Hamilton's rule meets the Hamiltonian: kin selection on dynamic characters

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SUMMARY

Many biological characters of interest are temporal sequences of decisions. The evolution of such characters is often modelled using dynamic optimization methods such as the maximum principle. A quantity central to these analyses is the 'Hamiltonian' function, named after the mathematician William R. Hamilton. On the other hand, evolutionary models in which individuals interact with relatives are usually based on Hamilton's rule, named after the evolutionary biologist William D. Hamilton. In this article we present a generalized maximum principle that includes the effects of interactions among relatives and we show that a time-dependent (dynamic) version of Hamilton's rule holds involving the Hamiltonian. This result brings together the power and generality of both the maximum principle and Hamilton's rule thereby providing a natural framework for understanding the evolution of 'dynamic' characters under kin selection.

1. INTRODUCTION

Optimization models have played an important role in theoretical evolutionary biology (Parker & Maynard Smith 1990). This approach usually begins by constructing a function that specifies the fitness of an individual for different values of a character of interest (e.g. clutch size), and then one seeks those character values that are evolutionarily stable. Such models are familiar to most evolutionary biologists and their construction is well understood.

Consider however, constructing an optimization model for a character that consists of a sequence of decisions over an interval of time. For example, suppose that an individual must 'decide' what proportion of its available resources to devote to growth versus reproduction each year. When weighing the costs and benefits of different decisions in any year, one must know the expected future reproductive output given different decisions and this entails knowing the optimal allocation strategy in future years. Such optimization problems are more difficult and require the less familiar techniques of dynamic optimization such as dynamic programming (Mangel & Clark 1988) or the maximum principle (Leon 1976; Schaffer 1983; Perrin & Sibly 1993). We refer to such characters as 'dynamic' characters.

Many important biological characters are dynamic. Examples include temporal patterns of resource allocation to growth and reproduction (i.e. general life history decisions; Leon 1976; Schaffer 1983; Perrin & Sibly 1993) and temporal patterns of behaviour (Houston *et al.* 1988; Mangel & Clark 1988). The maximum principle and dynamic programming have

provided much insight into the evolution of these characters.

Parallel to this body of literature has been the development of the theory of kin selection and Hamilton's rule (Hamilton 1964a). Most kin selection models consider the evolution of single decisions (characters) and can therefore be constructed in a routine way using a simple optimization or ESS approach (Taylor & Frank 1996). Although the concept of kin selection was initially introduced to explain the evolution of various social behaviours (Hamilton 1964a, b), its principles are important for the evolution of all characters whenever individuals preferentially associate with kin, or when the movements of individuals result in some form of population structuring (e.g. patch structuring).

But how are we to model dynamic characters and kin selection together? For example, consider the evolution of the resource allocation strategy in an annual plant. Individual plants can greatly affect the growth and reproduction of neighbours through competition for light and nutrients, and often these neighbours are relatives (Kelly 1996). Predictions for resource allocation strategies that ignore interactions with kin are clearly inadequate. Another example is the evolution of temporal virulence schedules of pathogens (Sasaki & Iwasa 1991). Pathogens within a host may to some degree be related and because they exploit a common resource, it is important to determine the effects of this relatedness on the evolution of virus replication schedules.

To our knowledge there are only two attempts to incorporate the effects of kin selection into models for the evolution of dynamic characters. Mirmirani & Oster (1978) modelled a specific case of the plant

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life history example mentioned above by constructing a differential game between two relatives. They provided predictions for that particular model but did not discuss a general approach for modelling the evolution of dynamic characters under kin selection. Recently, McNamara *et al.* (1994) have addressed this issue by demonstrating how to construct kin selection models for the evolution of dynamic characters numerically, using dynamic programming. Their results also concern interactions between two individuals; however, in their model only one of the two individuals was allowed to make decisions.

Our intention here is to present a straightforward analytical procedure for constructing kin selection models of dynamic characters that is based on the maximum principle. By straightforward we mean that it can be routinely applied in exactly the same way as the maximum principle. We show that in such models, an interesting dynamic version of Hamilton's rule holds, involving the so-called Hamiltonian function of the maximum principle. Our focus is on models of patch-structured populations where individuals 'play the field' (Maynard Smith 1982).

The remainder of this article is organized as follows. In §2 and §3 we briefly review Hamilton's rule for single decisions and the maximum principle, respectively. Section 4 then presents a generalization of the maximum principle that includes interactions among relatives. There we present a dynamic version of Hamilton's rule. Lastly, §5 discusses the range of applicability of this approach, as well as some shortcomings and possible future extensions.

2. HAMILTON'S RULE FOR SINGLE DECISIONS

Here we review the ideas of inclusive fitness and Hamilton's rule for single decisions. Consider a character, u, that can take any value in the interval from zero to one. For example, in a sex ratio model u might represent the proportion of all offspring produced that are male. Suppose that the population is patch structured and that an individual's fitness, $W(u, \bar{u})$ depends on its own value of u and the patch average, $\bar{u}$. This form of interaction is often termed 'playing the field' (Maynard Smith 1982).

Hamilton's rule characterizes the ESS value of u as follows. First imagine a population monomorphic at $u = u^*$, and consider the inclusive fitness effect, ΔW_{incl} of an actor altering its strategy slightly (locally) from u^* to $u = u^* + \delta$, where δ is small and positive. ΔW_{incl} is defined to be the weighted sum of the fitness effects on all individuals affected by the change in strategy (including the actor), where the weight for each individual is the relatedness of that individual to the actor (Hamilton 1964a; Hamilton 1970; Grafen 1991). Here, the actor will affect its own fitness through a change in both u and $\bar{u}$, and the sum of these effects is $(\partial W/\partial u) + (1/N)(\partial W/\partial \bar{u})$. In this expression N is the number of individuals in a patch and the derivatives are evaluated at $u = u^*$. The actor also affects the remaining $N-1$ individuals

in the patch through the change in $\bar{u}$, and weighting this effect for individual i by its relatedness to the actor r_i gives the sum of these effects to be

$$\left(\frac{\partial W}{\partial \bar{u}}\right)\left(\frac{1}{N}\right)\sum_{i\neq actor} r_i.$$

Thus the total inclusive fitness effect is

$$\Delta W_{incl} = \left[\left(\frac{\partial W}{\partial u}\right) + R\left(\frac{\partial W}{\partial \bar{u}}\right)\right]_{u=u^*},$$

where R is the relatedness between two randomly chosen individuals on the patch (with replacement). So defined, ΔW_{incl} can be regarded as the change in inclusive fitness resulting from a unit increase in u from u^*.

Hamilton's rule states that $\Delta W_{incl} > 0$ if selection favours values of u that are larger than u^*. Similarly, $\Delta W_{incl} < 0$ if selection favours values of u that are smaller than u^*. Therefore we have: if u^* is an ESS then,

$$\left.\begin{array}{ll}
\text{if } 0 < u^* < 1 & \text{then } \Delta W_{incl} = 0, \\
\text{if } u^* = 0 & \text{then } \Delta W_{incl} \leqslant 0, \\
\text{if } u^* = 1 & \text{then } \Delta W_{incl} \geqslant 0.
\end{array}\right\} \qquad (1)$$

3. DYNAMIC CHARACTERS AND THE MAXIMUM PRINCIPLE

Although the results to be presented here and in §4 are general, we phrase our exposition in the context of a model for the evolution of energy allocation to growth and reproduction in an annual plant. This context aids intuition and it is a dynamic optimization problem with a long history (Cohen 1971; Denholm 1975; Mirmirani & Oster 1978; King & Roughgarden 1982a, b; Iwasa & Roughgarden 1984). We begin by considering a population that is patch structured with patches of size N, and we will assume the population is monomorphic. We also assume that the population lacks all forms of class structure (e.g. sex, age, etc.). So, for example, although individual plants within a patch age as the season progresses, no two individuals differ in age.

Now imagine that an individual plant must 'choose' an energy allocation strategy at each point in time over a season of length T (from this point onward we assume continuous time). Let $y(t)$ denote individual size, $u(t)$ $(0 \leqslant u(t) \leqslant 1)$ the proportion of resources devoted to growth at time t, and $f(t, y(t), u(t))$ the rate of reproductive output at time t. Here we allow reproductive output to depend directly on time as well as through the individual's size and allocation strategy at time t. We use the total reproductive output over the season as a measure of the individual's fitness; i.e.

$$W = \int_0^T f(t, y(t), u(t))\, \mathrm{d}t. \qquad (2)$$

Suppose also that an individual's size changes with time according to the growth equation

$$\frac{\mathrm{d}y}{\mathrm{d}t} = g(t, y(t), u(t)), \quad y(0) = y_0. \qquad (3)$$

Here we also allow the growth rate of an individual to depend directly on time as well as on its size and the allocation strategy at time t. The maximum principle then constructs the so-called Hamiltonian function, $H = f + \lambda g$, i.e.

$$H(t, y(t), u(t), \lambda(t)) = f(t, y(t), u(t))$$
$$+ \lambda(t) g(t, y(t), u(t)), \qquad (4)$$

using a 'costate' variable $\lambda(t)$, and provides the following necessary conditions for the strategy $u^*(t)$ to be optimal:

(i) $\quad \dfrac{\partial H}{\partial y} = -\dfrac{\mathrm{d}\lambda}{\mathrm{d}t}, \quad \lambda(T) = 0, \qquad (5\,a)$

(ii) $\quad H(t, y^*, u^*, \lambda) = \max\limits_{u \in [0,1]} H(t, y^*, u, \lambda), \qquad (5\,b)$

where the arguments of functions have been suppressed (Knowles 1981; Pinch 1993; Perrin & Sibly 1993; Bulmer 1994).

The maximum principle may seem somewhat abstract but it is rich in biological interpretation (Leon 1976; Perrin & Sibly 1993). The Hamiltonian is constructed by introducing a 'costate' variable $\lambda(t)$ that is closely related to the state variable $y(t)$. The costate variable $\lambda(t)$ can be interpreted as the marginal return in future fitness of a free increment in size at time t, when using the optimal allocation strategy (Iwasa & Roughgarden 1984; Perrin & Sibly 1993). Equation $(5\,a)$ specifies how this marginal value changes over time. The terminal value $\lambda(T)$ is zero because that is the marginal return in future fitness of an increment in size at the end of the season. Equation $(5\,b)$ states that u should be chosen so that the Hamiltonian is maximized in u at all times, hence the name maximum principle. This strategy is found by integrating the differential equation $(5\,a)$ backward in time from T with u chosen such that condition $(5\,b)$ is always satisfied. A local necessary condition corresponding to $(5\,b)$ is

$$\left.\begin{array}{ll} \text{if } 0 < u^* < 1 & \text{then } \partial H/\partial u = 0, \\[4pt] \text{if } u^* = 0 & \text{then } \partial H/\partial u \leqslant 0, \\[4pt] \text{if } u^* = 1 & \text{then } \partial H/\partial u \geqslant 0, \end{array}\right\} \qquad (5\,c)$$

where $(\partial H/\partial u)$ is evaluated at u^* in each case.

4. A MAXIMUM PRINCIPLE UNDER KIN SELECTION

Now we suppose that the fitness of an individual also depends on the group mean size $\bar{y}$ and strategy $\bar{u}$ (i.e. individuals 'play the field') and that individuals

of the group are related. In general, an individual's fitness is now given by

$$W = \int_0^T f(t, y(t), \bar{y}(t), u(t), \bar{u}(t))\,\mathrm{d}t, \qquad (6)$$

where the sizes $y_i(t)$ of all individuals in the group, $i = 1, \ldots, N$ obey the same growth equation

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = g(t, y_i(t), \bar{y}(t), u_i(t), \bar{u}(t)), \quad y_i(0) = y_0. \qquad (7)$$

Consider a monomorphic population using the optimal strategy, $u^*(t)$ and define the Hamiltonian

$$H(t, y, \bar{y}, u, \bar{u}, \lambda_y, \lambda_{\bar{y}}) = f(t, y, \bar{y}, u, \bar{u})$$
$$+ \lambda_y(t) g(t, y, \bar{y}, u, \bar{u}) + \lambda_{\bar{y}}(t) g(t, \bar{y}, \bar{y}, \bar{u}, \bar{u}). \qquad (8)$$

As in § 3, $\lambda_y(t)$ is the marginal return of a free increment in *individual size* at time t. Now, however, we have introduced a second 'costate' variable, $\lambda_{\bar{y}}$ that corresponds to the group mean state variable, $\bar{y}$. $\lambda_{\bar{y}}(t)$ is the marginal return to the individual of a free increment in *group mean size* at time t. If the dependence of an individual's fitness on the group mean size results from competitive effects, we might expect $\lambda_{\bar{y}}(t)$ to be negative.

To characterize the ESS allocation strategy we again imagine a population monomorphic at $u^*(t)$, and we consider the inclusive fitness effect of an individual altering its allocation strategy slightly at time t. Note that now the inclusive fitness effect $\Delta W_{\mathrm{incl}}(t)$ is a function of time. This effect is quite complicated because changes in allocation strategy at time t not only affect reproductive output at time t, but at all future times as well. In fact there are six different pathways through which a change in allocation strategy at time t affects fitness (figure 1). The sum of all of these effects can, however, be computed easily using the Hamiltonian (equation (8)). In fact figure 1 shows that

$$\Delta W_{\mathrm{incl}}(t) = \left[\left(\frac{\partial H}{\partial u}\right) + R\left(\frac{\partial H}{\partial \bar{u}}\right)\right]_{u(t)=u^*(t)}.$$

This suggests the following theorem.

Theorem 4.1. *Let $u^*(t)$ denote the optimal strategy, R the relatedness of two randomly chosen individuals within a patch (with replacement), and $\Delta W_{\mathrm{incl}}(t)$ the inclusive fitness effect of a (local) mutant strategy at time t. If $u^*(t)$ is an ESS then*

(i) $\quad \dfrac{\partial H}{\partial y} = -\dfrac{\mathrm{d}\lambda_y}{\mathrm{d}t}, \quad \lambda_y(T) = 0, \qquad (9\,a)$

$\qquad \dfrac{\partial H}{\partial \bar{y}} = -\dfrac{\mathrm{d}\lambda_{\bar{y}}}{\mathrm{d}t}, \quad \lambda_{\bar{y}}(T) = 0, \qquad (9\,b)$

(ii) $\left.\begin{array}{ll} \textit{if } 0 < u^* < 1 & \textit{then } \Delta W_{\mathrm{incl}}(t) = 0, \\[4pt] \textit{if } u^* = 0 & \textit{then } \Delta W_{\mathrm{incl}}(t) \leqslant 0, \\[4pt] \textit{if } u^* = 1 & \textit{then } \Delta W_{\mathrm{incl}}(t) \geqslant 0, \end{array}\right\} \quad (9\,c)$

where everything is evaluated in a monomorphic population (i.e. $y = \bar{y} = y^*$, $u = \bar{u} = u^*$).

TOTAL EFFECT

Δu — changes reproductive output of actor at time t → f_u f_u **a1**

changes actor's growth rate at time t → g_u — changes actor's future size → changes actor's future reproductive output → λ_y $g_u \lambda_y$ **a2**

changes group mean allocation strategy

changes future mean size in group → $\frac{1}{N}$ changes future reproductive output of all group members → $\lambda_{\bar{y}}$ $\displaystyle\sum_i g_u \frac{1}{N} \lambda_{\bar{y}} r_i = R g_u \lambda_{\bar{y}}$ **a3**

$\frac{1}{N}$ — changes reproductive output of all group members at time t → $f_{\bar{u}}$ $\displaystyle\sum_i f_{\bar{u}} \frac{1}{N} r_i = R f_{\bar{u}}$ **b1**

changes growth rate of all group members at time t → $g_{\bar{u}}$ — changes future size of all group members → changes future reproductive output of all group members → λ_y $\displaystyle\sum_i g_{\bar{u}} \frac{1}{N} \lambda_y r_i = R g_{\bar{u}} \lambda_y$ **b2**

changes future mean size in group → changes future reproductive output of all group members → $\lambda_{\bar{y}}$ $\displaystyle\sum_i g_{\bar{u}} \frac{1}{N} \lambda_{\bar{y}} r_i = R g_{\bar{u}} \lambda_{\bar{y}}$ **b3**

$$\Delta W_{incl} = f_u + \lambda_y g_u + R[f_{\bar{u}} + \lambda_y g_{\bar{u}} + \lambda_{\bar{y}}(g_u + g_{\bar{u}})]$$

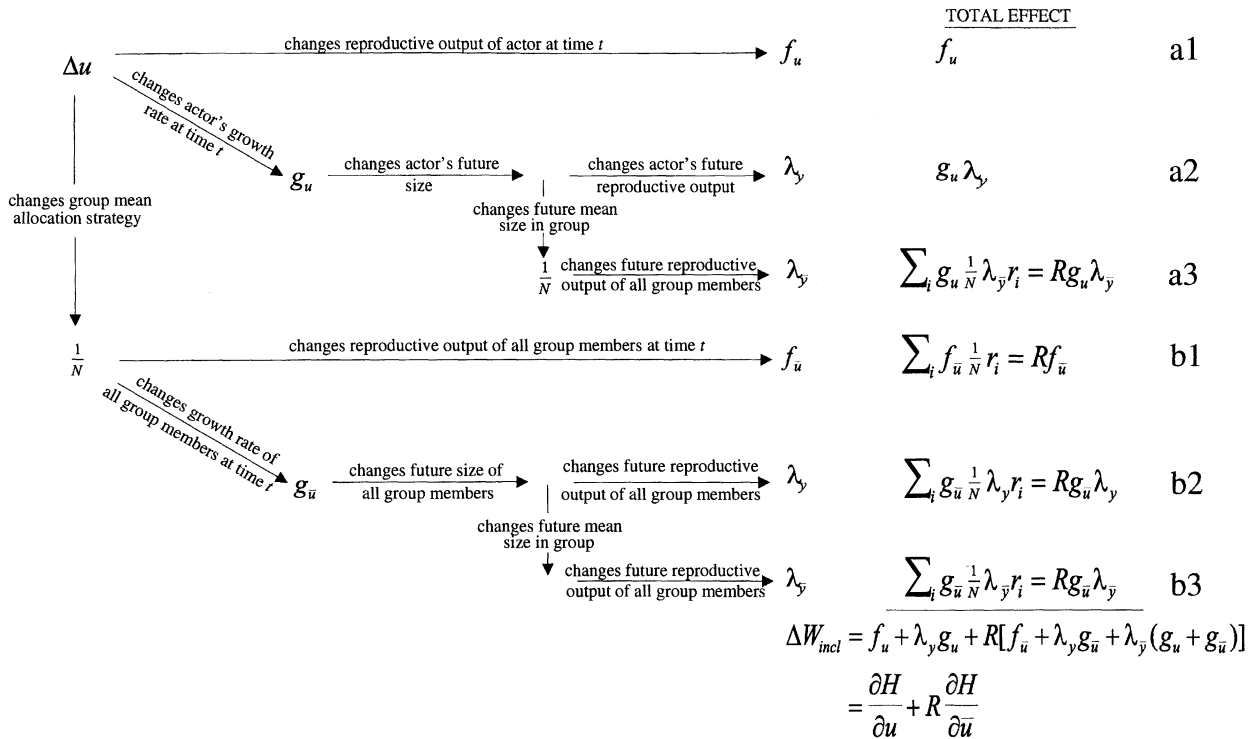$$= \frac{\partial H}{\partial u} + R \frac{\partial H}{\partial \bar{u}}$$

Figure 1. Six pathways through which an individual's inclusive fitness is affected by a change in its allocation strategy at time t. Pathways a1, a2 and a3 arise through the effects of changing $u(t)$. Pathways b1, b2 and b3 arise because of the change in the patch average allocation strategy $\bar{u}(t)$ that results from the individual changing its own strategy. This individual is one of N individuals in the patch and therefore changing its u by one unit will change $\bar{u}$ by $(1/N)$ units.

A thorough proof turns out to be quite lengthy and involves formulating the model as a standard control problem with one *genotypic* control variable and $N+1$ state variables, and then applying the standard maximum principle and evaluating the results in a monomorphic population. Figure 1 however, serves as a partial, heuristic proof.

Notice the similarity of conditions ($9c$) with those for inclusive fitness models of single decisions (equation (1)). By defining the costate variables $\lambda_y(t)$ and $\lambda_{\bar{y}}(t)$ and introducing the Hamiltonian (equation (8)), the complicated dynamic kin selection problem is converted into a temporal sequence of simple static kin selection problems where the Hamiltonian now serves as the fitness function. The result is that Hamilton's rule must be satisfied at each point in time along the ESS strategy $u^*(t)$. $(\partial H/\partial u)$ is the effect on fitness when an individual varies its own strategy $u(t)$ and $(\partial H/\partial \bar{u})$ is the effect on the fitness of each group member of varying the population mean strategy $\bar{u}(t)$. Of course to determine the inclusive fitness effect at any point in time (i.e. $\Delta W_{incl}(t) = [(\partial H/\partial u) + R(\partial H/\partial \bar{u})]_{u(t)=u^*(t)}$) one needs to know the values of the marginal return functions $\lambda_y(t)$ and $\lambda_{\bar{y}}(t)$ at that point in time. Equations ($9a$), ($9b$) specify the time dynamics of these marginal returns when the optimal strategy is used, just as equation ($5a$) specified the dynamics of the marginal return for an increment in y in § 3.

To take a concrete example, suppose the plant's production rate, $b(y,\bar{y})$, depends on both y and $\bar{y}$,

and that there is a constant size-independent mortality rate μ. The rate of reproductive output at time t is therefore $f(y,\bar{y},u) = (1 - u)e^{-\mu t}b(y,\bar{y})$, and the growth rate at time t is $g(y_i,\bar{y},u) = ub(y_i,\bar{y})$. In this example f and g are independent of $\bar{u}$ and therefore pathways b1, b2 and b3 of figure 1 disappear. Now form the Hamiltonian

$$H = (1-u)e^{-\mu t}b(y,\bar{y}) + \lambda_y ub(y,\bar{y}) + \lambda_{\bar{y}}\bar{u}b(\bar{y},\bar{y}). \quad (10)$$

Assuming that $b(y,\bar{y}) > 0$, condition ($9c$) is

if $0 < u^* < 1$ (mixed allocation),
$$\text{then } \lambda_y(t) + \lambda_{\bar{y}}(t)R = e^{-\mu t}, \quad (11a)$$

if $u^* = 0$ (pure reproduction),
$$\text{then } \lambda_y(t) + \lambda_{\bar{y}}(t)R \leqslant e^{-\mu t}, \quad (11b)$$

if $u^* = 1$ (pure growth),
$$\text{then } \lambda_y(t) + \lambda_{\bar{y}}(t)R \geqslant e^{-\mu t}. \quad (11c)$$

The right-hand side of inequalities ($11a$)–($11c$) is the inclusive fitness effect of a unit increment in reproduction at time t; it decays exponentially through mortality. The left-hand side is the inclusive fitness effect of a unit increment in size. If an individual's size was increased at time t it would gain $\lambda_y(t)$ through its own size increase, plus $\lambda_{\bar{y}}(t)R$ through the effect that this size increase has on all group members from the change in $\bar{y}$. Condition ($11a$) says that if mixed allocation is an ESS over some interval of time, then the inclusive fitness effect of a unit

increment in growth must equal that of reproduction. Condition (11 b) says that if a pure reproduction strategy is an ESS over some interval of time, then the inclusive fitness effect of a unit investment in reproduction must be at least as big as that of growth (and vice versa for condition (11 c)).

Under a minor technical assumption, it is relatively easy to show that $u^*(t) = 1$ up until some time t^* and then $u^*(t) = 0$ from that time onward, where t^* is defined by the equation

$$t^* = T + \frac{1}{\mu} \ln \left(1 - \left(\mu \Big/ \left(\frac{\partial b}{\partial y} + R \frac{\partial b}{\partial \bar{y}} \right) \right) \right). \quad (12)$$

5. DISCUSSION

The maximum principle is an important tool for addressing problems of dynamic optimization. Its use in evolutionary biology arises naturally in many contexts because many biological characters of interest are 'dynamic' (Perrin & Sibly 1993). Similarly, Hamilton's rule is an important conceptual and analytical tool for understanding evolution in the context of kin selection. Its use in evolutionary biology also has been widespread and fruitful. The ideas presented in this paper are an attempt to unify these two tools so that the insights available through each might be combined.

One of the nice results is the dynamic version of Hamilton's rule (equation (9 c)). Using the Hamiltonian as the fitness function, Hamilton's rule must be satisfied at all times (see also McNamara *et al.* 1994). The simplicity of this result is appealing. Because dynamic optimization models are often computationally difficult even without kin selection, it is significant that the incorporation of kin selection still results in a functional analytical tool. Additionally, the dynamic version of Hamilton's rule can serve as a conceptual tool as well, even without obtaining explicit solutions for the ESS strategy $u^*(t)$ (e.g. see equations (11 a)–(11 c)).

Although our exposition was couched largely in terms of the evolution of general life history attributes, these ideas can be used to construct kin selection models for the evolution of any dynamic character. For example, we are using these ideas to model the evolution of temporal patterns of cooperation or altruism (Day & Taylor 1997). Most previous theoretical accounts for the evolution of cooperation seek a single, evolutionarily stable level of cooperation. However, when individuals interact over a period of time, maintaining a constant level of cooperation or altruism is not necessarily the best strategy.

Although there are a wide variety of biological questions that can be addressed using this framework, certain caveats should also be born in mind. Our assumption of a monomorphic population greatly simplifies the results but it also implies an underlying degree of symmetry among group members that may not always be valid. For example, the approach would have to be altered if there are asymmetric interactions between different types of individuals

within a group. This is an important extension that we are presently exploring.

Additionally, the present results make the assumption that relatedness, R, remains constant over the interval of time in question. Since R is the average relatedness over all patch members including the actor, this assumption is problematical if the number of individuals within the patch changes. Thus for models which include mortality (such as the plant life history example above) this assumption is reasonable only if mortality is regarded primarily as 'patch' mortality or if the number of individuals within a patch is large and individual mortality rates are low. Dynamic models which allow patch size, and thus relatedness, to change through time are mathematically more difficult but are biologically important and we are currently considering how to extend the present results in this direction.

Also, the above results have been presented for univariate 'state' and 'control' variables, $y(t)$ and $u(t)$. For many biological questions, one requires multivariate state and control variables to adequately describe individuals (e.g. perhaps an individual can allocate resources to several different organs; there would need to be a state and control variable for each). In the proof of the above theorem we extend the approach to allow for vector state and control variables as well as more general fitness functions (Day & Taylor, unpublished results).

Lastly, we note that in the above formulation, the allocation strategy (or control variable) $u(t)$ is considered to be genetically programmed for each individual. That is, each individual is programmed with a strategy $u(t)$ that it uses throughout the season and individuals do not deviate from this course of action (an 'open-loop' strategy; Basar & Olsder 1982). This will be accurate only to the extent that the system is deterministic and individuals cannot change their strategy during the season in response to their current situations. Including the effects of stochasticity increases the complexity of models significantly. The ESS strategy then must be specified in a conditional or feedback form to account for all possible situations that an individual might encounter at all times (a 'closed-loop' strategy; Basar & Olsder 1982). In such cases one would likely have to employ numerical procedures.

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