with incorporating these heterogeneous effects into a model is that such systems are often far more complicated than their homogeneous counterparts. The variables are functions of at least two quantities (time and distance) and analytical results are difficult to obtain. Computer simulation often provides the only way ahead.

Numerical studies of environmental heterogeneous systems, usually using cellular automata (analytical analysis of morphological models involving reaction-diffusion equations has had success [3]), have shown a rich structure of population dynamical behaviour. Such environments are not continuous, but divided up into a number of patches. On each patch an automata is placed, which is allowed to interact with its neighbouring automata. It then reacts to the presence of its neighbours by changing its "state" following some predetermined set of rules. Nowak and May [4] showed that such a scheme applied to the Prisoner's Dilemma game can lead to chaotic spatial dynamics. Similarly, Hassell *et al.* [5] have looked at insect populations in general and have also shown that chaotic behaviour can result. However, chaotic behaviour need not always result from a heterogeneous environment, and the heterogeneous property can have a stabilising effect upon a previously unstable homogeneous system. For example, Hassel *et al.* [6] and Ives [7] have used heterogeneous environments to stabilise host-parasite dynamics while Gyllenberg *et al.* [8] have studied the stabilising effect of migration upon previously local populations.

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Keeping with the idea of patches as opposed to continuously changing environments, the simplest possible heterogeneous system that can be considered contains just two homogeneous patches. Although such a system is only going to be able to model very coarse scale differences in the background, it is nonetheless useful. The two patches could correspond to urban and rural environments, or to neighbouring environments in a beach dune system, or to micro-climates such as a dry hot rock versus a cool, damp crack. With such a system it is interesting to ask; does such a simple heterogeneous environment have important consequences for the population dynamics which are not seen for homogeneous environments?

We have taken a simple two patch system and using aggregation techniques [9] and corresponding assumptions about the time-scales of processes, we have tried to answer this question. Section 2 gives a summary of the model and the equations used, Section 3 discusses the dynamics of the migration between the patches, Section 4 looks at the game dynamics on each patch and the stability of the various solutions. Finally, Section 5 looks at the effects of the heterogeneity before the important points of the analysis are discussed.

2. THE TWO PATCH MODEL

The general schema for the model is shown in Figure 1. Two homogeneous patches, labelled by 1 and 2 each have a population of individuals, $n_1(t)$ for Patch 1 and $n_2(t)$ for Patch 2. These individuals are all of the same species, and are identical in all but their behavioural traits. Thus, they all compete for the same ecological niches, such as food sources, mating partners, sleeping areas, etc., and it will be the effectiveness of their different behaviours at coping with this competition that will be of interest. The environmental conditions on each patch are not necessarily the same, bringing in a possible component of heterogeneity into the model. The two environments are not isolated since migration is allowed between the patches.
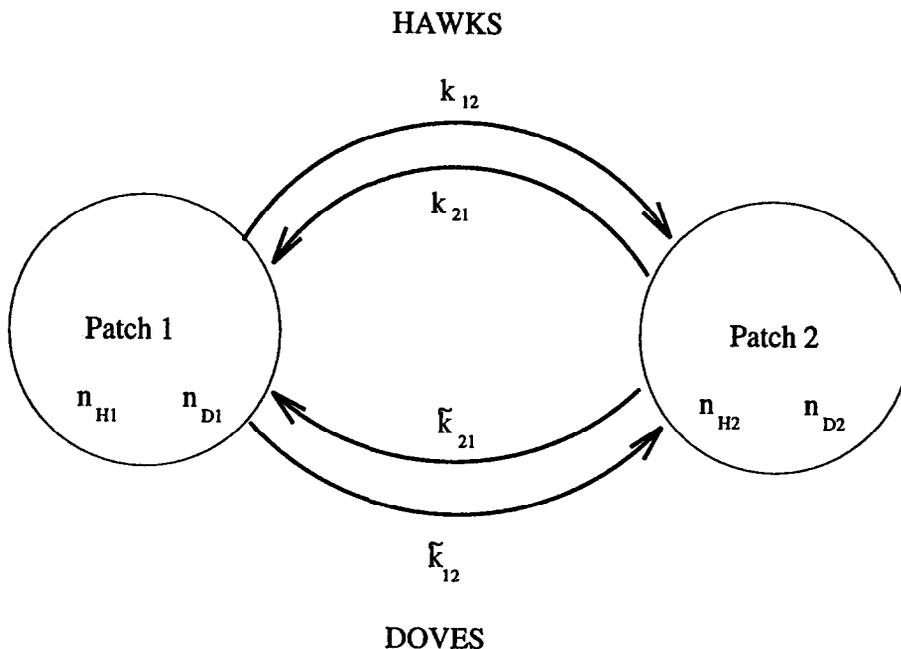
HAWKS

Figure 1. A schema of the two patch model. Two homogeneous patches, labelled 1 and 2. Migration is allowed between the patches.

Local to each patch, the dynamics follow the usual hawk-dove game. In this game an individual can follow one of two possible strategies, either "hawk" or "dove". A "hawk" strategy entails strong dominant behaviour. In clashes with other individuals (where a clash could be a fight for

territory, or a mate, or food, etc.) a hawk will persevere until the bitter end, reasoning that to "win" the encounter is the most important goal. On the other hand, a "dove" strategy can be more conservative. In an encounter with another individual, a dove will be willing to give way to his opponent if the clash is likely to dispense too much of his energy. A dove reasons that conservation of personal resources is a better strategy than winning at all cost. Thus, if a hawk and a dove were to meet the hawk would always succeed, while in encounters with a like-minded individual success will only be 50% of the time. This gives a hawk-dove payoff matrix as shown in Figure 2.

Strategy of Adversary

	Hawk	Dove
Hawk	$\dfrac{G-C}{2}$	G
Dove	0	$\dfrac{G}{2}$

Strategy Payoff

Figure 2. The "hawk-dove" payoff matrix. G is the average gain of winning a conflict and C is the cost incurred by adopting a hawk strategy in a conflict.

The total payoff of an individuals strategy is assumed to have a direct effect upon their reproductive success. Thus, the rate of change of a strategy's population can be written in terms of the payoff matrix and the numbers of individuals. Then combining the migration and game theory, we can write down the dynamical equations governing the total population as

$$\varepsilon\frac{d}{dt}n_{H1} = \overbrace{(k_{21}n_{H2} - k_{12}n_{H1})}^{\text{Migratory dynamics}} + \overbrace{\varepsilon\frac{n_{H1}}{n_{H1}+n_{D1}}\left[\frac{G_1-C_1}{2}n_{H1} + G_1 n_{D1}\right]}^{\text{Game dynamics}}, \tag{1}$$

$$\varepsilon\frac{d}{dt}n_{D1} = \left(\tilde{k}_{21}n_{D2} - \tilde{k}_{12}n_{D1}\right) + \varepsilon\frac{n_{D1}}{n_{H1}+n_{D1}}\frac{G_1}{2}n_{D1}, \tag{2}$$

$$\varepsilon\frac{d}{dt}n_{H2} = -(k_{21}n_{H2} - k_{12}n_{H1}) + \varepsilon\frac{n_{H2}}{n_{H2}+n_{D2}}\left[\frac{G_2-C_2}{2}n_{H2} + G_2 n_{D2}\right], \tag{3}$$

$$\varepsilon\frac{d}{dt}n_{D2} = -\left(\tilde{k}_{21}n_{D2} - \tilde{k}_{12}n_{D1}\right) + \varepsilon\frac{n_{D2}}{n_{H2}+n_{D2}}\frac{G_2}{2}n_{D2}, \tag{4}$$

where subscripts H and D are short for Hawk and Dove, respectively, and 1 and 2 refer to Patches 1 and 2, respectively. k_{12} and $\tilde{k}_{21}$ are, respectively, the migration rates of hawk individuals and dove individuals from Patch 1 to Patch 2, G_1 is the strategic gain of winning an encounter in Patch 1, C_1 is the strategic cost of being a hawk in Patch 1, and n_{H1} is the number of hawks in Patch 1. ε is a "small" parameter, whose significance will be described later. All other variables have a similar significance following their subscripts.

Even though there are just two patches, the solution of these equations is complicated. We propose a simplification by assuming that migration is a relatively frequent affair compared with the generation time (i.e., the time-scale for the hawk-dove game dynamics). This assumption is equivalent to assuming that $\varepsilon \ll 1$, and then using the two *time-scales* as a means of decomposing

the dynamical system following the techniques outlined by Auger and Rousserie [9]. Using the decomposed system analytical headway is much easier.

By adding equation (1) to equation (3), we obtain the equation governing the total hawk population n_H. This variable is independent of the migratory dynamics and is governed solely by the slow game dynamics. By adding equations (2) and (4) a similar result is obtained for n_D. Thus, there are two slow variables, the total hawk population n_H and the total dove population n_D.

3. THE MIGRATORY DYNAMICS

Since the migration is assumed to be the fastest dynamics of the system, to a first approximation [9–11] the equations (1)–(4) can be written as

$$\varepsilon \frac{d}{dt} n_{H1} = (k_{21} n_{H2} - k_{12} n_{H1}), \tag{5}$$

$$\varepsilon \frac{d}{dt} n_{D1} = \left(\tilde{k}_{21} n_{D2} - \tilde{k}_{12} n_{D1} \right), \tag{6}$$

$$\varepsilon \frac{d}{dt} n_{H2} = -(k_{21} n_{H2} - k_{12} n_{H1}), \tag{7}$$

$$\varepsilon \frac{d}{dt} n_{D2} = - \left(\tilde{k}_{21} n_{D2} - \tilde{k}_{12} n_{D1} \right). \tag{8}$$

Since migration is a conservative process, the variables n_H and n_D are the first integrals of the migratory system. This allows us to express the equilibrium, towards which the fast system relaxes, in terms of n_H and n_D, giving

$$n_{H1} = \frac{k_{21}}{k_{12} + k_{21}} n_H, \tag{9}$$

$$n_{H2} = \frac{k_{12}}{k_{12} + k_{21}} n_H, \tag{10}$$

$$n_{D1} = \frac{\tilde{k}_{21}}{\tilde{k}_{12} + \tilde{k}_{21}} n_D, \tag{11}$$

$$n_{D2} = \frac{\tilde{k}_{12}}{\tilde{k}_{12} + \tilde{k}_{21}} n_D. \tag{12}$$

This solution is stable so long as $k_{12} + k_{21} > 0$ and $\tilde{k}_{12} + \tilde{k}_{21} > 0$. Physically we expect k_{12}, k_{21}, $\tilde{k}_{12}$, and $\tilde{k}_{21}$ to be greater than zero. Thus, the realistic solution is always stable, which is required if we are to proceed and analyse the slow dynamics using the techniques mentioned above.

If migration is symmetrical between the two patches, then $k_{12} = k_{21}$ and $\tilde{k}_{12} = \tilde{k}_{21}$ giving $n_{H1} = n_{H2} = n_H/2$ and $n_{D1} = n_{D2} = n_D/2$, respectively. Since the symmetrical case is likely to be close to the biologically reality, we introduce two new parameters, $2\bar{r} = 1 - n_{H1}/n_H - n_{D1}/n_D$ and $2r = n_{H1}/n_H - n_{D1}/n_D$. The symmetrical migration corresponds to $\bar{r}$ and r both zero. Just $r = 0$ corresponds to the case where the migratory rates of hawks and doves are identical. Just $\bar{r} = 0$ is the case when the asymmetrical migration rates for the hawks are reserved for the doves. Using these new parameters, the behaviour close to symmetry can be easily calculated. The physical limits of $\bar{r}$ and r are, $1/2 \leq \bar{r} \leq -1/2$ and $-1 \leq r \leq 1$.

4. THE GAME DYNAMICS

We now turn to the slow part of the system. By adding equations (1)–(3), and similarly for equations (2) and (4), the equations for the slow dynamics are written down. The phase plane for the two slow variables, n_H and n_D, can be viewed as a 2-dimensional surface in the 4-dimensional

phase space of the entire system. On this surface, the fast variables are at their equilibrium values given by the solutions of (9)–(12).

Since there is no limiting term for the total population n, there is no nontrivial stationary solution for n. Following the usual hawk-dove analysis, we look at the ratio $x = n_H/n$ of hawk individuals to the total population. For a single patch, the dynamics of x are well known [1,12]. There are a maximum of three stationary solutions for x, the stability of which depend upon the ratio of the cost to the gain. The point $x = 0$ is always unstable, the point $x = 1$ is stable so long as $G > C$, while the point $x = G/C$ is stable so long as $G < C$. For two patches, the number of possible stationary solutions is now four. This can be seen by looking at the equation for x,

$$\frac{dx}{dt} = \frac{n^2}{2n_1 n_2} x(1-x)f(x),$$

where

$$f(x) = \alpha x^2 + \beta x + \gamma,$$

$$\alpha = -\bar{C}r\left(2\bar{r} - r\right) + \frac{c}{4}r\left(1 + 4\bar{r}^2 - 4r\bar{r} + r^2\right) - gr^3,$$

$$\beta = 2\bar{r}r\bar{G} - \frac{\bar{C}}{4}\left[1 - 4\bar{r}\left(\bar{r} + r\right) + 3r^2\right] + \frac{g}{4}r\left[5r^2 + 4\bar{r}\left(2r - \bar{r}\right) - 1\right]$$
$$- \frac{c}{8}\left(3r - 2\bar{r} + 8\bar{r}^3 - 4\bar{r}^2 r - 2\bar{r}r^2 + r^3\right),$$

$$\gamma = \left[1 - (2\bar{r} + r)^2\right]\left[\frac{\bar{G}}{4} - \frac{g}{8}\left(2\bar{r} + 3r\right)\right],$$

where $\bar{G} = (G_1 + G_2)/2$, $g = G_1 - G_2$, $\bar{C} = (C_1 + C_2)/2$, and $c = C_1 - C_2$. The multiplying term $n^2/(n_1 n_2)$ in equation (13) can be written purely in terms of x, and has no dependence upon the total population. Since this term is strictly positive, it has no effects upon the stability of the equilibrium points. Equation (13) has two stationary solutions at $x = 0$ and $x = 1$ and two others at the roots of the polynomial $f(x)$, which we shall call x_1 and x_2 (where $x_1 \leq x_2$). The difference with the one patch case lies in $f(x)$. For just one patch, $f(x)$ is linear in x, while in our case $f(x)$ has the possibility of being quadratic. If $G_1 = G_2$ and $C_1 = C_2$ or if $\bar{r} = r = 0$, then $\alpha = 0$ and $f(x)$ is similar in its properties to the single patch case.

4.1. The Stability of the Stationary Solutions

Even before the values of x_1 and x_2 are known, we can say something about the stability of the solutions.

$x = 0$ is stable if

$$2\bar{G} < g\left(3r + 2\bar{r}\right),$$

which if simplified by saying that $G_1 = G_2 = G$ tells us that $x = 0$ is never stable, except when $G = 0$. In this case, the solutions stability is determined at second order in x, and although this is technically always unstable (since leading order terms of x^2 are never stable), for realistic cases ($x > 0$) $x = 0$ may appear to be stable. These results are in fact true even when $G_1 \neq G_2$, thus the solution $x = 0$ is only stable for a very special case, which turns out to be when migration is forbidden, one patch contains only dove individuals with a positive gain, and the other a gain of zero.

$x = 1$ is stable if

$$\cdot\,\alpha + \beta + \gamma > 0.$$

If this is simplified by saving that $G_1 = G_2 = G$ and $C_1 = C_2 = C$, then the $x = 1$ solution is stable only when $G/C > 1$ as is expected from the single patch result.

$x = x_1$ is stable if

$$x_1(1 - x_1)g(x_1) < 0,$$

where

$$g(x_1) = \begin{cases} \alpha(x_1 - x_2), & \text{if } \alpha \neq 0, \\ \beta, & \text{if } \alpha = 0. \end{cases}$$

$x = x_2$ is only a solution if $\alpha \neq 0$. In this case, it is always unstable if it lies within the physical constraints (i.e., $0 \leq x_2 \leq 1$) and if $\alpha > 0$. The exception to this case is when $x_1 = x_2$, in which case the stability is determined at second order.

4.2. The Simplified Case $r = 0$

The case when $r = 0$ corresponds physically to the fact that the migration rates of the doves are proportional to those of the hawks. Calculating the coefficients for the polynomial $f(x)$ gives,

$$\alpha = 0, \tag{18}$$

$$\beta = -\left(1 - 4\bar{r}^2\right) \frac{(\bar{C} - c\bar{r})}{4}, \tag{19}$$

$$\gamma = \left(1 - 4\bar{r}^2\right) \frac{(\bar{G} - g\bar{r})}{4}. \tag{20}$$

Since $\alpha = 0$, this case has only three stationary solutions, just like the standard homogeneous result. In fact, the similarity between the single patch result and this case is even closer, since if we rewrite the parameters such that

$$G = \left(1 - 4\bar{r}^2\right)\left(\bar{G} - g\bar{r}\right), \tag{21}$$

$$C = \left(1 - 4\bar{r}^2\right)\left(\bar{C} - c\bar{r}\right), \tag{22}$$

we have exactly the single patch equations, where G is the homogeneous gain and C is the homogeneous cost. This should not really be that surprising, since if the migratory rates for the hawks and the doves are the same, we can "sum" the two patches and consider them as one big patch. The composite parameters are given by the right-hand sides of the relations (21) and (22).

Since the analysis of the homogeneous case is well known, we just review the results. The system has three stationary solutions at $x_a = 0$, $x_b = 1$, and $x_c = G/C$. The solution x_a is always unstable for positive values of the gain and cost (negative values of gain or cost do not have an obvious physical interpretation). If the gain G is greater than the cost then solution $x_c > 1$, and thus lies outside the physically realistic domain. In this case, the solution x_b is always stable (again we just consider positive values of G and C). For $G < C$, the solution x_c enters into the physical domain, and becomes stable while the solution x_b becomes unstable. Thus for $G < C$, the stable state is to have a mixture of hawks and doves in a ratio given by G and C.

5. EFFECTS OF HETEROGENEITY

Even if the conditions upon the two patches differ, the final state of the population may not be very different from the homogeneous case, as we saw in the last section. The homogeneity becomes important when the parameter α is nonzero. Then the similarities between our model and the homogeneous case come to an end, since the polynomial $f(x)$ now has two roots, giving a total of four stationary solutions.

The heterogeneity of our model is described by three parameters, c, g, and r. If $c \neq 0$, then the cost of following a hawk-like strategy varies between the two patches. If $g \neq 0$, then it is the gain involved in winning a confrontation with another individual which differs, while if $r \neq 0$, then the rates of migration between the two patches for the hawks and the doves are no longer the same. The parameter $\bar{r}$, although it describes the asymmetry between the migration rates, does not significantly alter the behaviour of the model if it is nonzero. As seen in the last section,
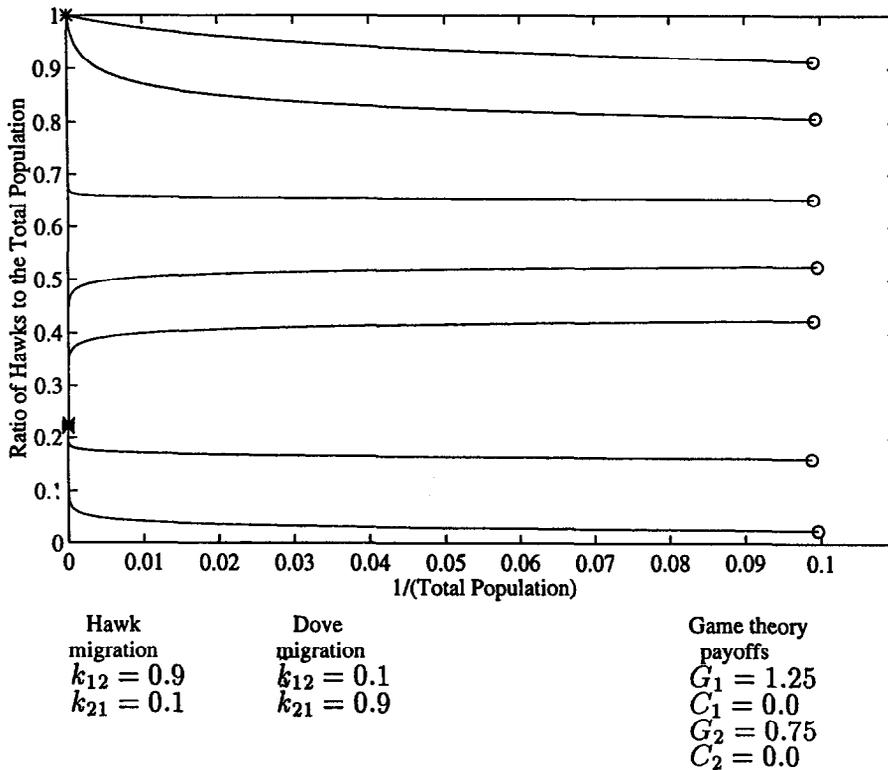
Figure 3. The ratio of hawks (x) plotted against the reciprocal of the total population. The heterogeneous model when $\alpha \neq 0$ and the two solutions x_1 and x_2 lie in the domain $x \in (0,1)$. Circles indicate starting values while the stars at $n = \infty$ indicate the stable stationary solutions $x_1 = 0.22$ and $x_2 = 0.64$. The total population tends to infinity because no ceiling has been imposed on the model. Depending upon the initial starting value of x, the population tends towards a purely hawk structure or a mixture of hawks and doves.

this is because the symmetry between the hawks and doves is still maintained, even if $\bar{r} \neq 0$. Heterogeneity introduces a wide range of dynamical behaviours which are not present in the homogeneous case. We review the situations, and discuss their physical significance.

First, if both the roots of $f(x)$ lie outside the domain $x \in [0,1]$, then it is possible that the solution $x = 0$ is stable while $x = 1$ is unstable, or vice versa (the stability of $x = 0$ is determined by equation (15)). So, the final population is either all doves or all hawks. This should be compared to the homogeneous case where only $x = 1$ (all hawks) was stable. Even if one patch apparently supports an obligate hawk-like population (e.g., $G_1 > C_1$), a suitably "poor" neighbouring patch (e.g., $G_2 \ll C_2$, G_1) combined with a suitably high migration rate is enough to make the hawk strategy inviable, and cause an obligate dove population.

If the solution x_1 lies in the domain $x \in (0,1)$, then we have the possibility of a mixed population, where hawk and dove individuals cohabit the same regions. So long as $\alpha > 0$, this mixed state is stable. Parameter changes can change the stability. If the quality of the environments alter or the migration becomes easier, effects may be seen in the stability of the population structure. A similar range of behaviours is possible when only x_2 lies in the range $x \in (0,1)$.

The most novel case is when both roots x_1 and x_2 lie in the physical domain $x \in (0,1)$. In this case, the final state of the population depends upon its starting state. If x_1 is stable, and hence x_2 unstable, then for an initial x sufficiently small, the population will tend towards the stable mixed state at x_1. However, if the initial x exceeds x_2, then the doves no longer have any possibility of surviving and the system converges upon an obligately hawk population. A numerical simulation illustrating this situation is given in Figure 3. This behaviour is caused by

a playoff between patch "quality" and migration. Consider a patch P_1, which favours an obligate hawk population (i.e., G_1 sufficiently greater than C_1), but where migration of hawks from this patch is much faster than their migration onto the patch, and where migration of doves onto the patch is much greater than their migration off the patch. Now, if we have enough hawks to start with they can capitalise upon the high dove concentrations on P_1 and the favourable environment, allowing the hawks to dominate on *both* patches. However, if the initial population of hawks is too small, then the handicap of the less favourable patch become impossible to compensate for and a mixed population results.

The complementary case would be when $\alpha < 0$, in which case x_1 is unstable. However, in this case, x_1 will not lie in the range $0 < x < 1$, and thus the two roots are no longer both in the physical range.

6. DISCUSSION

The aggregation techniques developed using ideas about time-scale hierarchies have permitted us to decompose the original system into a fast migratory part and a slow game-dynamics part. Assuming stability of the fast dynamics, their equilibrium solution was placed into the slow dynamics in order to obtain the dynamics of the full system. It has been possible to obtain analytical results from what, in general, is a complicated system.

The heterogeneous model does contain, as a special case, the homogeneous single patch model, as it should. As for the single patch, if parameters of the two patch model, such as the migration rates or the gains and costs, are changed then a previously stable solution can become unstable, and vice versa. As an example, such parameter change could arise from human intervention, or from the slow natural evolution of the environment. The general dynamics of the heterogeneous model are considerably richer than those of the homogeneous model, and new effects are seen. The effects of adding a second patch, alters the dynamics in a nontrivial way. New stationary solutions appear and existing solutions can have their stability properties altered. For example, the presence of a stable obligate dove strategy is allowed, albeit in a very special circumstance, and two stable physically realistic solutions can occur, where as only one is allowed in the homogeneous case.

Although such a simple model is not going to show the type of chaotic behaviour seen by Nowak and May [4] and Hassell *et al.* [5], it does start to show dependencies upon the initial conditions. This is interesting because no parameters have to change in order that the final state changes. Only a shift in the variables of the model is required. For instance, a mixed population could be turned into a purely hawk population with a suitable input of hawk-like individuals while a population, originally destined to be obligately hawk, may become mixed if there is a sudden cull of hawk individuals. Other situations are conceivable.

The question of whether such effects occur in real populations has yet to be shown. The next stage of this work will be to apply these ideas to real populations whose individuals are free to undertake local migrations in order to change their habitat. Extensions of the migratory part of the model to various other patch geometries (e.g., cyclic or branching patters), higher numbers of patches, and populations with carrying capacities, may also be possible. The game theory part could also be adapted, for example, to include three strategies games, bimatrix dynamics, such as a battle of the sexes or density dependent payoffs. Our present work shows that heterogeneous environments, even as simple as the one studied here, can have novel consequences which must be important if ecology is going to study realistic situations.

APPENDIX
DETAILS OF THE CALCULATION OF f(x)

In order to pass between the full equations (1)–(4) for the system to the equation (13) for the slow dynamics of $x = n_H/n$, the steps are complicated, but mathematically straightforward. Our

calculations were originally done by hand, and then checked and further cases examined using the mathematical computer package, MAPLE V. The fast dynamics are calculated, as explained in Section 3, giving the variables n_{H1}, n_{H2} in terms of n_H, and n_{D1}, n_{D2} in terms of n_D. Once this is done, we can turn to the slow game dynamics. Adding equation (1) to equation (3), and equation (2) to equation (4) gives,

$$\frac{d}{dt}n_H = \frac{n_{H1}}{n_{H1}+n_{D1}}\left[\frac{G_1-C_1}{2}n_{H1}+G_1 n_{D1}\right] + \frac{n_{H2}}{n_{H2}+n_{D2}}\left[\frac{G_2-C_2}{2}n_{H2}+G_2 n_{D2}\right], \quad (23)$$

$$\frac{d}{dt}n_D = \frac{n_{D1}}{n_{H1}+n_{D1}}\frac{G_1}{2}n_{D1} + \frac{n_{D2}}{n_{H2}+n_{D2}}\frac{G_2}{2}n_{D2}, \quad (24)$$

for the evolutionary equations of n_H and n_D, where all the parameters are described in the introduction. For realistic cases, where the populations are positive, the only stationary solution is when $n_H = n_D = 0$ and this is found to be unstable. Thus, there is no stable stationary solution for the whole system. To proceed, we change variables to be $n = n_H + n_D$, the total population, and $x = n_H/n$, the proportion of this populations which is hawk-like. The dynamical equations for these new variables are

$$\frac{dn}{dt} = \frac{dn_H}{dt} + \frac{dn_D}{dt}, \quad (25)$$

$$\frac{dx}{dt} = \frac{(1-x)}{n}\frac{dn_H}{dt} - \frac{x}{n}\frac{dn_D}{dt}. \quad (26)$$

The total population is found to have only one stationary point at $n = 0$ which is unstable, but the equation for x, which is independent of n has a more complicated behaviour. This far into the game-dynamics, nothing is really new. All these ideas have been well studied before. What we must now do is rewrite equation (26) explicitly in terms of x. First of all, we treat the ratios n_{H1}/n_H, n_{H2}/n_H, n_{D1}/n_D, and n_{D2}/n_D as parameters since they depend only upon the constant migration rates. It is quickly seen that the right-hand side of equation (26) can have a common factor of $x(1-x)$ brought out to give us

$$\frac{dx}{dt} = \frac{n^2}{2n_1 n_2}x(1-x)\left\{\left[(G_1-C_1)\left(\frac{n_{H1}}{n_H}\right)^2 r_2 + (G_2-C_2)\left(\frac{n_{H2}}{n_H}\right)^2 r_1\right.\right.$$

$$\left. - 2G_1\frac{n_{H1}}{n_H}\frac{n_{D1}}{n_D}r_2 - 2G_2\frac{n_{H2}}{n_H}\frac{n_{D2}}{n_D}r_1 + G_1\left(\frac{n_{D1}}{n_D}\right)^2 r_2 + G_2\left(\frac{n_{D2}}{n_D}\right)^2 r_1\right]x \quad (27)$$

$$\left. 2G_1\frac{n_{H1}}{n_H}\frac{n_{D1}}{n_D}r_2 + 2G_2\frac{n_{H2}}{n_H}\frac{n_{D2}}{n_D}r_1 + G_1\left(\frac{n_{D1}}{n_D}\right)^2 r_2 + G_2\left(\frac{n_{D2}}{n_D}\right)^2 r_1\right\},$$

where $r_1 = (n_{H1}+n_{D1})/n$ and $r_2 = (n_{H2}+n_{D2})/n$, which are used to simplify the representation, are functions linear in x. The term inside the curly brackets is quadratic in x, and is the function $f(x)$ in equation (13). Thus, all that remains to be done is rewrite this bracket in a more convenient form. First, we change the parameters so that we can easily look at nonsymmetric cases. We define new parameters, $G, g, C, c, \bar{r}, r$, such that

$$G = \frac{G_1 + G_2}{2}, \quad (28)$$

$$g = G_1 - G_2, \quad (29)$$

$$C = \frac{C_1 + C_2}{2}, \quad (30)$$

$$c = C_1 - C_2, \quad (31)$$

$$\bar{r} = \frac{1}{2}\left(1 - \frac{n_{H1}}{n_H} - \frac{n_{D1}}{n_D}\right), \quad (32)$$

$$r = \frac{1}{2}\left(\frac{n_{H1}}{n_H} - \frac{n_{D1}}{n_D}\right). \quad (33)$$

In the symmetric case when both patches are the same and the migration rates are equally balanced, $g = c = \bar{r} = r = 0$. Now, we collect the terms inside the curly bracket of equation (27) into powers of x and write them as shown in equations (13),(14).

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