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A Generalization of Pontryagin's Maximum Principle for Dynamic Evolutionary Games among Relatives

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We present two theorems that generalize Pontryagin's maximum principle to the setting of dynamic evolutionary games between genetically related individuals. The two theorems correspond to two types of interactions among individuals: patch-structured populations in which individuals locally ''play the field'' and pairwise interactions. These generalizations can be used in the same way that Pontryagin's maximum principle is used and they are valid for diploid organisms under a single locus, diallelic genetic model. These generalizations involve an interesting, dynamic version of Hamilton's Rule from inclusive fitness theory. We illustrate how these theoretical results can be applied by modeling the evolution of lifetime resource allocation to growth and reproduction in an annual plant when there is competition for resources among related individuals. © 2000 Academic Press

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1. INTRODUCTION

The formalization of inclusive fitness theory by W. D. Hamilton in 1964 (Hamilton, 1964) is a milestone in the development of evolutionary biology. In particular, the principles of inclusive fitness and Hamilton's Rule have offered tremendous insight into the evolution of social behavior. Subsequent extensions of this theory have demonstrated that the concepts of inclusive fitness have a scope of applicability much larger than social behavior. Theoretical work has progressed to the point whereby quite sophisticated models can be routinely constructed that incorporate different classes of individuals (e.g., age classes) as well as different forms of population structure (e.g., patch structure, pairwise interactions,

lattice structures) (Charlesworth and Charnov, 1981; Bulmer, 1994; Taylor and Frank, 1996).

Parallel to this body of theory has been the development of models for the evolution of dynamic characters, i.e., characters that consist of a sequence of decisions. For example, one of the most studied of such characters is the lifetime pattern of resource allocation to growth and reproduction (Roff, 1992; Stearns, 1992; Kozlowski, 1992). This is the so-called general life history problem (Cohen, 1971; Leòn, 1976; Schaffer, 1983) and it has been addressed using the techniques of dynamic optimization such as Pontryagin's maximum principle (PMP) and dynamic programming (Kozlowski, 1992; Perrin and Sibly, 1993). There are many other examples of dynamic characters in behavioral ecology as well (Houston and McNamara, 1987; Houston *et al.*, 1988).

These two areas of theoretical evolutionary biology have developed largely independently of one another, although there have been some attempts at combining

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the insights gained from each. For example, McNamara *et al.* (1994) have described how to construct dynamic kin-selection models with interactions between two related individuals using dynamic programming. Their results were used to explore food provisioning in birds, but because the method they developed was limited to the case where only one individual makes "decisions," it cannot be used to explore the consequences of frequency-dependent selection where all individuals exhibit the character of interest.

To our knowledge, there is only one published example of a model for the evolution of dynamic characters when selection is frequency-dependent and where there are interactions among related individuals. This is a model developed by Mirmirani and Oster (1978) to explore the evolution of plant resource allocation strategies under competition. Mirmirani and Oster formulated their model as a differential game between two plants. They included the effects of relatedness by constructing an expression for the inclusive fitness of each plant by analogy with Hamilton's Rule (1964), and they then used PMP to calculate the evolutionarily stable strategy (ESS) of both plants. It is now known, however, that even in simple univariate models, calculating the ESS using an inclusive fitness expression can produce incorrect results compared with those of explicit genetic models (Grafen, 1979; Hines and Maynard-Smith, 1979; Mesterton-Gibbons, 1996; Day and Taylor, 1998a). Therefore, the genetic validity of Mirmirani and Oster's (1978) results is unclear. Furthermore, Mirmirani and Oster's model considered competition between two plants, but it would be useful to be able to model situations where more than two individuals interact. Additionally, their model was tailored to plant life history evolution, and it would also be useful to have a simple, general modeling approach that works for the evolution of any dynamic (i.e., time-dependent) character and that is guaranteed to be genetically accurate in the context of a single locus, diallelic, additive genetic model.

The purpose of this article is therefore to derive such an approach. In particular, we prove two theorems that generalize Pontryagin's maximum principle to the setting of dynamic evolutionary games among genetically related individuals (one of which was presented in simplified form without proof in Day and Taylor, 1997). These two theorems correspond to two different types of interactions: interactions in patch-structured populations (metapopulations) and pairwise interactions (like those of the Mirmirani and Oster model). These theorems are derived from an explicit, single-locus genetic model, and they can be used to calculate ESSs of evolutionary models for a very wide variety of dynamic

characters. One of our primary findings is that some simple results analogous to Hamilton's Rule can be derived in this dynamic setting. In particular, the generalized maximum principle presented here is completely analogous to the standard maximum principle and it can be applied in exactly the same way. As it turns out, this generalized maximum principle involves a time-dependent version of Hamilton's Rule. We also present an example of how to apply these results by modeling the evolution of lifetime resource allocation to growth and reproduction in an annual plant when there is competition for resources among related individuals. In the discussion we also use these general theoretical results to illustrate that, although Mirmirani and Oster's (1978) modeling approach is not genetically correct, coincidentally, it does happen to provide the correct results in that instance.

Below are five remaining sections. In Section 2 an example of an evolutionary model is presented to motivate the theory. The third section gives a brief summary of the standard PMP. The fourth section then presents the two theorems for modeling dynamic evolutionary games between genetic relatives: one for patch-structured populations and one for pairwise interactions. The fifth section demonstrates how these mathematical results can be used to analyze the model of Section 2, and last Section 6 is a discussion.

2. A MOTIVATIONAL EXAMPLE

Consider an annual plant (e.g., *Impatiens capensis*) that grows, reproduces, and dies within a single season of length T. Often it will be the case that the performance of a plant depends on the characteristics of a few plants within its immediate surrounding area (Kelly, 1996, 1997). To capture this effect, suppose that the plant population consists of a large number of patches containing n individuals each and that competitive interactions occur among plants within patches but not between patches. Limited dispersal among patches results in the plants within any particular patch being genetically related. Now focus on a particular individual, and let $y(t)$ denote its size at time t and $\bar{y}(t)$ denote the average plant size in its patch.

Also, suppose that each plant produces resources through photosynthesis, and these resources can be used for either growth or reproduction. Consequently, each plant must divide its resources between these two functions at all times during the season. Let $u(t)$ denote the proportion of resources devoted to growth at time

$t(0 \leqslant u(t) \leqslant 1)$, and suppose that a plant's rate of production of resources through photosynthesis, $b(y, \bar{y})$, depends on both its own size, y, and the average plant size in its patch, $\bar{y}$. We assume that a plant's production increases with its own size (i.e., $\partial b/\partial y > 0$), but because of competition, its production decreases with an increase in the average plant size of the patch (i.e., $\partial b/\partial \bar{y} < 0$). The growth rate of each plant is given by

$$\frac{dy}{dt} = u(t)\, b(y(t),\, \bar{y}(t)) \qquad y(0) = y_0. \qquad (1)$$

A plant's rate of reproductive output at time t is given by

$$(1 - u(t))\, b(y(t),\, \bar{y}(t)), \qquad (2)$$

and therefore its total reproductive output over the season is

$$\int_0^T (1 - u(t))\, b(y(t),\, \bar{y}(t))\, dt, \qquad (3)$$

and u is to be chosen to maximize this.

This model is similar, to that presented by Mirmirani and Oster (1978), and it is an example of a patch-structured population in which individuals "play the field" locally. What is the evolutionarily stable resource allocation strategy? If there were no interactions among individuals (i.e., if b did not depend on $\bar{y}$), then this problem can be tackled using Pontryagin's maximum principle. But because of these interactions, and because the interacting individuals are genetically related, this approach is not appropriate. Below we present a generalization of PMP for this type of model, but before doing so, we first review the standard version of PMP.

3. PONTRYAGIN'S MAXIMUM PRINCIPLE

We refer to the time-dependent function, $u(t)$, as a control variable and the time-dependent function $y(t)$ as a state variable. In the previous section, these functions had specific biological interpretations. Here we leave the interpretation of these variables open, but the control variable is still the variable that is directly evolutionarily labile. We also generalize the state variable in this section by allowing it to be a vector.

Let $\mathbf{y}(t)$ denote an individual's p-dimensional state vector, defined within $\mathbb{E}^p$ (p-dimensional Euclidean space) and $u(t)$ denote the individual's control variable, defined within some (closed) interval $U = [a_0, a_1]$. We will refer to those control variables, $u(t)$, that are piecewise continuous and lie within U as feasible controls. Now suppose an individual's fitness can be expressed in the form

$$W(t_0, \mathbf{y}(t_0); u) = \int_{t_0}^{t_1} f(t, \mathbf{y}(t), u(t))\, dt + \Phi(\mathbf{y}(t_1)), \qquad (4)$$

where t_0 and t_1 are the initial and final points of the interval of time being considered. Here Φ is a scalar-valued function of a vector variable, $\Phi: \mathbb{E}^p \to \mathbb{E}^1$, and f is a scalar valued function of three arguments, $f: \mathbb{E}^1 \times \mathbb{E}^p \times \mathbb{E}^1 \to \mathbb{E}^1$. The second term in (4) is the fitness of an individual with a state vector $\mathbf{y}(t_1)$ at the final time, and the first term adds up the fitness accrued to an individual from the beginning of the time interval to the end (Kamien and Schwartz, 1991; Bulmer, 1994). Expression (4) applies to the case where interactions among individuals are ignored.

Now suppose that the state vector obeys a system of differential equations of the form

$$dy_s/dt = g_s(t, \mathbf{y}(t), u(t)) \qquad y_s(t_0) = y_{s0}, \qquad (5)$$

where the index $s = 1, ..., p$, and $g_s: \mathbb{E}^1 \times \mathbb{E}^p \times \mathbb{E}^1 \to \mathbb{E}^1$. Define the Hamiltonian function as

$$H(t, \mathbf{y}, u, \lambda) = f(t, \mathbf{y}, u) + \lambda(t)' \cdot \mathbf{g}(t, \mathbf{y}, u), \qquad (6)$$

where $\lambda(t)$ is a p-dimensional, time-dependent vector of costate (multiplier) variables (one for each state variable), $\mathbf{g}(t, \mathbf{y}, u)$ is a p-dimensional vector of the differential Eqs. (5), and $\lambda' \cdot \mathbf{g}$ denotes the inner product (the prime denotes transpose). Biologically, it is interesting to note that the elements of $\lambda(t)$, i.e., $\lambda_s(t)$, can be interpreted as the marginal return in future fitness of an increase in state variable $y_s(t)$ at time t (Leòn, 1976; Iwasa and Roughgarden, 1984; Perrin and Sibly, 1993; Day, 1998).

DEFINITION 3.1. An optimal control, $u^*(t)$, is defined to be a feasible control that renders the objective functional (in this case (4)), a maximum over the set of all feasible controls.

DEFINITION 3.2. Suppose $\eta(t)$ is a feasible deviation from the control $u^*(t)$, meaning that $u^*(t) + \eta(t)$ is a feasible control. It follows that, if h is a scalar and

$0 \leqslant h \leqslant 1$, then $u^*(t) + h\eta(t)$ is also a feasible control. $u^*(t)$ is defined to be a weak optimal control if

$$\left.\frac{dW(t_0, \mathbf{y}(t_0); u^*(t) + h\eta(t))}{dh}\right|_{h=0} \leqslant 0 \qquad (7)$$

for all feasible deviations, $\eta(t)$.

Notice that the dependence of W on h enters directly through the integrand, $f(t, \mathbf{y}(t), u^*(t) + h\eta(t))$, as well as indirectly through $\mathbf{y}(t)$ in the integrand as a result of the differential Eqs. (5). The existence of (7) is guaranteed provided that f and $\mathbf{g}$ are smooth enough (as we assume below); the direct dependence through f then poses no problem, and $\mathbf{y}(t)$ will be differentiable in the parameter h as demonstrated in Perko (1991, Theorem 2, Section 2.3, p. 83). It should also be stressed that, although the definition of a weak optimal control has been presented in terms of a specific objective functional, W (i.e., (4)), this definition holds for any objective functional of with the appropriate substitution of W in (7). Notice that the condition that $u^*(t)$ be an optimal control is stronger than the condition that it be a weak optimal control. Therefore, if $u^*(t)$ is an optimal control, then it is also a weak optimal control. This also follows directly from the following two theorems.

THEOREM 3.1 (Pontryagin's Maximum Principle). *Suppose that fitness is given by Expression* (4), *and the state variables,* $y_s(t)$, *are governed by the differential Eq.* (5). *Furthermore, suppose that the functions* f *and* g_s *are continuous and have continuous first derivatives in* t, y_s, *and* u, *and that* Φ *is continuous and has continuous first derivatives in* y_s. *If* u^* *is an optimal control then it is necessary that there exist a continuous, nonzero costate vector* $\boldsymbol{\lambda}(t)$ *that is a function of time, such that the following conditions are satisfied:*

$$-\frac{d\lambda_s}{dt} = \frac{\partial H}{\partial y_s}$$
$$\lambda_s(t_1) = \frac{\partial \Phi}{\partial y_s}(t_1) \qquad \text{for all} \quad s = 1, ..., p \qquad (8)$$

$$\max_{u \in U} H(t, \mathbf{y}, u, \boldsymbol{\lambda}) = H(t, \mathbf{y}, u^*, \boldsymbol{\lambda}). \qquad (9)$$

In (9) $\mathbf{y}$ *and* $\boldsymbol{\lambda}$ *refer to the state and costate vectors generated by the optimal control. Condition* (9) *states that the optimal control is such that the Hamiltonian is maximized in the control variable at all times. Notice that we can state conditions that must hold for* (9) *to hold in terms of the first order effect:*

$$\text{if} \quad a_0 < u^* < a_1 \qquad \text{then} \quad \left.\frac{\partial H}{\partial u}\right|_{u=u^*} = 0 \qquad (10)$$

$$\text{if} \quad u^* = \quad a_0 \qquad \text{then} \quad \left.\frac{\partial H}{\partial u}\right|_{u=u^*} \leqslant 0 \qquad (11)$$

$$\text{if} \quad u^* = \quad a_1 \qquad \text{then} \quad \left.\frac{\partial H}{\partial u}\right|_{u=u^*} \geqslant 0. \qquad (12)$$

For a proof of Theorem 3.1 see Leitmann (1966, 1981), Sagan (1969), Fleming and Rishel (1975), Knowles (1981), and Pinch (1993).

The maximum principle actually introduces one other costate variable, λ_0 (a scalar), that is multiplied to the function f in the Hamiltonian (Leitmann, 1966; Fleming and Rishel, 1975). As part of the necessary conditions of the maximum principle, this scalar must either be zero or positive, and hence it is usually scaled to be either zero or 1. The reason for this additional costate variable is that, when the problem of interest has $p \neq 1$, it can be the case that the optimal control is fully specified without considering the objective functional (4). This case is termed abnormal (Leitmann, 1981; Fleming and Rishel, 1975; Knowles, 1981), and we will ignore it and assume that, in all cases of interest, $\lambda_0 = 1$. The reasoning is that, if in some problem $\lambda_0 = 0$, then the fitness function for the problem would play no role in determining the optimal strategy, and this suggests that the problem is poorly formulated from a biological standpoint.

THEOREM 3.2. *Under the conditions of Theorem* 3.1, *if* $u^*(t)$ *is a weak optimal control, then conditions* (8) *and* (10)–(12) *must hold* (*but not necessarily condition* (9)).

Proof (Theorem 3.2). The proof follows that of Kamien and Schwartz (1991, Part II, Sections 2 and 10). We calculate the total differential, $\delta W(t_0, \mathbf{y}(t_0); u^*(t) + h\eta(t))$ at $h = 0$, and require that it be nonpositive. Following Kamien and Schwartz (1991),

$$\delta W = \int_{t_0}^{t_1} \sum_{s=1}^{p} \left\{ \frac{\partial f}{\partial y_s} + \sum_{i=1}^{p} \lambda_i \frac{\partial g_i}{\partial y_s} + \frac{d\lambda_s}{dt} \right\} \delta y_s$$
$$+ \left\{ \frac{\partial f}{\partial u} + \sum_{i=1}^{p} \lambda_i \frac{\partial g_i}{\partial u} \right\} \delta u \, dt$$
$$- \sum_{s=1}^{p} \lambda_s(t_1) \, \delta y_s(t_1) + \sum_{s=1}^{p} \frac{\partial \Phi}{\partial y_s}(t_1) \, \delta y_s(t_1) \qquad (13)$$
$$= \int_{t_0}^{t_1} \sum_{s=1}^{p} \left\{ \frac{\partial H}{\partial y_s} + \frac{d\lambda_s}{dt} \right\} \delta y_s + \left\{ \frac{\partial H}{\partial u} \right\} \delta u \, dt$$
$$+ \sum_{s=1}^{p} \left(\frac{\partial \Phi}{\partial y_s}(t_1) - \lambda_s(t_1) \right) \delta y_s(t_1), \qquad (14)$$

where δy_s and δu are the variations in y_s and u caused by a change in h. Now we define $\lambda_s(t)$ so that

$$\frac{d\lambda_s}{dt} = -\frac{\partial H}{\partial y_s} \quad \lambda_s(t_1) = \frac{\partial \Phi}{\partial y_s}(t_1). \tag{15}$$

This is Condition (8) of Theorem 3.1. With this definition, having $dW/dh \leqslant 0$ requires that

$$\int_{t_0}^{t_1} \frac{\partial H}{\partial u} \delta u \, dt \leqslant 0 \tag{16}$$

for all feasible variations, δu. As in Kamien and Schwartz (1991) it can be shown that under the control constraint $a_0 \leqslant u \leqslant a_1$, Condition (16) implies Conditions (10)–(12).

Q.E.D.

4. THE GENERALIZED MAXIMUM PRINCIPLE

4.1. An Underlying Genetic Model

To account for the effect of relatedness among interacting individuals, it is necessary to work with a genetic model. In this section we describe the genetic model that forms the foundation of our results, both for interactions in patch-structured populations and for pairwise interactions. However, one of the most important features of the theorems presented in Sections 4.2 and 4.3 below is that all of the genetic details of the model are encapsulated in a single, biologically meaningful (and relatively easy to measure) parameter: genetic relatedness.

The genetic model is a single-locus, diallelic model for a diploid organism, and, in keeping with the conceptual framework of game theory, one allele (termed the mutant) is rare. We imagine that the common (resident) allele in the population, say "a," codes for some control strategy, $\hat{u}(t)$, and the rare mutant allele, "A," codes for a different strategy, $u(t)$. Under diploidy every individual will have either zero, one, or two copies of the mutant allele. Let g_x be a random variable that denotes the genotype of individual x and that takes a value of either 0, $\frac{1}{2}$, or 1 corresponding to these three cases, respectively. Therefore, $E[g_x] \triangleq \bar{g}$ is the mutant allele frequency in the population. Allowing for inbreeding, the three genotypes occur with frequencies

$$\begin{array}{ll} \text{AA} & (1-\psi)\,\bar{g}^2 + \psi\bar{g} \\ \text{Aa} & 2(1-\psi)\,\bar{g}(1-\bar{g}) \\ \text{aa} & (1-\psi)(1-\bar{g})^2 + \psi(1-\bar{g}), \end{array} \tag{17}$$

where ψ is Wright's inbreeding coefficient (i.e., the probability that homologous copies of a gene are identical by descent) (Crow and Kimura, 1970). Next, define $W^{\mathrm{AA}}(u, \hat{u})$ and $W^{\mathrm{Aa}}(u, \hat{u})$ to be the average fitness of a mutant homozygote and heterozygote, respectively, and $W^{\mathrm{aa}}(\hat{u})$ to be the average fitness of a resident-type homozygote. We will assume that allelic effects are additive, meaning that $W^{\mathrm{Aa}}(u, \hat{u}) = W^{\mathrm{AA}}(\frac{u+\hat{u}}{2}, \hat{u})$ (we also have $W^{\mathrm{aa}}(\hat{u}) = W^{\mathrm{AA}}(\hat{u}, \hat{u})$). The equation for allele frequency change is

$$\frac{\Delta \bar{g}}{\bar{g}} = \frac{1}{\bar{W}}(W^{\mathrm{A}} - \bar{W}), \tag{18}$$

where $\bar{W}$ is the population mean fitness, and W^{A} is the marginal fitness of the mutant allele (Crow and Kimura, 1970);

$$W^{\mathrm{A}} = \{(1-\psi)\,\bar{g} + \psi\}\ W^{\mathrm{AA}}(u, \hat{u})$$
$$+ \{(1-\psi)(1-\bar{g})\}\ W^{\mathrm{Aa}}(u, \hat{u}). \tag{19}$$

We are concerned with the limiting case where the mutant allele is rare, so as $\bar{g} \to 0$, Eq. (18) becomes

$$\frac{\Delta \bar{g}}{\bar{g}} = \frac{1}{W^{\mathrm{aa}}(\hat{u})}(\psi\,W^{\mathrm{AA}}(u, \hat{u})$$
$$+ (1-\psi)\,W^{\mathrm{Aa}}(u, \hat{u}) - W^{\mathrm{aa}}(\hat{u})). \tag{20}$$

To proceed further, the average genotypic fitnesses, $W^{\mathrm{AA}}(u, \hat{u})$, $W^{\mathrm{Aa}}(u, \hat{u})$, and $W^{\mathrm{aa}}(\hat{u})$ must be further specified. Because of interactions among individuals, these genotypic fitnesses will depend on how the mutant alleles are distributed throughout the population. For example, knowing that an individual has genotype AA is not enough to know its expected fitness. We must also know the genotype (and thereby the phenotype) of those individuals with which it interacts. This, in turn, will depend on the population structure and dispersal behavior being considered. It might also depend on the mutant strategy, u, and the resident strategy, $\hat{u}$. To keep the modeling approach as general as possible, we leave all of these dependencies unspecified, and we simply assume that once the mutant allele enters the population (by mutation for example), the probabilities of different types of mutant individuals interacting with one another (e.g., a heterozygote with a heterozygote) reach a statistical quasi-equilibrium while the allele is still rare. It is this statistical equilibrium that is used to calculate the expected genotypic fitnesses when the mutant allele is rare. We note, however, that for such an equilibrium to

exist, it must often be assumed that the mutant has a small effect so that fitness differences are small. This point is considered more thoroughly in the Discussion.

Given Eq. (20) we can now define an evolutionarily stable strategy.

DEFINITION 4.1.   A strategy, u^*, is an ESS if

$$\psi W^{AA}(u, u^*) + (1 - \psi) W^{Aa}(u, u^*) \qquad (21)$$

is maximized in u at $u = u^*$, in other words, if the marginal fitness of a rare mutant strategy is maximized at $u = u^*$.

The logic behind Definition 4.1 is that, if the population is fixed for an allele that codes for u^*, then from Eq. (20), no mutant allele coding for $u \neq u^*$ can invade the population because $\Delta \bar{g}/\bar{g} < 0$ for all such alleles (Day and Taylor, 1998a). Also notice that, to use (21) to characterize ESSs, we only need to specify the two mutant genotypic fitnesses, W^{AA} and W^{Aa}.

4.2. Patch-Structured Populations

We now consider the first of two types of interactions: patch-structured populations in which individuals locally play the field. We begin by setting up a general model of a patch-structured population and then present a theorem that provides necessary conditions that an ESS must satisfy. Section 4.2.1 then presents the proof of this theorem. Again we emphasize that one of the most important features of the theorem is that all of the genetic details enter only through a single parameter which is the genetic relatedness.

Consider a patch-structured population and suppose that an individual's fitness depends on its own state variable, $y(t)$, the patch mean state variable, $\bar{y}(t)$, its own control variable, $u(t)$, and the patch mean control variable, $\bar{u}(t)$. Denote the patch size by n and allow patch members to be related. In general we suppose that an individual's fitness can be specified by an expression of the form

$$\int_{t_0}^{t_1} f(t, y(t), \bar{y}(t), u(t), \bar{u}(t)) \, dt + \Phi(y(t_1), \bar{y}(t_1)). \quad (22)$$

Again suppose that the control variable, $u(t)$, is piecewise continuous and that it lies within some closed interval $U = [a_0, a_1]$. Assume that the state variable of each individual, i, obeys the same differential equation,

$$\frac{dy_i}{dt} = g(t, y_i(t), \bar{y}(t), u_i(t), \bar{u}(t)) \qquad y_i(t_0) = y_0. \quad (23)$$

Notice that here, $\bar{y}$ and $\bar{u}$ are the means of all the y_i and u_i, respectively, within the patch. *Define* a Hamiltonian for the current problem as

$$\begin{aligned} H(t, &\theta, \bar{\theta}, \zeta, \bar{\zeta}, \lambda_y, \lambda_{\bar{y}}) \\ &\triangleq f(t, \theta, \bar{\theta}, \zeta, \bar{\zeta}) + \lambda_y g(t, \theta, \bar{\theta}, \zeta, \bar{\zeta}) \\ &\quad + \lambda_{\bar{y}} g(t, \bar{\theta}, \bar{\theta}, \bar{\zeta}, \bar{\zeta}). \end{aligned} \quad (24)$$

Here λ_y is a costate variable corresponding to the state variable, y, and we have introduced the costate variable, $\lambda_{\bar{y}}$, corresponding to the average state variable, $\bar{y}$. Last (Day and Taylor, 1997), define the inclusive fitness effect of an individual (termed the actor) increasing its control variable slightly from the current, resident value, $\hat{u}(t)$, at time t (denoted by $\Delta W_{incl}(t)$), as

$$\Delta W_{incl}(t)|_{\hat{a}} \triangleq \left[\frac{\partial H}{\partial \zeta} + \bar{r} \frac{\partial H}{\partial \bar{\zeta}} \right]_{\theta = \bar{\theta} = y^*, \, \zeta = \bar{\zeta} = \hat{a}}, \quad (25)$$

where $\bar{r}$ is the relatedness of a randomly chosen patch member (including the possibility of it being the actor itself) to the actor (Michod and Hamilton, 1980). y^* is the state variable generated by the ESS control, $u^*(t)$, in a monomorphic population through differential Eq. (23), i.e.,

$$\begin{aligned} \frac{dy^*}{dt} &= g(t, y^*(t), y^*(t), u^*(t), u^*(t)) \\ y^*(t_0) &= y_0. \end{aligned} \quad (26)$$

THEOREM 4.1.   *Consider the model outlined above. Suppose the organism in question is diploid, and allelic effects are additive. Further, suppose that the functions f and g are continuous and have continuous first derivatives in t, y, $\bar{y}$, u, and $\bar{u}$, and Φ is continuous and has continuous first derivatives in y and $\bar{y}$. Suppose that the Hamiltonian, H, is given by (24), and $\Delta W_{incl}(t)|_{\hat{a}}$ is given by (25). If $u^*(t)$ is an ESS, then it is necessary that there exist continuous, nonzero costate variables, λ_y and $\lambda_{\bar{y}}$, that are functions of time, such that the following conditions are satisfied*:

$$-\frac{d\lambda_y}{dt} = \frac{\partial H}{\partial \theta} \qquad \lambda_y(t_1) = \frac{\partial \Phi}{\partial y}(t_1) \qquad (27)$$

$$-\frac{d\lambda_{\bar{y}}}{dt} = \frac{\partial H}{\partial \bar{\theta}} \qquad \lambda_{\bar{y}}(t_1) = \frac{\partial \Phi}{\partial \bar{y}}(t_1) \qquad (28)$$

$$\text{if} \quad a_0 < u^* < a_1 \qquad \text{then} \quad \Delta W_{incl}(t)|_{u^*} = 0 \quad (29)$$

$$\text{if} \quad u^* = a_0 \qquad \text{then} \quad \Delta W_{incl}(t)|_{u^*} \leqslant 0 \quad (30)$$

$$\text{if} \quad u^* = a_1 \qquad \text{then} \quad \Delta W_{incl}(t)|_{u^*} \geqslant 0, \quad (31)$$

where (27) and (28) are evaluated at $\zeta = \bar{\zeta} = u^*$ and $\theta = \bar{\theta} = y^*$, i.e., λ_y, $\lambda_{\bar{y}}$, and all y_i are the costate and state variables corresponding to a monomorphic population at the ESS, $u^*(t)$. Conditions (27) and (28) specify the time dynamics of the costate variables λ_y and $\lambda_{\bar{y}}$. Conditions (29)–(31) are a version of Hamilton's Rule for dynamic games between relatives (Day and Taylor, 1997).

4.2.1. *Proof of Theorem* 4.1. We will use Definition 4.1 to derive the necessary conditions presented in Theorem 4.1. Recall that (21) is the expected fitness of a randomly selected mutant allele. In particular, with probability ψ such an allele will be in a homozygote and therefore have fitness $W^{\text{AA}}(u, \hat{u})$. With probability $(1 - \psi)$ it will be in a heterozygote and therefore have fitness $W^{\text{Aa}}(u, \hat{u})$. Thus we need to specify $W^{\text{AA}}(u, \hat{u})$ and $W^{\text{Aa}}(u, \hat{u})$ for a patch-structured population. In what follows it will be convenient to refer to the individual that houses the randomly chosen mutant allele as the "focal" individual.

Suppose the focal individual is a mutant homozygote. This homozygote will exist in a particular patch type, where patch type refers to the total number of heterozygous and homozygous mutants in the patch. There are a finite number of patch types for this focal homozygous mutant, say ω_{AA}, and we label them as $k = 1, ..., \omega_{\text{AA}}$. Similar considerations apply if the focal individual is heterozygous and there will again be a finite number of patch types, say ω_{Aa}. Label these as $k = \omega_{\text{AA}} + 1, ..., \omega_{\text{AA}} + \omega_{\text{Aa}}$. Now label all individuals in a k-patch from $i = 1$ to n in a consistent way so that all individuals labeled ik are genetically identical. Now, letting P_k and p_k be the probabilities that the focal mutant homozygote or heterozygote is found in a k-patch then, using (22), we have

$$W^{\text{AA}}(u, \hat{u}) = \sum_{k=1}^{\omega_{\text{AA}}} P_k \left\{ \int_{t_0}^{t_1} f(t, y_{Ik}, \bar{y}_k, u, \bar{u}_k) \, dt \right.$$
$$\left. + \Phi(y_{Ik}, \bar{y}_k) \right\} \quad (32)$$

$$W^{\text{Aa}}(u, \hat{u}) = \sum_{k=\omega_{\text{AA}}+1}^{\omega_{\text{AA}}+\omega_{\text{Aa}}} p_k \left\{ \int_{t_0}^{t_1} f\left(t, y_{Ik}, \bar{y}_k, \frac{u+\hat{u}}{2}, \bar{u}_k\right) dt \right.$$
$$\left. + \Phi(y_{Ik}, \bar{y}_k) \right\}. \quad (33)$$

A few comments about notation are required here. We use y_{Ik} to denote the state variable of the focal individual, and $\bar{u}_k = \frac{1}{n} \sum_i u_{ik}$ and $\bar{y}_k = \frac{1}{n} \sum_i y_{ik}$. Also, u_{ik} denotes the control strategy of an ik individual, and this can be either u, $(u + \hat{u})/2$, or $\hat{u}$ depending on whether it is a

homozygote mutant, heterozygote, or homozygote normal, respectively. Notice that y_{Ik} will be identical to one of the y_{ik} because the focal individual is included in the calculation of the mean. This is true for the control variable as well. Last, we point out that the probabilities P_k, p_k, and ψ are determined by the way in which the mutant alleles are distributed throughout the population. These probabilities come from the statistical quasi-equilibrium that was mentioned near the end of Section 4.1. Therefore, in general they will depend upon the entire mutant and resident control functions, $u(t)$ and $\hat{u}(t)$, from t_0 to t_1. In particular, they will be functionals of $u(t)$ and $\hat{u}(t)$, having the form

$$\int_{t_0}^{t_1} \xi(u(t), \hat{u}(t)) \, dt \quad (34)$$

for some function, $\xi(\cdot, \cdot)$. Now, using (32) and (33), Expression (21) is

$$W \triangleq \int_{t_0}^{t_1} \left\{ \psi \sum_{k=1}^{\omega_{\text{AA}}} P_k f(t, y_{Ik}, \bar{y}_k, u, \bar{u}_k) \right.$$
$$+ (1 - \psi) \sum_{k=\omega_{\text{AA}}+1}^{\omega_{\text{AA}}+\omega_{\text{Aa}}} p_k f\left(t, y_{Ik}, \bar{y}_k, \frac{u+\hat{u}}{2}, \bar{u}_k\right) \right\} dt$$
$$+ \psi \sum_{k=1}^{\omega_{\text{AA}}} P_k \Phi(y_{Ik}, \bar{y}_k)$$
$$+ (1 - \psi) \sum_{k=\omega_{\text{AA}}+1}^{\omega_{\text{AA}}+\omega_{\text{Aa}}} p_k \Phi(y_{Ik}, \bar{y}_k). \quad (35)$$

Also, the state variable of each individual ik obeys differential Eq. (23), i.e.,

$$\frac{dy_{ik}}{dt} = g(t, y_{ik}(t), \bar{y}_k(t), u_{ik}(t), \bar{u}_k(t))$$
$$y_{ik}(t_0) = y_0. \quad (36)$$

The notation in (35) can be greatly simplified by defining $\sigma_k(u, \hat{u}) \triangleq \psi P_k + (1 - \psi) p_k$ where $p_k = 0$ for $k = 1, ..., \omega_{\text{AA}}$ and $P_k = 0$ for $k = \omega_{\text{AA}} + 1, ..., \omega_{\text{AA}} + \omega_{\text{Aa}}$ (notice that here we explicitly display the dependence of this probability distribution on $u(t)$ and $\hat{u}(t)$). Also, we define $v_k \triangleq u$ for $k = 1, ..., \omega_{\text{AA}}$ and $v_k \triangleq (u + \hat{u})/2$ for $k = \omega_{\text{AA}} + 1, ..., \omega_{\text{AA}} + \omega_{\text{Aa}}$. Notice that v_k is the control variable of the focal individual, given that it occurs in a patch of type k. Therefore, (35) can be written

$$W = \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k(u, \hat{u}) \, f(t, y_{Ik}, \bar{y}_k, v_k, \bar{u}_k) \, dt$$

$$+ \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k(u, \hat{u}) \, \Phi(y_{Ik}, \bar{y}_k). \tag{37}$$

Expression (21) is now completely specified, and we can use Definition 4.1 to characterize the ESS control, $u^*(t)$. In particular, if we set $\hat{u}(t) = u^*(t)$, then Expression (37) must be maximized in $u(t)$ at $u(t) = u^*(t)$. This maximization problem is quite complex because the control variable $u(t)$ appears not only in the function f as in standard dynamic optimization problems, but also in the functionals $\sigma_k(u, \hat{u})$ (which themselves have the form (34)). Therefore, the objective functional (37) is not in the form of a standard dynamic optimization problem. This motivates us to define an additional expression:

$$W_0 \triangleq \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \hat{\sigma}_k \, f(t, y_{Ik}, \bar{y}_k, v_k, \bar{u}_k) \, dt$$

$$+ \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \hat{\sigma}_k \, \Phi(y_{Ik}, \bar{y}_k), \tag{38}$$

where $\hat{\sigma}_k \triangleq \sigma_k(\hat{u}, \hat{u})|_{\hat{u}=u^*}$. Expression (38) differs from (37) only in that the probability distribution, $\sigma_k(u, \hat{u})$, is evaluated at $u = \hat{u} = u^*$ so that (38) *is* in the form of a standard dynamic optimization problem, and therefore it is a problem to which Theorem 3.2 can be applied.

With this setup, the structure of the proof of Theorem 4.1 consists of the proof of each of a series of four implications:

(i) u^* is an ESS $\Rightarrow u^*$ is an optimal control for W (expression (37));

(ii) u^* is an optimal control for $W \Rightarrow u^*$ is a weak optimal control for W;

(iii) u^* is a weak optimal control for $W \Rightarrow u^*$ is a weak optimal control for W_0;

(iv) u^* is a weak optimal control for $W_0 \Rightarrow u^*$ satisfies Theorem 4.1.

Implication (i) follows directly from Definitions 3.1 and 4.1. Implication (ii) follows directly from Definitions 3.1 and 3.2. Therefore, we need only demonstrate that implications (iii) and (iv) are true. The proof of implication (iii) is contained in the following lemma.

LEMMA 4.1 (Proof of Implication (iii)). *The proof consists of demonstrating that $dW/dh = dW_0/dh$ at $h = 0$. In Expression* (37) *for W, $\sigma_k(u, \hat{u})$, $f(t, y_{Ik}, \bar{y}_k, v_k, \bar{u}_k)$, and $\Phi(y_{Ik}, \bar{y}_k)$ are all functions of h, and, as noted in Definition* 3.2, *this dependence enters through both the*

control variable and the state variable. For the present purposes, however, all that matters is that the derivative with respect to h exist at $h = 0$, and this is guaranteed as discussed in Definition 3.2. Therefore, to simplify notation we display the dependence on h as $\sigma_k[h]$, $f_k[h]$, and $\Phi_k[h]$ (this notation is used in the proof of this lemma only). Thus (37) and (38) can be written

$$W = \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[h] \, f_k[h] \, dt + \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[h] \, \Phi_k[h]$$

$$\tag{39}$$

and

$$W_0 = \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[0] \, f_k[h] \, dt \, dt$$

$$+ \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[0] \, \Phi_k[h]. \tag{40}$$

Now calculating,

$$\frac{dW}{dh}\bigg|_{h=0} = \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \left(\frac{d\sigma_k[0]}{dh} f_k[0] + \sigma_k[0] \frac{df_k[0]}{dh} \right) dt$$

$$+ \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \left(\frac{d\sigma_k[0]}{dh} \phi_k[0] + \sigma_k[0] \frac{d\Phi_k[0]}{dh} \right)$$

$$= \int_{t_0}^{t_1} \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[0] \frac{df_k[0]}{dh} \, dt$$

$$\tag{41}$$

$$+ \sum_{k=1}^{\omega_{AA}+\omega_{Aa}} \sigma_k[0] \frac{d\Phi_k[0]}{dh}. \tag{42}$$

The second equality, *follows from the fact that $f_k[0]$ and $\Phi_k[0]$ are independent of k and that, because $\sum_k \sigma_k[h] = 1$ for all h, we also have that $\sum_k \frac{d\sigma_k[0]}{dh} = 0$. Calculating dW_0/dh at $h = 0$ also gives* (42).

All that remains in the proof of Theorem 4.1 is to prove implication (iv). This is done simply by noting that, because u^* is a weak optimal control for W_0 (from implication [iii]), we can apply the results of Theorem 3.2 to W_0. Implication (iv) then follows directly. It turns out, however, that applying Theorem 3.2 to W_0 involves a considerable amount of calculation. The reason is that, although the only control and state variables that appear in (38) are y_{Ik}, $\bar{y}_k$, v_k, and $\bar{u}_k$, these variables alone are not sufficient to apply Theorem 3.2 because the differential equation governing $\bar{y}_k$ (not shown) involves all the y_{ik} and u_{ik}. Therefore, Theorem 3.2 must be applied using

all the y_{ik} and u_{ik}, and this high dimensionality results in somewhat tedious calculations. These are presented in the Appendix, and they complete the proof of Theorem 4.1.

4.3. Pairwise Interactions

There is an analogous version of Theorem 4.1 for pairwise interactions as well. Suppose an individual's fitness depends on its own state variable, $y(t)$, the state variable of one other individual, $\tilde{y}(t)$, its own control variable, $u(t)$, and the control variable of the other individual, $\tilde{u}(t)$. In particular, suppose an individual's fitness can be specified by an expression of the form

$$\int_{t_0}^{t_1} f(t, y(t), \tilde{y}(t), u(t), \tilde{u}(t))\, dt + \Phi(y(t_1), \tilde{y}(t_1)). \quad (43)$$

Suppose that the control variables, u and $\tilde{u}$, are piecewise continuous and must lie within some closed interval, $U = [a_0, a_1]$. Assume that the state variable of the individual in question obeys the differential equation

$$\frac{dy}{dt} = g(t, y(t), \tilde{y}(t), u(t), \tilde{u}(t)) \qquad y(t_0) = y_0, \quad (44)$$

and the state variable of the other individual obeys the same differential equation with the variables y and $\tilde{y}$ (and u and $\tilde{u}$) interchanged. Now *define* a Hamiltonian function for the current problem as

$$H(t, \theta, \tilde{\theta}, \zeta, \tilde{\zeta}, \lambda_y, \lambda_{\tilde{y}})$$
$$\triangleq f(t, \theta, \tilde{\theta}, \zeta, \tilde{\zeta}) + \lambda_y g(t, \theta, \tilde{\theta}, \zeta, \tilde{\zeta})$$
$$+ \lambda_{\tilde{y}} g(t, \tilde{\theta}, \theta, \tilde{\zeta}, \zeta). \quad (45)$$

Here $\lambda_{\tilde{y}}$ is a costate variable corresponding to the state variable, $\tilde{y}$. Also, notice that the form of the Hamiltonian defined here for pairwise interactions is slightly different than that defined for interactions in a patch-structured population (i.e., (24)). Last, define the inclusive fitness effect of an individual (termed the *actor*) increasing its control variable slightly from $\hat{u}$ at time t (denoted by $\Delta W_{\mathrm{incl}}(t)$), as

$$\Delta W_{\mathrm{incl}}(t)|_{\hat{u}} = \left[\frac{\partial H}{\partial \zeta} + \bar{r}\frac{\partial H}{\partial \tilde{\zeta}} \right]_{\theta = \tilde{\theta} = y^*,\, \zeta = \tilde{\zeta} = \hat{u}}, \quad (46)$$

where $\bar{r}$ is the relatedness of the other individual to the actor, and y^* is the state variable generated by the ESS control, $u^*(t)$, through differential Eq. (44).

THEOREM 4.2. *Suppose the organism in question is diploid and allelic effects are additive. Further, suppose that the functions f and g are continuous and have continuous first derivatives in t, y, $\tilde{y}$, $\tilde{u}$, and $\tilde{u}$ and that Φ is continuous and has continuous first derivatives in y and $\tilde{y}$. Suppose that the Hamiltonian, H, is given by (45), and $\Delta W_{\mathrm{incl}}(t)|_{\hat{u}}$ is given by (46). If u*(t) is an ESS, then it is necessary that there exist continuous, nonzero costate variables, λ_y and $\lambda_{\tilde{y}}$, that are functions of time, such that the following conditions are satisfied*:

$$-\frac{d\lambda_y}{dt} = \frac{\partial H}{\partial \theta} \qquad \lambda_y(t_1) = \frac{\partial \Phi}{\partial y}(t_1) \quad (47)$$

$$-\frac{d\lambda_{\tilde{y}}}{dt} = \frac{\partial H}{\partial \tilde{\theta}} \qquad \lambda_{\tilde{y}}(t_1) = \frac{\partial \Phi}{\partial \tilde{y}}(t_1) \quad (48)$$

$$\text{if} \quad a < u^* < b \qquad \text{then} \quad \Delta W_{\mathrm{incl}}(t)|_{u^*} = 0 \quad (49)$$

$$\text{if} \quad u^* = a \qquad \text{then} \quad \Delta W_{\mathrm{incl}}(t)|_{u^*} \leqslant 0 \quad (50)$$

$$\text{if} \quad u^* = b \qquad \text{then} \quad \Delta W_{\mathrm{incl}}(t)|_{u^*} \geqslant 0, \quad (51)$$

where (47) and (48) are evaluated at $\zeta = \tilde{\zeta} = u^*$ and $\theta = \tilde{\theta} = y^*$, i.e., λ_y, $\lambda_{\tilde{y}}$, y, and $\tilde{y}$ are the costate and state variables corresponding to a monomorphic population at the ESS, u*. Conditions (47) and (48) specify the time dynamics of the costate variables λ_y and $\lambda_{\tilde{y}}$. Conditions (49)–(51) are again a version of Hamilton's Rule for dynamic games between relatives.

The proof of this theorem is analogous to that of Theorem 4.1.

5. THE EVOLUTION OF RESOURCE ALLOCATION STRATEGIES

To illustrate the use of the above theorems, we now analyze the resource allocation model introduced in Section 1. Mirmirani and Oster (1978) have analyzed a similar model for a special case of the function b and for pairwise interactions among plants using a differential game between two players. We discuss their model further in Section 6.

Using Theorem 4.1, the Hamiltonian (24) for this problem is

$$H(\theta, \bar{\theta}, \zeta, \bar{\zeta}, \lambda_y, \lambda_{\tilde{y}})$$
$$= (1 - \zeta)\, b(\theta, \bar{\theta}) + \lambda_y \zeta b(\theta, \bar{\theta}) + \lambda_{\tilde{y}} \bar{\zeta} b(\bar{\theta}, \bar{\theta}). \quad (52)$$

Now, applying Theorem 4.1 gives the following necessary conditions that an ESS, $u^*(t)$, must satisfy:

$$-\frac{d\lambda_y}{dt} \triangleq \frac{\partial H}{\partial \theta} = (1-u^*)\frac{\partial b}{\partial y} + \lambda_y u^* \frac{\partial b}{\partial y} \qquad \lambda_y(T)=0 \quad (53)$$

$$-\frac{d\lambda_{\bar{y}}}{dt} \triangleq \frac{\partial H}{\partial \bar{\theta}} = (1-u^*)\frac{\partial b}{\partial \bar{y}} + \lambda_y u^* \frac{\partial b}{\partial \bar{y}} + \lambda_{\bar{y}} u^* \left(\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}}\right)$$

$$\lambda_{\bar{y}}(T)=0 \qquad\qquad (54)$$

and

if $0 < u^* < 1$ then $\Delta W_{\text{incl}}(t)|_{u^*} = 0$ (55)

if $u^* = 0$ then $\Delta W_{\text{incl}}(t)|_{u^*} \leqslant 0$ (56)

if $u^* = 1$ then $\Delta W_{\text{incl}}(t)|_{u^*} \geqslant 0$,   (57)

where

$$\Delta W_{\text{incl}}(t)|_{u^*} = \left[\frac{\partial H}{\partial \zeta} + \bar{r}\frac{\partial H}{\partial \bar{\zeta}}\right]_{\theta=\bar{\theta}=y^*, \zeta=\bar{\zeta}=u^*} \qquad (58)$$

$$= b(\lambda_y + \bar{r}\lambda_{\bar{y}} - 1). \qquad (59)$$

If (59) is positive then $u^* = 1$, and if it is negative then $u^* = 0$. This follows from (55)–(57) which is a dynamic version of Hamilton's Rule.

Now to solve for the ESS schedule, $u^*(t)$, we work backward in time from $t = T$. From differential Eqs. (53) and (54) we can see that

$$\Delta W_{\text{incl}}(T)|_{u^*} = -b. \qquad (60)$$

Therefore, from Conditions (55)–(57), $u^*(T) = 0$. Also notice that λ_y and $\lambda_{\bar{y}}$ are continuous and therefore $\Delta W_{\text{incl}}(t)|_{u^*}$ is continuous as well from (59). It follows that either $\Delta W_{\text{incl}}(t)|_{u^*} < 0$ for all t or else there is some interval $(t^*, T]$ in which $\Delta W_{\text{incl}}(t)|_{u^*} < 0$ where t^* is defined by

$$\Delta W_{\text{incl}}(t^*)|_{u^*} = 0. \qquad (61)$$

We will assume that the latter is true (otherwise $u^*(t) = 0$ for all time). Thus using (59) in (61) gives

$$\lambda_y(t^*) + \bar{r}\lambda_{\bar{y}}(t^*) - 1 = 0. \qquad (62)$$

Now because $\Delta W_{\text{incl}}(t)|_{u^*} < 0$ in the interval $(t^*, T]$, $u^*(t) = 0$ on this interval from (56). As a result, Eq. (1) implies that y^* is constant in this interval, and therefore $b(y^*, y^*)$ is constant in this interval as are its derivatives.

Therefore differential Eqs. (53) and (54) have the solutions

$$\lambda_y(t) = \frac{\partial b}{\partial y} \cdot (T-t) \qquad (63)$$

$$\lambda_{\bar{y}}(t) = \frac{\partial b}{\partial \bar{y}} \cdot (T-t) \qquad (64)$$

in this interval. Also, since $\lambda_y(T) = 0$ and $\lambda_{\bar{y}}(T) = 0$, we have

$$\lambda_y(t) > 0 \qquad (65)$$

$$\lambda_{\bar{y}}(t) < 0 \qquad (66)$$

on this interval from the assumptions about how $b(y, \bar{y})$ changes with changes in y and $\bar{y}$.

Now, since b is not zero, using (63) and (64) in (62), t^* satisfies

$$\frac{\partial b}{\partial y} \cdot (T-t^*) + \bar{r}\frac{\partial b}{\partial \bar{y}} \cdot (T-t^*) - 1 = 0 \qquad (67)$$

or

$$t^* = T - \frac{1}{\dfrac{\partial b}{\partial y} + \bar{r}\dfrac{\partial b}{\partial \bar{y}}}. \qquad (68)$$
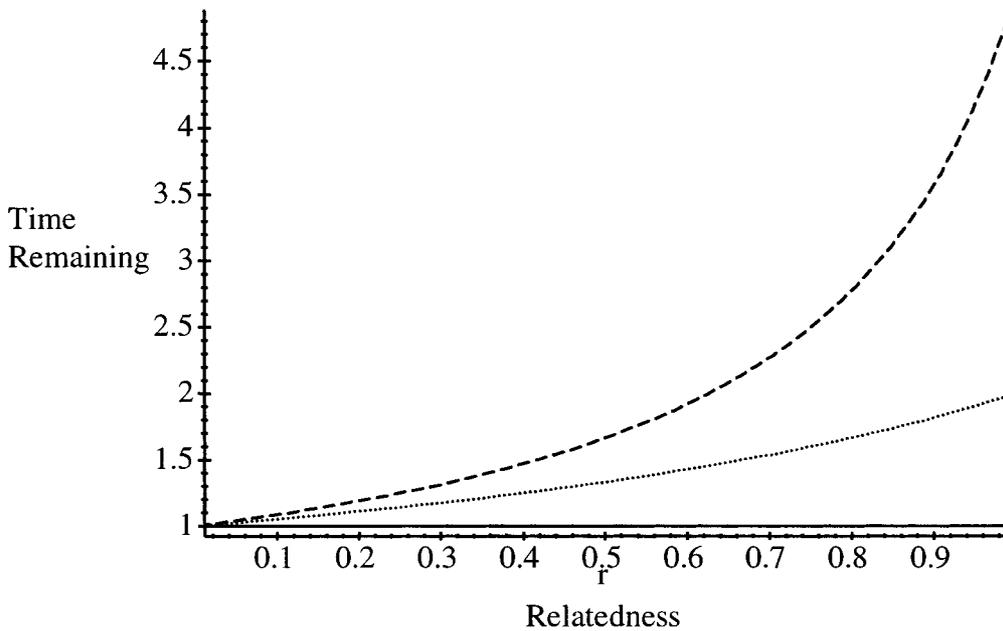
For a feasible t^* to exist we assume that

$$\frac{\partial b}{\partial y} + \bar{r}\frac{\partial b}{\partial \bar{y}} > 0 \qquad (69)$$

for all $0 < \bar{r} \leqslant 1$. In particular, we assume

$$\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}} > 0. \qquad (70)$$

Now we must determine what happens prior to t^*. A singular control (Bell and Jacobsen, 1975) results if $\Delta W_{\text{incl}}(t)|_{u^*} = 0$ over some interval of time, $[t^{**}, t^*]$. For this to occur, the time derivative of $\Delta W_{\text{incl}}(t)|_{u^*}$ (from the left) must be zero at $t = t^*$, i.e.,

$$\left[\frac{d}{dt}\Delta W_{\text{incl}}(t)|_{u^*}\right]_{t=t^*} = 0 \qquad (71)$$

FIG. 1. Time remaining when switching to reproduction. The vertical axis is time remaining and the horizontal axis is the relatedness of two randomly chosen patch members with replacement. Solid line, $\alpha = 0$; dotted line, $\alpha = 0.5$; dashed line, $\alpha = 0.8$.

or, by (59),

$$\frac{db}{dt}(\lambda_y + \bar{r}\lambda_{\bar{y}} - 1) + b\left(\frac{d\lambda_y}{dt} + \bar{r}\frac{d\lambda_{\bar{y}}}{dt}\right) = 0. \quad (72)$$

From (62) this requires that

$$\frac{d\lambda_y}{dt} + \bar{r}\frac{d\lambda_{\bar{y}}}{dt} = 0, \quad (73)$$

which, using differential Eqs. (53) and (54), and noting that $\lambda_y = 1 - \bar{r}\lambda_{\bar{y}}$ from (62) when $\Delta W_{\text{incl}}(t)|_{u*} = 0$, requires

$$\frac{\partial b}{\partial y} + \bar{r}\frac{\partial b}{\partial \bar{y}} = u^*\bar{r}\left\{\lambda_{\bar{y}}\frac{\partial b}{\partial \bar{y}}(\bar{r} - 1)\right\}. \quad (74)$$

Notice that u^* would have to be negative for this equality to hold, which is not feasible. Therefore a singular control is not possible, and thus in some interval prior to t^*, $u^* = 1$.

We now show that $\Delta W_{\text{incl}}(t)|_{u*} > 0$ at all times prior to t^*, which, from Conditions (55)–(57), implies that $u^* = 1$ at all times prior to t^*. Because $b > 0$ by assumption, we can see from (59) that we simply need to show that $\lambda_y - \bar{r}\lambda_{\bar{y}} - 1 > 0$ at all times prior to t^*.

From what we have shown above, $u^* = 1$ in some time interval immediately prior to t^*. Therefore, differential Eqs. (53) and (54) are

$$-\frac{d\lambda_y}{dt} = \lambda_y\frac{\partial b}{\partial y} \qquad \lambda_y(t^*) > 0 \quad (75)$$

$$-\frac{d\lambda_{\bar{y}}}{dt} = \lambda_y\frac{\partial b}{\partial \bar{y}} + \lambda_{\bar{y}}\left(\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}}\right) \qquad \lambda_{\bar{y}}(t^*) < 0 \quad (76)$$

in this interval, where the conditions on $\lambda_y(t^*)$ and $\lambda_{\bar{y}}(t^*)$ follow from (65) and (66). Now $\lambda_y + \bar{r}\lambda_{\bar{y}} - 1$ will increase backward in time from t^* in this interval if
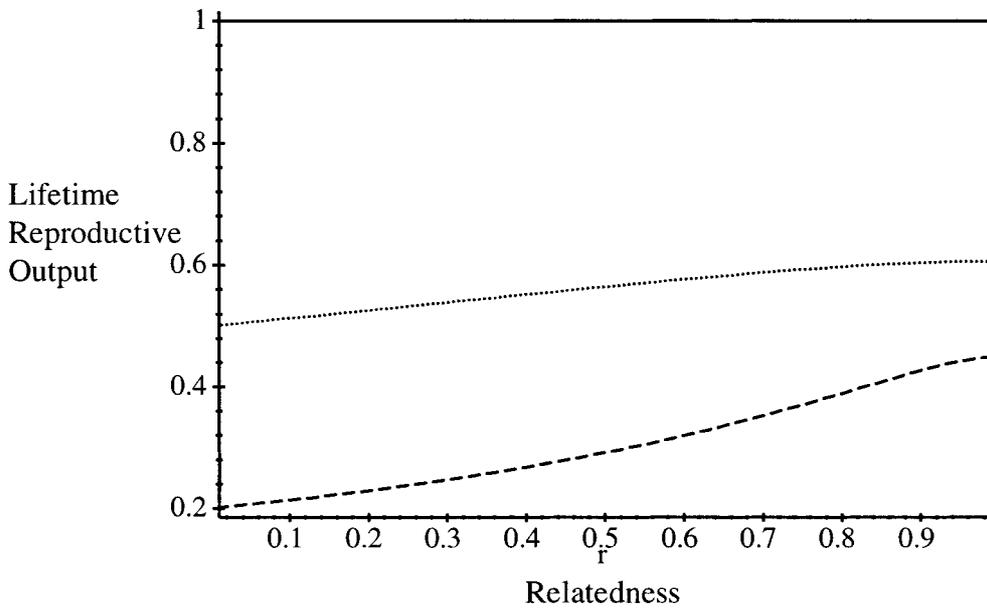
$$\frac{d}{dt}\left[\lambda_y + \bar{r}\lambda_{\bar{y}} - 1\right]$$

$$= -\lambda_y\left(\frac{\partial b}{\partial y} + \bar{r}\frac{\partial b}{\partial \bar{y}}\right) - \lambda_{\bar{y}}\bar{r}\left(\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}}\right) < 0. \quad (77)$$

For ease of handling, we write the right-hand side of the equality in (77) as

$$-(\lambda_y A + \lambda_{\bar{y}} B). \quad (78)$$

Now A and B are both positive from (69) and (70), and we also have that $A > B$ because calculating $A - B$ gives

$$\frac{\partial b}{\partial y} + \bar{r}\frac{\partial b}{\partial \bar{y}} - \bar{r}\left(\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}}\right) = (1 - \bar{r})\frac{\partial b}{\partial y}, \quad (79)$$

FIG. 2. Lifetime reproductive output. The vertical axis is reproductive output and the horizontal axis is the relatedness of two randomly chosen patch members with replacement. Solid line, $\alpha = 0$; dotted line, $\alpha = 0.5$; dashed line, $\alpha = 0.8$.

which is positive. Therefore,

$$\lambda_y A + \lambda_{\bar{y}} B > (\lambda_y + \lambda_{\bar{y}}) B, \tag{80}$$

because $\lambda_y > 0$. Hence, $\lambda_y A + \lambda_{\bar{y}} B$ will be positive as t moves backward from t^* if we can show that $\lambda_y + \lambda_{\bar{y}}$ is positive for such t. The time dynamics of $\lambda_y + \lambda_{\bar{y}}$ are given by

$$\frac{d\lambda_y}{dt} + \frac{d\lambda_{\bar{y}}}{dt} = -(\lambda_y + \lambda_{\bar{y}}) \left(\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}} \right), \tag{81}$$

and since $\lambda_y + \lambda_{\bar{y}} > 0$ at t^* and $\frac{\partial b}{\partial y} + \frac{\partial b}{\partial \bar{y}} > 0$, $\lambda_y + \lambda_{\bar{y}}$ increases backward in time from t^*. Therefore, t^* as defined by Eq. (68) is the only time in $[0, T]$ at which $\Delta W_{\text{incl}}(t)|_{u^*} = 0$. The ESS allocation strategy, $u^*(t)$, consists of a period of pure growth ($u^* = 1$) up until t^* and then a switch to a period of pure reproduction ($u^* = 0$) from t^* until the end of the season, T.

As a specific example, suppose

$$b(y, \bar{y}) = y - \alpha \bar{y}, \tag{82}$$

where $0 \leqslant \alpha < 1$. Then Eq. (68) for the switching time from pure growth to pure reproduction is

$$t^* = T - \frac{1}{1 - \bar{r}\alpha}. \tag{83}$$

Notice that if $1/(1 - \bar{r}\alpha) > T$ then the ESS is to never grow since $\Delta W_{\text{incl}} < 0$ for all time. From this equation we can see that the time remaining in the season when the switch occurs, $T - t^*$, does not depend on the length of the season, but it does depend on the relatedness parameter, $\bar{r}$, as well as the competition parameter, α. In fact, higher relatedness (higher values of $\bar{r}$) and stronger competitive effects (higher values of α) both result in an earlier switching time (Fig. 1). Stronger competition decreases the value of a unit increase in size and therefore the ESS is to begin reproducing earlier. Similarly, higher relatedness also decreases the (inclusive) value of a unit increase in size because it has a negative effect on other patch-mates through competition, and this negative effect is more important (evolutionarily) if relatedness is high. In this sense, an individual exhibiting an earlier switching time can be viewed as being more altruistic since it is sacrificing some of its own reproductive potential for the benefit of others. Greater altruism is selected for when relatedness is high.

Another way to depict this is by plotting an individual's total reproductive output as a function of the intrapatch relatedness, $\bar{r}$. This is calculated as

$$\int_0^T (1 - u^*(t))(1 - \alpha) y^*(t^*) \, dt$$

$$= (1 - \alpha) y_0 \exp \left((1 - \alpha) \left(T - \frac{1}{1 - \bar{r}\alpha} \right) \right) \left(\frac{1}{1 - \bar{r}\alpha} \right), \tag{84}$$

which is plotted in Fig. 2. It can be seen that the total reproductive output of each plant (or the patch as a whole) is maximized when $\bar{r} = 1$ and that stronger competition results in lower ESS reproductive output.

6. DISCUSSION

We have presented two theorems that can be used to construct models of dynamic evolutionary games between relatives. As mentioned earlier, the work of Mirmirani and Oster (1978) is the only published example, to our knowledge, of such a model. In their model, relatedness was included in a differential game heuristically by constructing an expression for an actor's inclusive fitness by analogy with Hamilton's Rule (their Eqs. 5). This expression was then maximized using Pontryagin's maximum principle (in the context of a differential game [Basar and Olsder, 1982]).

Hamilton's Rule is a phenotypic result in that the only reference it makes to genetics is through relatedness. Nevertheless, it works (i.e., it gives the same predictions as a genetic model under certain assumptions) because it is derived from a genetic model. In the same sense, Mirmirani and Oster's (1978) approach is phenotypic as well because it is based on the phenotypic result of Hamilton's Rule. Their approach was not derived from a genetic model directly, however, and consequently it was unclear whether it is genetically valid. Further doubt is cast on their approach by the fact that, in simple univariate models, maximizing an individual's inclusive fitness sometimes gives erroneous results (Grafen, 1979; Hines and Maynard-Smith, 1979; Mesterton-Gibbons, 1996; Day and Taylor, 1998a).

A comparison of the approach for constructing dynamic games between relatives derived here (which *is* genetically valid) with the approach of Mirmirani and Oster (1978) reveals that their approach is, in general, incorrect. The expression for inclusive fitness that is maximized in their approach (Mirmirani and Oster, 1978; Eqs. 5) is substantially different (and much simpler) than the expression that is maximized in a genetic model (our Eq. 37). The genetic details of the phenotypic approach are contained in the single composite parameter of relatedness, whereas the genetic details of Expression (37) enter in an explicit, mechanistic way through the probability distribution, $\sigma_k(u, \hat{u})$. This distribution contains complete information about how the mutant alleles are distributed throughout the population whereas relatedness does not. As a result there are two levels on

which maximizing the phenotypic expression of Mirmirani and Oster will differ from maximizing the genetic expression. First, the relatedness parameter of the phenotypic approach is treated as a constant when in fact such genetic properties will depend upon the strategies u and $\hat{u}$. Accounting for this dependence on u is what makes maximizing the genetic Expression (37) much more difficult. Second, suppose we ignore the dependence of σ_k on u and simply work directly with Expression (38). Then we can apply Theorem 4.1 to this expression. In doing so, the application of (9) to (38) nevertheless leads to a much more complicated condition than when it is applied to the phenotypic expression used by Mirmirani and Oster (see Eqs. [4.69] and [4.70] of Day, 1998). The reason is that, from a genetic standpoint, more information is required to use this general maximization condition for characterizing $u^*(t)$ than that which is contained in the relatedness parameter.

It turns out, however, that it is possible to obtain conditions that $u^*(t)$ must satisfy which do involve relatedness as the sole genetic parameter. The key to doing so is to focus on the first-order, necessary conditions that must be satisfied by $u^*(t)$ when Expression (37) is maximized. These are the conditions given by Theorems 4.1 and 4.2. Therein lies the utility of implications (ii) and (iii) in the proof of Theorem 4.1. Implication (ii) shows that u^* is necessarily characterized by first-order conditions, and implication (iii) shows that such first-order conditions will be the same whether we acknowledge the dependence of σ_k on u or not. Consequently, by applying Theorem 3.2 (which contains only first-order conditions) to (38), it is possible to obtain a result in which all the genetic details of the model are encapsulated by the single parameter of relatedness. Problems arise only if we try to obtain more general results by using Condition (9) of Theorem 3.1, because this requires information about the distribution of mutant alleles that is not contained in relatedness. As already mentioned, similar conclusions have been reached in the context of (static) univariate games between relatives (Grafen, 1979; Hines and Maynard-Smith, 1979; Mesterton-Gibbons, 1996; Day and Taylor, 1998a).

Interestingly, Mirmirani and Oster (1978) used the first-order conditions that correspond to the maximization of their phenotypic expression for inclusive fitness, and such first-order conditions happen to coincide with those for the maximization of the correct, genetic expression derived here (Day, 1998). Consequently, although their general approach is not genetically accurate, their focus on first-order necessary conditions resulted in conclusions that, coincidentally, happen to be valid. It is possible, however, to obtain some of the results of

Mirmirani and Oster more directly using Theorem 4.2 (Day, 1998). Furthermore, Theorem 4.1 provides a simple approach for extending the dynamic model of Mirmirani and Oster (1978) to allow for interactions among more than two plants (Section 5).

This also brings up an important assumption mentioned briefly in Section 4.1. In describing the genetic model, we assumed that the distribution of mutant alleles in the population reaches a statistical quasi-equilibrium. This is described by the probability distribution, $\sigma_k(u, \hat{u})$. What this means is that $\sigma_k(u, \hat{u})$ is the probability distribution that is attained after the mutant allele has been introduced at very low frequency and the movements of such mutant alleles have reached a statistical equilibrium. For it to be sensible to use this equilibrium, it is often necessary to assume that the mutant allele has a small effect (i.e., u is. close to $\hat{u}$) because otherwise, a significant change in allele frequency might occur before such an equilibrium is reached. This poses no problem for Theorems 4.1 and 4.2, however, because, being phrased as first-order conditions, these theorems implicitly consider only mutants of small effect. It is also significant that relatedness in these theorems is calculated using the distribution $\hat{\sigma}_k$. This is the distribution that would be attained if the mutant allele were neutral. Calculations of relatedness for neutral alleles are generally much simpler than for nonneutral alleles because simple arguments based on identity by descent can be used.

A particularly striking result to emerge from our analysis is the dynamic version of Hamilton's Rule, for example, Conditions (29)–(31). This is completely analogous to the scalar (static) version of Hamilton's Rule (Hamilton, 1964; Day and Taylor, 1997) except with the Hamiltonian playing the role of the fitness function. This rule can be applied just as the static version of Hamilton's Rule is applied and it provides the same degree of power for analyzing evolutionary models. In particular, to obtain a conceptual understanding of the factors at play in determining the ESS, it is not always necessary to even explicitly calculate u^*. Rather one can simply calculate the inclusive fitness effect and interpret each of the terms to understand the balance that must be struck along the ESS control at each point in time (Day and Taylor, 1997).

The theorems presented here can be used to address a very wide variety of evolutionary questions. Several models have been constructed to help understand the evolution of resource allocation strategies in annual plants (Cohen, 1971; Denholm, 1975; Mirmirani and Oster, 1978; King and Roughgarden, 1982a,b; Iwasa and Roughgarden, 1984). The generalization of the maximum principle presented here has allowed us to easily extend these analyses to more realistic scenarios that include competition between related individuals. In plants this is likely to be important because plants are sessile, seed dispersal is often limited, and individuals can have large effects on the resource acquisition ability of neighbors through shading.

Of course, Theorems 4.1 and 4.2 can be applied to any evolutionary model for a dynamic character, not only problems involving the evolution of resource allocation strategies. For example, Theorem 4.1 has been used to model the evolution of temporal patterns of cooperation and altruism (Day and Taylor, 1998b). Most models for the evolution of cooperation and altruism are static and seek a single ESS level of cooperation or altruism. If a group of individuals can interact over a period of time, however, then there is no reason to expect that the ESS level of cooperation or altruism should remain the same over the entire period. Theorem 4.1 was used to determine the factors that promote different levels of cooperation and altruism over time, and these results might prove useful for understanding the evolution of temporal patterns such as the breakdown in cooperation that occurs in some annual bumblebee colonies as the season progresses (van der Bloom 1985; Duchateau and Velthuis, 1988). Interestingly, they have implications for the evolution of meiotic nondisjunction and trisomy in humans as well (Day and Taylor, 1998c). Similarly, the evolution of a pathogen's temporal schedule of virulence within a host might fall into this category. Previous work has examined the evolution of virulence schedules in detail but has ignored relatedness among virus strains within a host (Sasaki and Iwasa, 1991). The above theorems provide a route to generalize these results by incorporating kin selection.

We close by mentioning a few caveats. First, all of the above results assume a symmetry among individuals that greatly simplifies the analysis. It would be very useful to have similar results for other, asymmetric interactions between individuals as well and we are currently exploring this possibility. Second, the above framework assumes that the control strategy used by an individual is genetically fixed. In other words, an individual is committed to a temporal strategy and cannot alter this strategy in relation to new information gained over time. In the language of differential games, the ESS strategy, u^*, is an open-loop solution (Basar and Olsder, 1982). Including the possibility of short time scale interactions and responses to learning greatly complicates models because the optimal strategy then has to be specified in a type of feedback (closed-loop) form. In other words, the ESS must be specified, conditional upon the state of the

individual and all interacting individuals at all times. At present obtaining results for such models still poses a considerable challenge. Similarly, incorporating stochasticity in the changes of state variables (Houston *et al.*, 1988) might also be more realistic for some models, but again this requires that the ESS be specified in a feedback form. Lastly our assumption of a single-locus diallelic model was made to derive results in the simplest possible genetic setting. Many inclusive fitness models employ this approach but it would be useful to explore more general (and realistic) genetic scenarios.

APPENDIX

For the dynamic optimization problem represented by W_0 (i.e., expression [38]), there are $(\omega_{AA} + \omega_{Aa})(n+1)$ state variables (i.e., y_{Ik} and y_{ik}) that we will keep track of and therefore we need to introduce as many costate variables, which we denote by λ_{Ik} and λ_{ik} where $i = 1, ..., n$ and $k = 1, ..., \omega_{aa} + \omega_{Aa}$. In what follows we will use the notation $f|_{ik}$ and $g|_{ik}$ to denote the functions f and g when evaluated at $y = y_{ik}$, $u = u_{ik}$ (and $\bar{y} = \bar{y}_k$, $\bar{u} = \bar{u}_k$). From (6), the Hamiltonian for this problem (which we denote by $\tilde{H}$) is

$$\tilde{H} = \sum_{k=1}^{\omega_{AA} + \omega_{Aa}} \hat{\sigma}_k f|_{Ik} + \sum_{k=1}^{\omega_{AA} + \omega_{Aa}} \lambda_{Ik} g|_{Ik}$$
$$+ \sum_{i=1}^{n} \sum_{k=1}^{\omega_{AA} + \omega_{Aa}} \lambda_{ik} g|_{ik}. \qquad (A1)$$

Applying Condition (8) for λ_{Ik} gives

$$-\frac{d\lambda_{Ik}}{dt} = \frac{\partial \tilde{H}}{\partial y_{Ik}} = \hat{\sigma}_k \frac{\partial f}{\partial y}\bigg|_{Ik} + \lambda_{Ik} \frac{\partial g}{\partial y}\bigg|_{Ik}$$
$$(A2)$$

$$\lambda_{Ik}(t_1) = \hat{\sigma}_k \frac{\partial \Phi}{\partial y}\bigg|_{Ik}. \qquad (A3)$$

Now evaluating this at $u = \hat{u} = u^*$, which from the state variable differential Eqs. (36) implies $y_{ik} = y_{Ik} = y^*$, gives

$$-\frac{d\lambda_{Ik}}{dt} = \hat{\sigma}_k \frac{\partial f}{\partial \bar{y}} + \lambda_{Ik} \frac{\partial g}{\partial \bar{y}} \qquad \lambda_{Ik}(t_1) = \hat{\sigma}_k \frac{\partial \Phi}{\partial \bar{y}}. \qquad (A4)$$

The $\omega_{AA} + \omega_{Aa}$ differential equations in (A4) can be added to give one differential equation for $\lambda_y \triangleq \sum_{k=1}^{\omega_{AA} + \omega_{Aa}} \lambda_{Ik}$:

$$-\frac{d\lambda_y}{dt} = \frac{\partial f}{\partial y} + \lambda_y \frac{\partial g}{\partial y} \qquad \lambda_y(t_1) = \frac{\partial \Phi}{\partial y}. \qquad (A5)$$

This is (27) of Theorem 4.1.

Applying condition (8) for λ_{ik} gives

$$-\frac{d\lambda_{ik}}{dt} = \frac{\partial \tilde{H}}{\partial y_{ik}} \qquad (A6)$$

$$= \hat{\sigma}_k \frac{\partial f}{\partial \bar{y}}\bigg|_{ik} \frac{1}{n} + \lambda_{Ik} \frac{\partial g}{\partial \bar{y}}\bigg|_{Ik} \frac{1}{n}$$

$$+ \lambda_{ik} \frac{\partial g}{\partial y}\bigg|_{ik} + \sum_{j=1}^{n} \lambda_{jk} \frac{\partial g}{\partial \bar{y}}\bigg|_{jk} \frac{1}{n} \qquad (A7)$$

and

$$\lambda_{ik}(t_1) = \hat{\sigma}_k \frac{1}{n} \frac{\partial \Phi}{\partial \bar{y}}\bigg|_{Ik}. \qquad (A8)$$

Evaluating this at $u = \hat{u} = u^*$, which from the state variable differential Eqs. (36) implies $y_{ik} = y_{Ik} = y^*$, gives

$$-\frac{d\lambda_{ik}}{dt} = \hat{\sigma}_k \frac{\partial f}{\partial \bar{y}} \frac{1}{n} + \lambda_{Ik} \frac{\partial g}{\partial \bar{y}} \frac{1}{n} + \lambda_{ik} \frac{\partial g}{\partial y} + \frac{\partial g}{\partial \bar{y}} \frac{1}{n} \sum_{j=1}^{n} \lambda_{jk}$$

$$\lambda_{ik}(t_1) = \hat{\sigma}_k \frac{1}{n} \frac{\partial \Phi}{\partial \bar{y}}. \qquad (9)$$

This is $(\omega_{AA} + \omega_{Aa}) n$ differential equations that can be reduced to one as follows. First, $\lambda_{ik} = \lambda_{jk}$ for all $i, j = 1, ..., n$. To see this define the variable $D = \lambda_{ik} - \lambda_{jk}$ for $i \neq j$. This satisfies the differential equation

$$\frac{dD}{dt} = \frac{d\lambda_{ik}}{dt} - \frac{d\lambda_{jk}}{dt} = -D \frac{\partial g}{\partial y} \qquad D(t_1) = 0. \quad (A10)$$

This has the unique solution $D \equiv 0$. Therefore, define $\lambda_{*k} \triangleq \lambda_{ik} = \lambda_{jk}$. Now write (A9) as

$$-\frac{d\lambda_{*k}}{dt} = \hat{\sigma}_k \frac{\partial f}{\partial \bar{y}} \frac{1}{n} + \lambda_{Ik} \frac{\partial g}{\partial \bar{y}} \frac{1}{n} + \lambda_{*k} \frac{\partial g}{\partial y} + \lambda_{*k} \frac{\partial g}{\partial \bar{y}}$$

$$\lambda_{*k}(t_1) = \hat{\sigma}_k \frac{1}{n} \frac{\partial \Phi}{\partial \bar{y}}. \qquad (A11)$$

This is now $(\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}})$ differential equations which can be reduced to one differential equation in $\lambda_{\bar{y}} \triangleq n \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \lambda_{*k}$:

$$-\frac{d\lambda_{\bar{y}}}{dt} = \frac{\partial f}{\partial \bar{y}} + \lambda_y \frac{\partial g}{\partial \bar{y}} + \lambda_{\bar{y}} \frac{\partial g}{\partial y} + \lambda_{\bar{y}} \frac{\partial g}{\partial \bar{y}} \tag{A12}$$

$$\lambda_{\bar{y}}(t_1) = \frac{\partial \Phi}{\partial \bar{y}}.$$

This is (28) of Theorem 4.1.

What remains is to derive (29)–(31) where $\Delta W_{\mathrm{incl}}(t)|_{\hat{u}}$ is given by (25). First, using the fact that $\lambda_y = \lambda_{Ik}/\hat{\sigma}_k$ and $\lambda_{\bar{y}} = n\lambda_{ik}/\hat{\sigma}_k$, $\tilde{H}$ can be written

$$\tilde{H} = \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k f(t, y^*, y^*, v_k, \bar{u}_k)$$

$$+ \lambda_y \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k g(t, y^*, y^*, v_k, \bar{u}_k)$$

$$+ \lambda_{\bar{y}} \frac{1}{n} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \sum_{i=1}^{n} g(t, y^*, y^*, u_{ik}, \bar{u}_k). \tag{A13}$$

Now, evaluating Conditions (10)–(12) we have,

$$\frac{\partial \tilde{H}}{\partial u}\bigg|_{u = \hat{u} = u^*} = \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \left(\frac{\partial f}{\partial u} \frac{dv_k}{du} + \frac{\partial f}{\partial \bar{u}} \frac{d\bar{u}_k}{du} \right)$$

$$+ \lambda_y \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \left(\frac{\partial g}{\partial u} \frac{dv_k}{du} + \frac{\partial g}{\partial \bar{u}} \frac{d\bar{u}_k}{du} \right)$$

$$+ \frac{\lambda_{\bar{y}}}{n} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k^u \sum_{i=1}^{n} \left(\frac{\partial g}{\partial u} \frac{du_{ik}}{du} + \frac{\partial g}{\partial \bar{u}} \frac{d\bar{u}_k}{du} \right) \tag{A14}$$

$$= \frac{\partial f}{\partial u} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \frac{dv_k}{du} + \frac{\partial f}{\partial \bar{u}} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \frac{d\bar{u}_k}{du}$$

$$+ \lambda_y \left(\frac{\partial g}{\partial u} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \frac{dv_k}{du} \right.$$

$$+ \frac{\partial g}{\partial \bar{u}} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \frac{d\bar{u}_k}{du} \right)$$

$$+ \lambda_{\bar{y}} \left(\frac{\partial g}{\partial u} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \frac{\hat{\sigma}_k}{n} \sum_{i=1}^{n} \frac{du_{ik}}{du} \right.$$

$$+ \frac{\partial g}{\partial \bar{u}} \sum_{k=1}^{\omega_{\mathrm{AA}} + \omega_{\mathrm{Aa}}} \hat{\sigma}_k \frac{d\bar{u}_k}{du} \right) \tag{A15}$$

$$= \frac{\partial f}{\partial u} \mathrm{E}_{\hat{\sigma}_k} \left[\frac{dv_k}{du} \right] + \frac{\partial f}{\partial \bar{u}} \mathrm{E}_{\hat{\sigma}_k} \left[\frac{d\bar{u}_k}{du} \right]$$

$$+ \lambda_y \left(\frac{\partial g}{\partial u} \mathrm{E}_{\hat{\sigma}_k} \left[\frac{dv_k}{du} \right] + \frac{\partial g}{\partial \bar{u}} \mathrm{E}_{\hat{\sigma}_k} \left[\frac{d\bar{u}_k}{du} \right] \right)$$

$$+ \lambda_{\bar{y}} \mathrm{E}_{\hat{\sigma}_k} \left[\frac{d\bar{u}_k}{du} \right] \left(\frac{\partial g}{\partial u} + \frac{\partial g}{\partial \bar{u}} \right), \tag{A16}$$

where $\mathrm{E}_{\hat{\sigma}_k}[\,\cdot\,]$ is the expectation weighted by the probability distribution, $\hat{\sigma}_k$. Equation (A16) has the same sign as

$$\frac{\partial f}{\partial u} + \lambda_y \frac{\partial g}{\partial u} + \frac{\mathrm{E}_{\hat{\sigma}_k} \left[\dfrac{d\bar{u}_k}{du} \right]}{\mathrm{E}_{\hat{\sigma}_k} \left[\dfrac{dv_k}{du} \right]} \left(\frac{\partial f}{\partial \bar{u}} + \lambda_y \frac{\partial g}{\partial \bar{u}} + \lambda_{\bar{y}} \left(\frac{\partial g}{\partial u} + \frac{\partial g}{\partial \bar{u}} \right) \right). \tag{A17}$$

The remainder of the proof will now show that $\bar{r}$ of Theorem 4.1 is equal to the coefficient of the parenthetical term in (A17), i.e., $\bar{r} = \mathrm{E}_{\hat{\sigma}_k}[\frac{d\bar{u}_k}{du}]/\mathrm{E}_{\hat{\sigma}_k}[\frac{dv_k}{du}]$. Recall that $\bar{r}$ is simply the relatedness of a randomly chosen patch member (including the possibility of it being the actor itself) to the actor when the mutant allele is rare.

By definition, the relatedness of a randomly chosen patch member to an actor is given by

$$\bar{r} = \frac{\mathrm{cov}(g_x, g_y)}{\mathrm{var}(g_x)}, \tag{A18}$$

where g_x is the genotype of an actor and g_y is the genotype of the randomly chosen patch member (Michod and Hamilton, 1980). Calculating the covariance, using, $\hat{\psi}$, $\hat{P}_k$, and $\hat{p}_k$ to denote the corresponding probabilities evaluated at $u = \hat{u} = u^*$ gives

$$\mathrm{cov}(g_x, g_y)$$

$$= \mathrm{E}[g_x g_y] - \mathrm{E}[g_x] \mathrm{E}[g_y]$$

$$= \mathrm{E}[g_x g_y \mid g_x = 1] \Pr\{g_x = 1\}$$

$$\quad + \mathrm{E}[g_x g_y \mid g_x = 1/2] \Pr\{g_x = 1/2\} - \bar{g}^2$$

$$= \mathrm{E}[g_y \mid g_x = 1]((1 - \hat{\psi}) \bar{g}^2 + \bar{g}\hat{\psi})$$

$$\quad + \tfrac{1}{2} \mathrm{E}[g_y \mid g_x = 1/2] \, 2(1 - \hat{\psi}) \, \bar{g}(1 - \bar{g}) - \bar{g}^2$$

$$= \bar{g}[\mathrm{E}[g_y \mid g_x = 1]((1 - \hat{\psi}) \bar{g} + \hat{\psi})$$

$$\quad + \mathrm{E}[g_y \mid g_x = 1/2](1 - \hat{\psi})(1 - \bar{g}) - \bar{g}] \tag{A19}$$

and calculating the variance gives

$$
\begin{aligned}
\mathrm{var}(g_x) &= \mathrm{E}[\,g_x^2\,] - \mathrm{E}[\,g_x\,]^2 \\
&= \tfrac{1}{4}2\bar{g}(1-\bar{g})(1-\hat{\psi}) + (1-\hat{\psi})\,\bar{g}^2 + \bar{g}\hat{\psi} - \bar{g}^2 \\
&= \bar{g}[\,\tfrac{1}{2}(1-\bar{g})(1-\hat{\psi}) + \hat{\psi} + (1-\hat{\psi})\,\bar{g} - \bar{g}\,].
\end{aligned}
\tag{A20}
$$

Therefore,

$$
\bar{r} = \frac{\left(\begin{array}{c} \mathrm{E}[\,g_y\,|\,g_x=1\,]((1-\hat{\psi})\,\bar{g}+\hat{\psi}) \\ +\,\mathrm{E}[\,g_y\,|\,g_x=1/2\,](1-\hat{\psi})(1-\bar{g}) - \bar{g} \end{array}\right)}{\tfrac{1}{2}(1-\bar{g})(1-\hat{\psi}) + \hat{\psi} + (1-\hat{\psi})\,\bar{g} - \bar{g}}
\tag{A21}
$$

and, for rare mutants,

$$
\lim_{\bar{g}\to 0}\bar{r} = \frac{\hat{\psi}\mathrm{E}[\,g_y\,|\,g_x=1\,] + (1-\hat{\psi})\,\mathrm{E}[\,g_y\,|\,g_x=1/2\,]}{\hat{\psi} + (1-\hat{\psi})\cdot\tfrac{1}{2}}.
\tag{A22}
$$

Now, from the definition of u_{ik}, du_{ik}/du is the genotype of an ik individual. More precisely, it is equal to 0, 1/2, or 1 depending on whether the individual is a normal type, a mutant heterozygote, or a mutant homozygote. Additionally, we have

$$
\frac{d\bar{u}_k}{du} = \frac{1}{n}\sum_{i=1}^{n}\frac{du_{ik}}{du},
\tag{A23}
$$

which is the expected genotype of a randomly chosen individual in a k patch. Therefore, $\mathrm{E}[\,g_y\,|\,g_x=1\,] = \sum_{k=1}^{\omega_{\mathrm{AA}}}\hat{P}_k\frac{d\bar{u}_k}{du}$ and $\mathrm{E}[\,g_y\,|\,g_x=1/2\,] = \sum_{k=\omega_{\mathrm{AA}}+1}^{\omega_{\mathrm{AA}}+\omega_{\mathrm{Aa}}}\hat{p}_k\frac{d\bar{u}_k}{du}$. Similarly, from the definition of v_k, we have that dv_k/du is the genotype of the focal individual (i.e., the actor). In particular, it is 1/2 if the actor is a heterozygote and it is 1 if the actor is a mutant homozygote. Consequently, (A22) can be written

$$
\lim_{\bar{g}\to 0}\bar{r} = \frac{\hat{\psi}\sum_{k=1}^{\omega_{\mathrm{AA}}}\hat{P}_k\dfrac{d\bar{u}_k}{du} + (1-\hat{\psi})\sum_{k=\omega_{\mathrm{AA}}+1}^{\omega_{\mathrm{AA}}+\omega_{\mathrm{Aa}}}\hat{p}_k\dfrac{d\bar{u}_k}{du}}{\hat{\psi}\sum_{k=1}^{\omega_{\mathrm{AA}}}\hat{P}_k\dfrac{dv_k}{du} + (1-\hat{\psi})\sum_{k=\omega_{\mathrm{AA}}+1}^{\omega_{\mathrm{AA}}+\omega_{\mathrm{Aa}}}\hat{p}_k\dfrac{dv_k}{du}}
\tag{A24}
$$

$$
= \frac{\mathrm{E}_{\hat{\sigma}_k}\left[\dfrac{d\bar{u}_k}{du}\right]}{\mathrm{E}_{\hat{\sigma}_k}\left[\dfrac{dv_k}{du}\right]}.
\tag{A25}
$$

The last equality follows from the definition of $\hat{\sigma}_k$. This demonstrates that Expression (A17) is equal to Expression (25), and using this in Conditions (10)–(12) produces Conditions (29)–(31) of Theorem 4.1. This completes the proof. As an aside, it is interesting that the coefficient of relatedness, $\mathrm{E}_{\hat{\sigma}_k}[\frac{d\bar{u}_k}{du}]/\mathrm{E}_{\hat{\sigma}_k}[\frac{dv_k}{du}]$, can be interpreted as the ratio of the expected genotype of a randomly selected patch member to the expected genotype of the focal individual, from the perspective of a mutant allele. In other words, it is a weighting of the fraction of a random patch member's genotype that is mutant to the fraction of the focal individual's genotype that is mutant, from the perspective of a mutant allele.

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