Inherited Fitness in the Hawk-Dove Model

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ABSTRACT

We examine a generalization of the standard Hawk-Dove evolutionary model in which we incorporate a proportional inheritance of Darwinian fitness. We discuss the behavior of the model analytically and numerically and, in particular, find regions of the parameter space corresponding to stable equilibria. We show a dependence of these equilibria on the relative values of the inheritance parameters and show the existence of periodic orbits not present in the original. Further, we show that fixed initial fitness values need not be assumed, as they are in the standard model, since these equilibrium fitness values will be sought out by the model itself. This demonstrates that frequency-based models may be resilient to certain changes in assumptions of inheritance mechanisms.

1. INTRODUCTION

The prevalence of conventional contests in animal populations is a persistent theme in biological theories of animal behavior. Quite often, contests between pairs of animals over food, habitat, mates, and so forth, take the form of highly ritualized display behavior so that more often than not these contests are settled without serious injury to either animal. For example, harbor seals display an array of contest behavior, from flipper movements to head thrusts, in order to establish hierarchical dominance for mating [12]. Aggressive behavior, such as biting, is rarely observed. Similarly, many species of deer rely on vocalization and lateral display to settle conflicts over territory [4], [7]. On occasion – usually when the contest pairs are most evenly matched – deer will charge each other, lock antlers, and push against each other. However, if

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during the charge, one animal turns his flank to his opponents sharp antlers, the other animal halts his potentially injurious attack and again resumes display (see [6] p. 57).

Such behavior may be beneficial for the species as a whole since it avoids self-inflicted mortality among the population. However, it is hard to see at first why such behavior is beneficial on the individual level. After all, a ruthlessly aggressive animal seeking to kill his opponent would inherit his opponents' territory, harem, and so forth, increasing his number of offspring. These offspring would then inherit the parent's aggressive behavior and reproduce at a greater rate than the less aggressive population.

Several explanations have been given for why such escalated contests remain relatively rare. Early theorists, such as Tinbergen [13], focused on the intimidating aspects of contest behavior, the notion being that one animal might use a show of aggression to frighten his opponent into giving up the resource without a fight. As Clutton-Brock and Albon point out [4], this theory has the weakness that "selection should favor those individuals that are not intimidated unnecessarily and which adjust their behaviour only to the probability of winning and the costs and benefits of fighting." Because of this, subsequent theories have viewed display behavior as a mutual assessment of quality, or "resource holding potential," which allows animals to avoid fighting if they are unlikely to win [4], [7], [10].

However, while this view of contest behavior as mutual assessment does a good job of explaining the prevalence of escalated contests when opponents are evenly matched, it does not completely explain the lack of aggression when opponents are not equally matched. After all, if an assessment

of resource holding potential can lead the inferior animal to choose to give up the resource, then so too could it lead the superior animal to attempt to injure its opponent.

Realizing the need for a theory of animal contest behavior that avoids questions of individual ethology, John Maynard-Smith used game theory to propose a solution to the problem that focuses on the evolutionary dynamics of the population as a whole [11]. The theory is presented in the form of an abstract population model consisting of a single species in two distinct phenotypes. The first phenotype, *Hawk*, displays aggressive behavior while the second, *Dove*, is passive. Under the assumptions of the model, Hawk always defeats Dove in contesting for a resource. Yet, in the long term, Hawks do not always come to dominate the population. Maynard-Smith's model showed for the first time how simple mathematical rules governing interaction and reproduction can lead to the evolution of a stable distribution of aggressive/passive behavior in a population with neither one dominating the other.

An important assumption of the Hawk-Dove model is that initial fitness of each generation is held constant. In other words, each generation starts with a uniform fitness and it is solely the results of the contests in each generation that determine the phenotypes' fitness prior to reproduction. This assumption, while justified for the purposes of examining the dynamics of the model in the simplest case, can be justifiably weakened in cases where the resource itself is heritable. For instance, if the resource is status-related, and if the status of the parents is heritable in some way by the offspring, then it is possible that the phenotype's initial fitness is not fixed, but rather depends on the phenotype's fitness in the previous generation. In this way, we may generalize the Hawk-Dove model to allow for inheritance of fitness as well as phenotype from one generation to the next.

For instance, dominance hierarchies have been shown to affect reproductive success in free-ranging groups of deer [2]. Since antler size is an honest signal of quality in contest situations, as shown in [9], [15], one might expect to find a relation between social rank and antler length in mature stags. However, no such correlation has been observed [2], [8]. One way to account for this is to view deer as employing the following contest strategy, "retreat if opponent is of higher quality, escalate otherwise." In this way, individual contest behavior can be separated from overall reproductive success. That is to say, the behavioral phenotype, aggressive vs. passive, is actually determined by a secondary hereditary phenotype, the length and complexity of the antlers [8]. Status, on the other hand, is more closely correlated with body size and nutritional state [2], [8]. Body size in deer is hereditary, is correlated with greater overall reproductive success, and has been shown to both reinforce, and be reinforced by, rank within the group [1], [2], [3], [8], [14]. Hence, in this case, an argument can be made that both the fitness of an individual and the individual's behavioral phenotype are independently inherited from the parent.

In this paper we examine the implications of allowing inheritance of fitness in the Hawk-Dove model. In particular, we focus on the case where inheritance of fitness between generations is proportional. That is, each successive generation will inherit a fixed percentage of the fitness of its parent. We show that there are notable differences between this model and the basic one. For instance, the stable states of the population are shown to depend on the relative values of the coefficients of proportional inheritance for each phenotype. If these coefficients are equal, the population equilibrium is identical to that of the basic model. If the inheritance coefficients are different, however, then the model attains new population equilibriums not achievable by a similarly parametrized basic Hawk-Dove model. Further, convergence to the equilibrium population state is demonstrated to be highly oscillatory in the generalized model and a bifurcation curve is shown to exist in the parameter space about which periodic orbits are achieved. The existence of such periodic orbits is unexpected since they rarely show up in game theoretic models, even those that allow multiple phenotypes. This gives an intriguing connection between our generalization of Smith's model and other population models that display periodic orbits such as logistic or Lotka-Volterra models.

Another interesting aspect of our analysis lies simply in the observation that the generalized model does not "blow up." After all, by allowing for proportional inheritance we are, in effect, adding a positive feedback to the system. Simply put, if in any generation one phenotype has a higher fitness than the other, then this difference in fitness will tend to be exaggerated in the next generation since

initial fitness of the offspring is proportional to reproductive fitness of the parent. This is analogous to situations in which the "haves" end up having more and the "have nots" having less. The fact that this added feedback does not destabilize the system indicates that frequency-based models may be resilient to certain perturbations in assumptions of genetic inheritance mechanisms.

Yet perhaps the similarities that exist between the two models are more interesting than the differences. For instance, we show for the generalized model that any population at frequency equilibrium must also be at fitness equilibrium, so that in the long term the model must return to the basic case where the initial fitness of each generation is constant. This gives a mathematical explanation for how a uniform initial fitness for all generations can arise naturally in frequency-dependent evolutionary models and need not be assumed.

In what follows, we first give a brief overview of the basic Hawk-Dove model following Maynard-Smith [11]. Next we discuss the effects of allowing proportional inheritance of fitness from one generation to the next. In particular, we focus on finding equilibria and determining their stability. Lastly, we show the results of numerical implementation of our model.

2. THE HAWK-DOVE GAME

The setting of the Hawk-Dove game comprises of three main components: (1) the players and their characteristics, (2) the assumptions regarding how the game will be played, and (3) the payoff parameters, presented in the form of a payoff matrix.

"Hawk" and "Dove" are not literally the two types of animals present in the population, but are the behavioral phenotypes of individuals in a single species population. More specifically, in any given contest between two individuals in a Hawk-Dove population, one can exhibit any or all of the three following behaviors:

(i) Display: a player presents itself as a contestant for the resource.

(ii) Escalate: a player engages in attacking and attempts to injure its opponent.

(iii) Retreat: a player gives up the resource to its opponent and flees.

Hawk is the strategy that will escalate until either (1) its opponent retreats or (2) *Hawk* sustains an injury, at which point it retreats and gives up the resource. *Dove* is the strategy that starts by displaying, but retreats as soon as its opponent escalates.

Besides delineating the behavioral characteristics of each phenotype, it is equally important to state the typical assumptions of the model. First of all, any individual in the population is either a Hawk or a Dove, not both. Second, the distribution of Hawks and Doves in the population is measured by their frequency, not the raw number of individuals. As such, in order to avoid unnecessary complications, the population is assumed to be infinite. Third, we assume there is random mixing of phenotypes before each contest. Fourth, the generations are discrete and there is no overlap between a parent's generation and its offspring's. Fifth, reproduction is asexual and strategies are inherited from the parent. Lastly, the offspring of both phenotypes have a common initial fitness, denoted W_0, and this initial fitness remains constant over all generations. Note that it is this last assumption that will be modified in subsequent sections.

In contesting over a resource, a Hawk will prevail over a Dove due to the fact that the aggressiveness of the former is favored over the passiveness of the latter. However, if two Hawks face each other, their mutual aggressive behavior will result in injury to one opponent, reducing the average fitness of the pair. A contest between a pair of Doves will result in no injury to either player, but rather a reduced increase in fitness due to the fact that both players will have to share the resource.

The matrix below summarizes the expected payoff, $E(X, Y)$, in the form of Darwinian fitness of strategy X against Y:

	H	D
H	$(V - C)/2$	V
D	0	$V/2$

Here V is the value of the resource being contested for, which is also the increase in fitness, while C is the cost to fitness due to injury. For instance, the payoff $E(\mathrm{H}, \mathrm{H}) = (V - C)/2$ represents the average payoff to a Hawk when it engages in a contest

against another Hawk: 50% of the time it will increase its fitness by V, and for the rest of the time it will sustain injury and decrease its fitness by C.

Let p be the frequency of the Hawk phenotype in the population. The fitness of Hawk, denoted by WH, is equal to the sum of the initial fitness W_0 and the average change in fitness after the contest. This averaged change for Hawk is the sum of the weighted average of the expected payoffs of Hawk against Hawk and Hawk against Dove. Similarly, we can express the fitness of Dove WD in the same way. Hence, the expressions for both WH and WD are:

$$WH = W_0 + p\,E(\mathrm{H,H}) + (1-p)E(\mathrm{H,D}) \quad (1)$$
$$WD = W_0 + p\,E(\mathrm{D,H}) + (1-p)E(\mathrm{D,D})\,. \quad (2)$$

Since the strategies are hereditary and are passed on from one generation to the next (either genetically or via some other mechanism), the frequency of Hawk in the next generation is given by

$$p' = \frac{p\,WH}{p\,WH + (1-p)WD}\,. \quad (3)$$

2.1 Dynamics of the Hawk-Dove Game

Let $p(n)$ denote the frequency of Hawk in the nth generation. Similarly, let $WH(n)$ and $WD(n)$ denote the after-contest fitnesses of the Hawk and Dove phenotypes in the nth generation. If initial frequency of Hawks, $p(0)$, is predetermined, then equations (1)–(3) together determine uniquely the sequence $p(0), p(1), p(2), \ldots$ that gives the frequency of Hawks in any generation. This sequence is given recursively by

$$p(n+1) = \frac{p(n)WH(n)}{p(n)WH(n) + (1-p(n))WD(n)} \quad (4)$$

where the expressions for WH and WD can be reduced from (1) and (2) to the following form

$$\begin{aligned} WH(n) &= W_0 + V - p(n)(V+C)/2 \\ WD(n) &= W_0 + (1-p(n))V/2\,. \end{aligned} \quad (5)$$

Applying (5) to (4) gives

$$p(n+1) = \frac{2W_0 + 2V - (V+C)p(n)}{2W_0 + V - Cp(n)^2}p(n)\,. \quad (6)$$

A population equilibrium is achieved when $p(n) = p(n+1) = p^*$. If we ignore the trivial equilibrium

$p^* = 0$, then equation (6) reduces to

$$C(p^*)^2 - (V+C)p^* + V = 0$$

which has solutions $p^* = V/C$, 1. If $V < C$, then $p^* = V/C$ is strictly between 0 and 1 and gives a unique nontrivial equilibrium. On the other hand, if $V \geq C$, then the system has only the trivial equilibriums $p^* = 0$, 1. In this case, the cost due to injury is less then the value of the resource, hence there is no downside to aggressive behavior, and Hawk will eventually dominate the population.

2.2 Stability of p* = V / C

Let F denote the real valued function given by

$$F(x) = \frac{(2W_0 + 2V)x - (V+C)x^2}{2W_0 + V - Cx^2}\,.$$

By (6) we have $p(n+1) = F(p(n))$. Moreover, the equilibrium $p^* = V/C$ is a fixed point of F. The equilibrium is said to be stable if for all δ in a neighborhood of p^*, we have $|F(p^* + \delta) - p^*| < \delta$. That is, if the system is perturbed from its equilibrium a distance δ, then in the next generation the frequency will be less than δ units away from the equilibrium. Since F is smooth near p^*, the mean value theorem gives, for every δ sufficiently small in absolute value, a value c between p^* and $p^* + \delta$ such that

$$F(p^* + \delta) - F(p^*) = \delta\,F'(c)\,.$$

Since $F(p^*) = p^*$, the equilibrium is stable if and only if $|F'(x)| < 1$ for all x in a δ-neighborhood of p^*. By continuity of F, this is equivalent to requiring that $|F'(p^*)| < 1$. But we can check that

$$F'(p^*) = \frac{2CW_0}{2CW_0 + V(C-V)}$$

which is clearly less than 1 in absolute value given that $V < C$.

3. PROPORTIONAL INHERITANCE OF FITNESS

As before, let $p(n)$ denote the frequency of Hawks in the nth generation. Let $WH(n)$ and $WD(n)$ denote the after-contest fitnesses of the Hawk and Dove populations, respectively. We add the following inheritance assumption: the starting fitness of the $(n+1)^{\mathrm{st}}$ generation is directly proportional to the after-contest fitness of the nth generation. Letting $\alpha, \beta \in [0,1]$ denote the corresponding proportional inheritance constants of Hawk and Dove,

respectively, the inheritance assumption is then expressed by the following equations:

$$WH(n) = \alpha\, WH(n-1) + V - p(n)\frac{V+C}{2}$$
$$WD(n) = \beta\, WD(n-1) + (1-p(n))V/2\,. \qquad (7)$$

Notice the difference between (7) and (5): where the previous equations had constant initial fitness in the nth generation, now the initial fitness is determined by the after-contest fitness of the previous generation and the proportionality coefficients α and β. The replicator equation in this model remains unchanged from (4):

$$p(n+1) = \frac{p(n)\,WH(n)}{p(n)\,WH(n) + (1-p(n))WD(n)}\,. \qquad (8)$$

3.1 Equilibria

We wish to find the equilibria of this system. The stability of the equilibria will be discussed in the following section. Suppose the system is at frequency-equilibrium so that $p(n) = p(n+1) = p^*$ for all n, where p^* is fixed in $[0,1]$. Then (8) implies

$$p^* = \frac{WH(n)p^*}{p^*WH(n) + (1-p^*)WD(n)} \qquad (9)$$

for all n. If we assume $p^* \neq 0, 1$ (i.e., p^* is a nontrivial equilibrium), then (9) implies $WH(n) = WD(n)$ for all n. Subtracting the equations in (7) then gives the following expression for the frequency equilibrium:

$$p^* = \frac{V}{C} + \frac{2}{C}(\alpha - \beta)WH(n)\,. \qquad (10)$$

In case $\alpha \neq \beta$, equation (10) implies that $WH(n)$ (and therefore also $WD(n)$) does not depend on n. That is, assuming $\alpha \neq \beta$, if the system is at frequency equilibrium, then the system must also be at fitness equilibrium. On the other hand, if $\alpha = \beta$, then (7) implies that

$$WH(n) = \alpha\, WH(n-1) + V - p^*\frac{V+C}{2}\,. \qquad (11)$$

This equation will have a unique stable fixed point W^* provided $\alpha < 1$. Moreover, the fixed point W^* will be positive if and only if the constant term from (11) is positive, which is equivalent to the condition

$$p^* < \frac{2V}{V+C}\,. \qquad (12)$$

Since (10) reduces to $p^* = V/C$ in the case $\alpha = \beta$, we see that the inequality in (12) reduces to $V <$

C. But this is precisely the condition required for $p^* = V/C \in (0,1)$.

Thus, we see that for $\alpha, \beta < 1$ the system given by equations (7)–(8) has a fixed point given by $p(n) = p^*$, $WH(n) = WD(n) = W^*$.

To solve for this fixed point, notice that the equations in (7) together imply

$$W^* = \frac{V(1-p^*)}{2(1-\beta)} = \frac{2V - (V+C)p^*}{2(1-\alpha)} \qquad (13)$$

which gives us the following expression for the frequency equilibrium:

$$p^* = \frac{V(1+\alpha-2\beta)}{C(1-\beta) + V(\alpha-\beta)}\,. \qquad (14)$$

After substituting this expression back into (13) we obtain

$$W^* = \frac{V/2}{1-\beta}\left(1 - \frac{V(1+\alpha-2\beta)}{C(1-\beta) + V(\alpha-\beta)}\right)\,. \qquad (15)$$

At this point we would like to find conditions on our parameters in order to guarantee that these solutions are realistic. Namely, we must insure that $0 < p^* < 1$ and $W^* > 0$. Notice, however, that $p^* < 1$ is equivalent to $W^* > 0$. Hence, we need only concern ourselves with insuring that $0 < p^* < 1$.

We will have $p^* > 0$ if the numerator and denominator in (14) are either both positive or both negative. The equation $V(1+\alpha-2\beta) = 0$, given by setting the numerator equal to 0, is a line in the $\alpha\beta$-plane passing through the points $(0, 1/2)$ and $(1,1)$. Likewise, the equation given by the denominator, $C(1-\beta) + V(\alpha-\beta) = 0$, is a line passing through the points $(0, C/(C+V))$ and $(1,1)$.

Under the assumption that $V < C$, it is easily verified that $0 < p^* < 1$ if and only if (α, β) lies in the region $R_1 = \{(\alpha, \beta) \mid \beta < \alpha/2 + 1/2\}$ (i.e., the point lies below both lines from the previous paragraph). On the other hand, if $V > C$, then we see that $0 < p^* < 1$ if and only if (α, β) lies in the region $R_2 = \{(\alpha, \beta) \mid \beta > \alpha/2 + 1/2\}$. These regions are shown in Figure 1.

In this way, the parameter space is decomposed into two regions, R_1 and R_2, in which realistic equilibriums exist depending on whether $V < C$ or $V > C$, respectively.
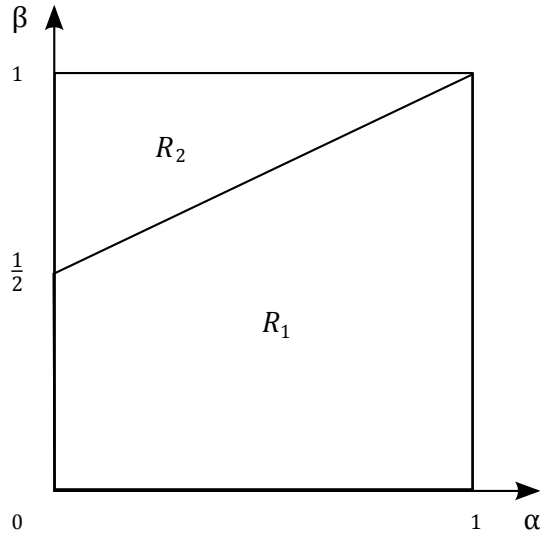
Figure 1: Regions of the parameter space corresponding to realistic equilibrium values.

3.2 Stability

We now seek to answer the question of stability of the fixed points given in the previous section. As a first step we rewrite the defining equations (7) and (8) as a system of three recursive equations

$$x_{n+1} = F(x_n, y_n, z_n)$$
$$y_{n+1} = G(x_n, y_n, z_n)$$
$$z_{n+1} = H(x_n, y_n, z_n)$$

where the functions F, G, and H are given by

$$F(x, y, z) = \frac{xy}{xy + (1 - x)z}$$

$$G(x, y, z) = \alpha y + \frac{xy(V - C)/2 + (1 - x)zV}{xy + (1 - x)z}$$

$$H(x, y, z) = \beta z + \frac{(1 - x)zV/2}{xy + (1 - x)z}.$$

The point (p^*, W^*, W^*) given by (14) and (15) is then a fixed point of this system.

The system is linearized via the Jacobian matrix:

$$J = \begin{bmatrix} \partial F/\partial x & \partial F/\partial y & \partial F/\partial z \\ \partial G/\partial x & \partial G/\partial y & \partial G/\partial z \\ \partial H/\partial x & \partial H/\partial y & \partial H/\partial z \end{bmatrix}$$

That is, if we denote the perturbation from equilibrium by $x'_n = x_n - p^*$, $y'_n = y_n - W^*$, and $z'_n = z_n - W^*$, then the perturbation in the next generation is given, up to a first approximation, by

$$\begin{bmatrix} x'_{n+1} \\ y'_{n+1} \\ z'_{n+1} \end{bmatrix} = J|_{(p^*, W^*, W^*)} \begin{bmatrix} x'_n \\ y'_n \\ z'_n \end{bmatrix}$$

Moreover, the fixed point (p^*, W^*, W^*) is stable if and only if the eigenvalues of $J|_{(p^*, W^*, W^*)}$ are all less than 1 in absolute value (for more details see [5], Section 2.9).

The characteristic polynomial of $J|_{(p^*, W^*, W^*)}$ is of degree 3 and sufficiently complicated to preclude solving for the eigenvalues in the general case. Instead, we will use the Jury test, which produces a finite set of conditions such that all conditions are satisfied if and only if the fixed point is stable. In our case, if we write the characteristic polynomial of $J|_{(p^*, W^*, W^*)}$ as

$$\chi_J(\lambda) = a_3 + a_2\lambda + a_1\lambda^2 + \lambda^3$$

(were we have multiplied by -1 in order to make the polynomial monic), then the Jury test gives the following conditions for stability (see p. 59 in [5]):

$$1 + a_1 + a_2 + a_3 > 0 \tag{16}$$
$$1 - a_1 + a_2 - a_3 > 0 \tag{17}$$
$$1 > |a_3| \tag{18}$$
$$|b_3| > |b_1| \tag{19}$$
$$|c_3| > |c_2| \tag{20}$$

where

$$b_1 = a_2 - a_3a_1 \qquad b_2 = a_1 - a_3a_2 \qquad b_3 = 1 - a_3^2$$
$$c_2 = b_3b_2 - b_1b_2 \qquad c_3 = b_3^2 - b_1^2.$$

At first, it should be pointed out the terms in the above inequalities can be shown to depend on the ratio $r = V/C$, rather than on V or C independently. However, the inequality in (16) is independent of r as well, and can be reduced to

$$(1 - \beta)(1 + \alpha - 2\beta) > 0.$$

This implies that all stable fixed points must correspond to parameters $(\alpha, \beta) \in R_1$. Recall that for points in R_1 to be realistic equilibria we must also have $V < C$. The inequalities in (17), (18), and (20) are similarly shown to be satisfied in region R_1.

The inequality in (19), however, is not satisfied on the full region, R_1, but rather on a subregion. In
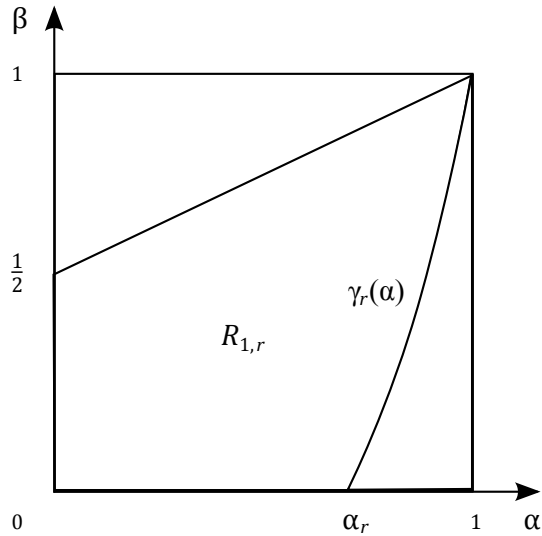
Figure 2: Division of R_1 into stable and unstable regions.

fact, for fixed $r > 1$ the quantity $z = |b_3/b_1|$ defines a surface over R_1 which intersects the plane $z = 1$ in a smooth curve.

Projecting onto the $\alpha\beta$-plane, we obtain a function $\beta = \gamma_r(\alpha)$. This curve defines the subregion $R_{1,r} \subseteq R_1$ that corresponds to stable fixed points of the system (see Figure 2). We find the point α_r at which this curve intersects the α-axis by solving for α in $|b_3/b_1|_{\beta=0} = 1$. Since this quantity is given by

$$|b_3/b_1|_{\beta=0} = \frac{\alpha + r}{2\alpha^2 + \alpha(1 + r)}$$

we find that

$$\alpha_r = \frac{1}{4}\left(\sqrt{8r + r^2} - r\right).$$

The equation for the curve $\gamma_r(\alpha)$ is somewhat unwieldy. However, it can be shown that $\gamma_r(\alpha)$ is always below the line $\beta = (\alpha - \alpha_r)/(1 - \alpha_r)$, which is the straight line connecting $(\alpha_r, 0)$ to $(1, 1)$. As $r \to 1$ we have $\alpha_r \to 1/2$. On the other hand, as $r \to \infty$ we have $\alpha_r \to 1$ and the region of stability, $R_{1,r}$, approaches the full region R_1.

The line $\alpha = \beta$ is inside $R_{1,r}$ for all r, hence the system is stable for all choices of $0 < \alpha = \beta < 1$. In fact, the eigenvalues of the Jacobian matrix can be found explicitly in this case. They are

$$\lambda = \alpha, \alpha \pm \sqrt{\alpha^2 - \alpha}$$

from which we verify $|\lambda| < 1$ directly. Further-

more, the existence of complex eigenvalues implies that this system will display oscillatory behavior near the equilibria (see [5], p. 25). This is verified numerically in the next section.

In addition, since the system changes stability when passing through the curve $\beta = \gamma_r(\alpha)$, we expect to find periodic orbits in this vicinity. This, too, is verified in the next section.

4. NUMERICAL SIMULATION

To verify the analytical results given above, we show the results of numerical implementation of the generalized model. As discussed above, realistic, non-trivial equilibria exist only when $V < C$. As such, all models are run under this assumption.

p : Current
q : Current
Equilibrium : Current
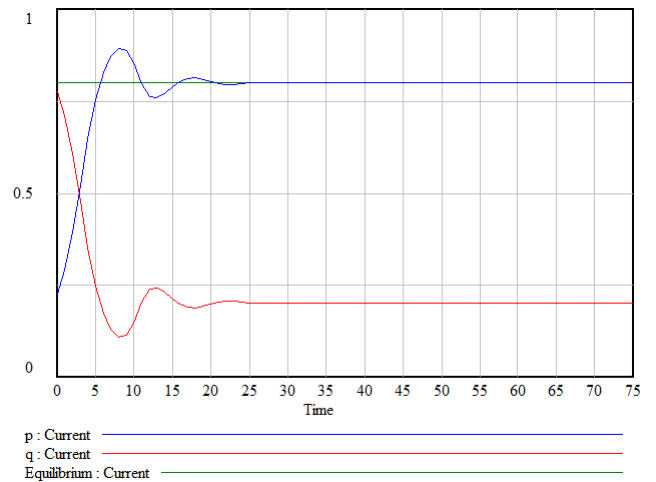
**Figure 3: Frequency over time for $p(0) = 0.225$, $V = 4$, $C = 5$, $\alpha = 0.64$, and $\beta = 0.64$.**

Figure 3 is representative of the frequency behavior of the model when $\alpha = \beta$. As stated previously, the line $\alpha = \beta$ is always inside $R_{1,r}$, which means the system is always stable for choices of $0 < \alpha = \beta < 1$. For this simulation we take $V = 4$ and $C = 5$, hence the stable equilibrium value in this case is $p^* = 0.8$. One thing to notice here is the presence of oscillations as the frequency approaches the equilibrium. This kind of behavior is due to the existence of complex eigenvalues and is not present in the standard model.

Figures 4 and 5 show the behavior of the model as the inheritance parameters leave the diagonal $\alpha = \beta$ and approach the bifurcation curve. Both the frequency and the fitness are shown. Notice the increase in oscillations from Figure 3. Notice also, that the equilibrium value here is different
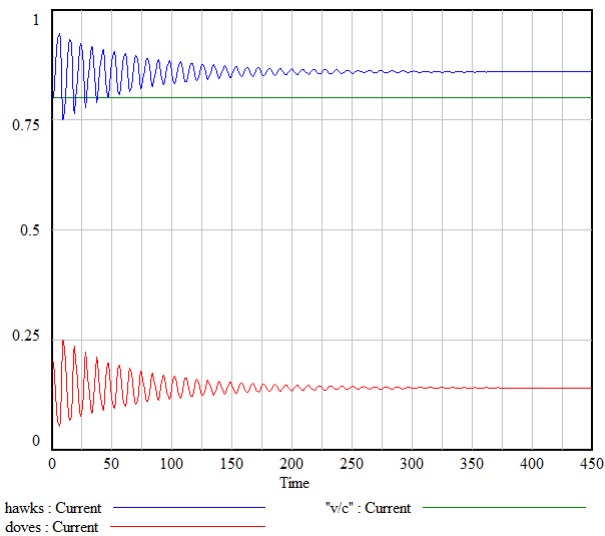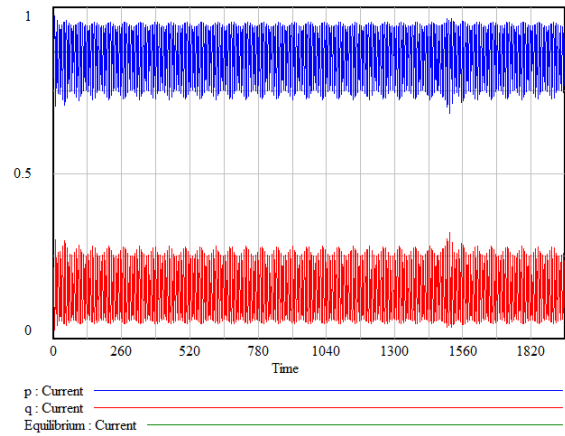
Figure 4: Frequency over time for $p(0) = 0.8$, $V = 4$, $C = 5$, $\alpha = 0.83$, and $\beta = 0.64$.

from that in Figure 3 due to equation (14) and the fact that $\alpha \neq \beta$. A similar picture results even if we start with $p(0) = p^*$. That is, the model begins in frequency-equilibrium, but does not remain there. This is due to the fact that the fitnesses WH and WD do not begin at their equilibrium values. In the long term, however, the population evolves to these equilibrium fitness values and at that point the population has a fixed initial fitness for all generations.
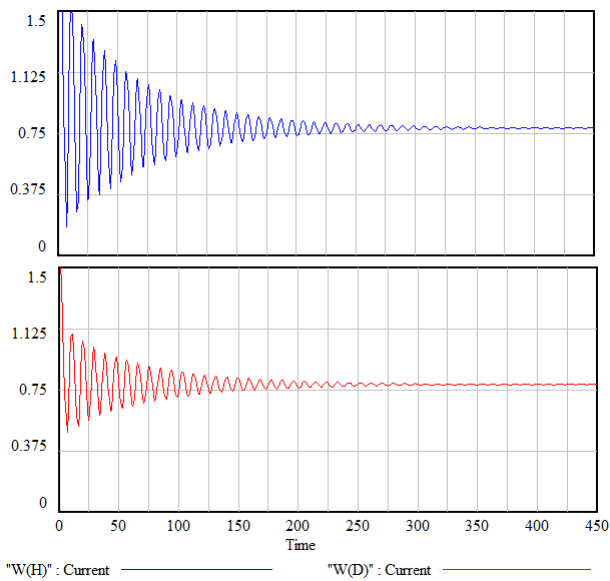

Figure 5: Fitness over time for $p(0) = 0.8$, $V = 4$, $C = 5$, $\alpha = 0.83$, and $\beta = 0.64$.

Figure 6 shows the periodic orbits that characterize the behavior of the model for parameters on the bifurcation curve. In this case there is no long term stability in the population, though the oscillations are regular about the equilibrium. Plots of the fitnesses WH and WD show similar oscillations. Notice that the model parameters in this case are very close to those in Figure 4. This indicates that the bifurcation curve is a Hopf-like bifurcation, wherein periodic orbits occur in a narrow window about the bifurcation, with stability being reattained upon perturbation of the system in the appropriate direction.

Figure 6: Frequency over time for $p(0) = 0.787$, $V = 4$, $C = 5$, $\alpha = 0.85$, and $\beta = 0.63$. Note: a perturbation has been introduced at time 1500.
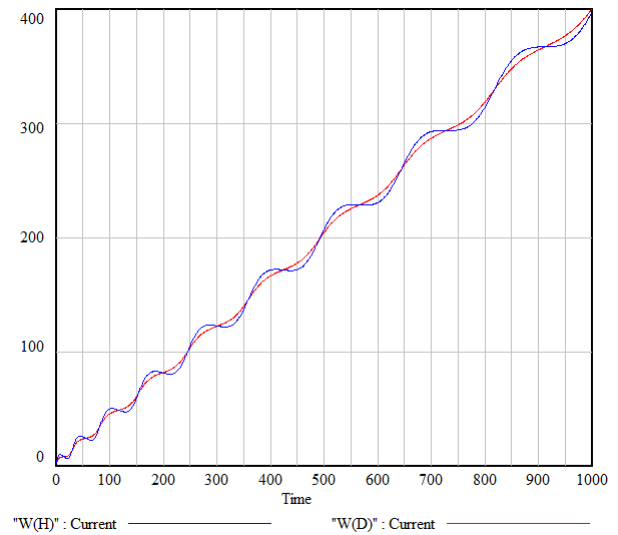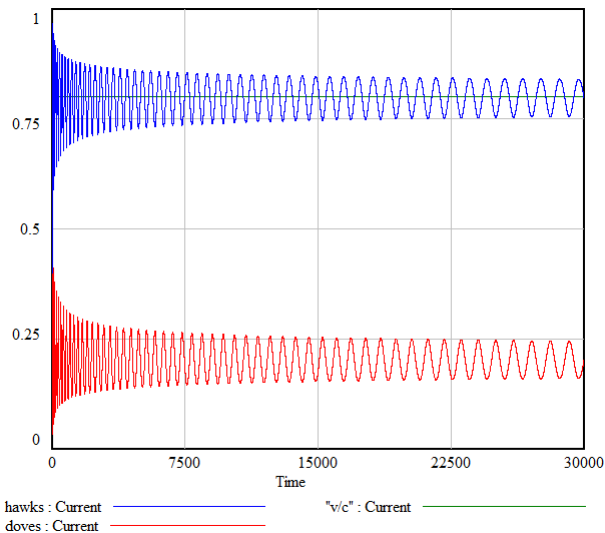

Figure 7: Fitness over time for $V = 4$, $C = 5$, $\alpha = \beta = 1$.

Though we did not discuss it above, it is interesting to note the behavior of the model when we set $\alpha = \beta = 1$. That is, we assume that fitness is fully and directly inherited from one generation to the next. In this case, equation (14) implies that $p^* = V/C$. Taking the limit as $\alpha, \beta \to 1$ in (13) we see that $W^* = \infty$. Moreover, equation (11) shows that the asymptotic behavior of the fitness is linear with slope given by

$$V - p^* \frac{V + C}{2} = \frac{V}{2}\left(1 - \frac{V}{C}\right) \, .$$

This behavior is confirmed numerically in Figure 7. Because the fitness can never achieve an infinite value, the system is never at equilibrium. Hence, the frequency of individuals in the population never stabilizes and, instead, always oscillates about is equilibrium as shown in Figure 8.

hawks : Current ———— "v/c" : Current ————
doves : Current ————

Figure 8: Frequency over time for $V = 4$, $C = 5$, $\alpha = \beta = 1$. Notice the persistence of the oscillations: the model has been computed to 30,000 generations.

5. CONCLUSION

By allowing proportional inheritance of fitness in the Hawk-Dove game we obtain a more complex system that displays both bifurcation and oscillatory phenomena. We showed that the steady states of the system depend on the relative value of the inheritance parameters. The standard non-trivial population equilibrium V/C is achieved only when these parameters are equal. Furthermore, and as long as the inheritance parameters stay sufficiently far away from the bifurcation curve in the parameter space, similar equilibrium values will be sought out by the system wherein fitness values for Hawk and Dove converge to steady states. For points in the parameter space near the bifurcation curve, the system displays periodic behavior and cannot obtain equilibrium.

These results have potential implications for populations that have previously been described using frequency-dependent models assuming a constant initial fitness (cf. [11], Ch. 6-9). For instance, while there is no *a priori* reason to allow different inheritance parameters to correspond to different display behavior, such an assumption could provide one explanation for why such populations are not always observed to be at equilibrium: inheritance parameters near the bifurcation curve lead to oscillations about the equilibrium rather than fast convergence as in the standard model.

The biological implications of this generalization for particular populations could also be the subject of further study. Good candidates for such a study would be populations, like deer, that exhibit status hierarchies in which individual status has a direct relationship to fitness and in which status is independent of display behavior.

The Hawk-Dove game is a simple model and is most often used as a first example to demonstrate the particular phenomena that can arise when using frequency-dependent models to describe biological populations. Because of this, it would be interesting to see how allowing proportional inheritance of fitness affects the dynamics of more complicated models which incorporate more than two strategies. For instance, preliminary numerical investigations show a dramatic increase in oscillatory phenomena when proportional inheritance of fitness is introduced in the Hawk-Dove-Retaliator model (cf. [11], p. 17).

In addition, it would be interesting to see if a similar analysis is possible for more general inheritance functions. This would show the extent to which the behavior of frequency-based models remains the same under changes in assumptions of genetic inheritance mechanisms.

6. ACKNOWLEDGMENTS

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