The Evolution of Temporal Patterns of Selfishness, Altruism, and Group Cohesion

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ABSTRACT: In intrademic selection models, individuals interact in groups, and this interaction phase is usually treated as a point in time. It is likely, however, that interactions take place over some time period. If selfishness is treated as a quantitative trait and this time period is explicitly considered, how does the evolutionarily stable strategy (ESS) level of selfishness or altruism change through time? Our main result is that, under biologically reasonable conditions, the ESS level of selfishness is expected to increase. Two of the assumptions behind this result are that there is a finite time horizon on the life of the group and that reproduction occurs continuously throughout the time period in question. If there is no time horizon or if all reproductive output is concentrated at the end of the time period, the ESS level of selfishness is constant. Our main result suggests that care must be taken when interpreting empirical data that is collected at different times and that altruism will often be most pronounced when groups first form. The model also demonstrates that, when individuals interact repeatedly over time, the evolution of altruism can be promoted through a mechanism other than reciprocity.

Keywords: altruism, selfishness, reproductive value, inclusive fitness, control theory, evolutionarily stable strategy.

Models of intrademic selection provide an important and simple tool for understanding the evolution of altruistic and selfish behavior (Price 1970, 1972; Hamilton 1975; Wilson 1975, 1980; Wade 1985; Frank 1986; Wilson 1990 and references therein). In these models, organisms are imagined to live in groups within a larger metapopulation, and variation within and among groups allows natural selection to act at both the individual and the group

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level. In perhaps the simplest scenario, an individual's fitness is assumed to increase with its degree of selfishness and to decrease as the average level of selfishness in the group increases (see, e.g., Frank 1995). Altruistic behavior can evolve if there is sufficient variation in average selfishness among groups. Group selection models and kin selection models of patch-structured populations can both be viewed as examples of intrademic selection models differing only in the way that they describe the variation within and among groups, the latter using principles of relatedness (Wade 1985; Breden 1990; Wilson and Dugatkin 1997).

In intrademic selection models, groups are formed from a global pool of individuals. Fitness-determining interactions then take place within these groups, and all reproductive output enters the global pool from which new groups form (Wilson 1990). Most models assume that each individual makes a single "decision" during the interaction phase. For example, supposing selfishness (or altruism) is a quantitative trait, each individual exhibits a single level of selfishness. This assumption is made largely for simplicity, but in many situations individuals are faced with the same "decision" repeatedly during the period of time that the group exists. For example, individuals in insect colonies can act altruistically or not continuously throughout the life of the colony. Similarly, when multiple strains of a virus infect a host, each virus can exhibit selfishness or not continuously throughout the period of infection. In such cases what is the evolutionarily stable strategy (ESS) temporal sequence of decisions? Should the level of selfishness predicted from models allowing single decisions simply be maintained over time, or should the level of selfishness increase or decrease during the existence of the group? If selfishness is expected to change, then care must be taken when interpreting empirical data. High selfishness might be found in one instance and low selfishness in another simply because the observations were made at different times. If so, this implies that altruism should be easiest to detect at a certain stage in a group's existence as well.

This aspect of the evolution of altruism appears to have received little attention, and it is the focus of the present article.

To address this question we need an intrademic selection model that allows individuals to vary their selfishness through time. One class of such models in which individuals are faced with the same "decision" repeatedly are those based on the game, iterated prisoner's dilemma (IPD; Axelrod and Hamilton 1981; Axelrod 1984; Brembs 1996). In these models, however, repeated interactions promote the evolution of altruism through reciprocity (Mesterton-Gibbons and Dugatkin 1992), whereas our purpose for examining repeated interactions is different. We assume that intrademic selection (group selection in Mesterton-Gibbons and Dugatkin 1992) is the primary factor responsible for the evolution of any altruistic behavior (rather than reciprocity), and within this context we wish to ask how the ESS level of selfishness changes during the existence of groups. Models based on IPD do not accommodate this type of question easily and consequently we use an alternative framework (Day and Taylor 1997). This framework is better suited to the question at hand, and, as it turns out, it also reveals that repeated interactions can promote the evolution of altruism through a mechanism other than reciprocity.

Even the simplest models that allow individuals to interact over a period of time are considerably complex. For example, determining which strategies are evolutionarily stable in the simplest versions of IPD is difficult (Farrell and Ware 1989). Because the question of interest here is more difficult yet, some simplifying assumptions are necessary to make any progress. Our primary simplification is that we do not allow individuals to learn. For example, in IPD, individuals can use knowledge of their opponent's past behavior in deciding what to do next; in fact it is learning that allows reciprocity (Axelrod and Hamilton 1981; Axelrod 1984). We assume that such learning is not possible and that individuals effectively "choose" their temporal strategy when the groups form. This assumption may be too restrictive for some situations, but in many cases it is not unreasonable. Obviously, if it is not possible to gain information from other individuals in the group, or if it is not possible to use available information, then this assumption is not problematic. It is also reasonable, however, when the plastic response of behavior to available information is slow relative to the duration of group existence. A wide range of traits can be considered within the framework of altruistic behavior, including dispersal rate (Hamilton and May 1977; Taylor and Frank 1996), sex ratio (Wilson and Colwell 1981), life-history characteristics (Mirmirani and Oster 1978; Day and Taylor 1997), virus replication

schedules (Eshel 1977; Axelrod and Hamilton 1981; Sasaki and Iwasa 1991; Frank 1992), and meiotic drive strategies (Axelrod and Hamilton 1981; Kloss and Nesse 1992; Day and Taylor 1998), to name a few. For many of these traits the assumption of a slow or nonexistent plastic response to available information is probably acceptable.

Neglecting learning can also provide many important benefits. Because models involving IPD have dominated the literature in this area we believe that it is worth considering the insight that can be provided by models with alternative simplifying assumptions (Dugatkin et al. 1992; Connor 1995). The assumption of no learning is a good choice for two reasons. First, it simplifies the model enough that we can easily increase its generality in other respects. For example, it allows for any degree of relatedness among the N members of each group, for a greater generality in fitness functions, and most important, it allows the behavior of group members to affect the likelihood of future interactions. Second, it removes the possibility of reciprocity as it occurs in IPD, and therefore we can determine how repeated interactions can enhance the evolution of altruism through different mechanisms. Also, perhaps equally important, it allows a model that is still amenable to an intuitive analysis.

The Basic Model

The model we develop is used as a general exploratory tool, similar to the way in which IPD has been used, and is not meant represent a specific biological system. It is helpful however, to have particular biological examples in mind when trying to intuit the results. Therefore, when appropriate, we use specific biological examples to illuminate key points. It should be borne in mind, however, that the model is intended to capture the general principles at play rather than the specific details of any particular system.

We follow the tradition of patch-structured ESS models by considering the fate of rare mutants in a monomorphic population (Maynard Smith and Price 1973; Maynard Smith 1982; Taylor and Frank 1996; Day and Taylor 1997). The modeling framework that we use is a combination of inclusive fitness theory (Hamilton 1964) and noncooperative dynamic game theory (Basar and Olsder 1982), as detailed in an earlier article of ours (Day and Taylor 1997). This framework provides an inclusive fitness approach for modeling dynamic games between relatives.

Suppose individuals associate into groups of size N and remain in these groups over a continuous period of time from 0 to T. We consider a single quantitative trait,

$z(t)$, which is interpreted as the degree of selfishness, and choose a scale of measurement so that z lies between 0 and 1. We take $z = 0$ to be the minimum possible selfishness (maximum altruism) and $z = 1$ to be the maximum possible selfishness (minimum altruism). Note that z is a function of time because we are interested in determining how the ESS value of z changes over the interval $0-T$. We also allow individuals within the group to be related and define R as the expected relatedness between two randomly chosen group members with replacement. Consequently, if groups are randomly formed, $R = 1/N$ (Frank 1996; Taylor and Frank 1996; Day and Taylor 1997). Altruism in such models is sometimes termed *weak altruism* (Wilson 1990). We also note that, the predictions of such phenotypic models of kin selection are compatible with those of more explicit genetic treatments provided that selection is weak and, in the case of diploidy, genetic effects are additive (various such results are summarized in Taylor 1996; T. Day and P. D. Taylor, unpublished data).

Following standard life-history theory (Roff 1992; Stearns 1992), we consider an individual's fitness to be the sum from 0 to T of its probability of survival to time t, $l(t)$, multiplied by its fecundity at time t, m, that is, $W = \int_0^T lmdt$. This assumes that reproductive output is realized continuously as it is produced over time (see Kozlowski and Wiegert 1986). Below, in the section titled "Variations of the Model," we consider an alternative scenario whereby all reproductive output is realized at the end of the time period. There we also consider the case where $T = \infty$. A finite time horizon, T, would apply to organisms for which the groups have a maximum life span. For example, this would be true for a patch-structured population of annual plants (e.g., *Impatiens capensis*) or a population of annual bumblebee colonies (e.g., *Bombus terrestris*), where T represents the end of the season. The case $T = \infty$ would apply when there is no fixed time horizon, as might be the case for populations that reproduce approximately continuously in an aseasonal environment. In either case, however, we assume that all reproductive output goes to form new groups, as is the case in all intrademic selection models.

How should survival, $l(t)$, be specified? It is helpful to distinguish between two types of mortality: patch mortality and individual mortality. It is probably reasonable to assume that there is some type of patch mortality because a high average selfishness might decrease the probability that the patch as a whole survives. For example, if the patch is a host organism, then a high average selfishness, $\bar{z}$, (e.g., resource exploitation) would increase the mortality rate of the host. Alternatively, a high average selfishness might result in the group dissociating sooner than would otherwise occur. Provided that members of the

dissociated group do not enter the global population, these two scenarios are equivalent. In this way, the strategies of group members affect the probability of future encounters with one another. At the same time, individuals within the patch might suffer variable mortality depending on their individual selfishness. Accounting for such individual mortality is very difficult because patch size will then change, and the calculation of an individual's expected fitness then entails knowledge of the probability distribution of patch size through time. Therefore, as a first attempt, we restrict attention to patch mortality only and assume that patch mortality rate at any time depends on $\bar{z}$ at that time (i.e., $\mu(\bar{z})$). The effect of allowing individual mortality as well is considered in the discussion. The probability that the patch survives until time t is, therefore,

$$l(t) = \exp\left(-\int_0^t \mu d\tau\right). \tag{1}$$

We allow an individual's fecundity, $m(z(t), \bar{z}(t))$, at any time to depend on its level of selfishness as well as on the average level of selfishness in its group at that time. With these assumptions, an individual using the temporal strategy $z(t)$ in a patch where the average temporal strategy is $\bar{z}(t)$ has a fitness given by

$$W(z, \bar{z}) = \int_0^T l(t)m(z(t), \bar{z}(t))dt. \tag{2}$$

To make it reasonable for z to represent selfishness we make the further restrictions:

$$d\mu/d\bar{z} > 0, \tag{3a}$$

$$\partial m/\partial z > 0, \tag{3b}$$

and

$$\partial m/\partial \bar{z} < 0. \tag{3c}$$

Inequality (3a) states that the patch mortality rate increases as the average selfishness in the patch increases. Inequalities (3b) and (3c) state that an individual's fecundity increases as its selfishness increases but decreases as the patch average selfishness increases. Thus if an individual decreased its selfishness at time t it would be sacrificing its own current reproduction to increase that of other individuals and also to increase the survival prospects and thereby the future reproduction of the patch as a whole.

The ESS level of selfishness over time can be determined from the fitness function (2) using a combination of inclusive fitness and control theory (Day and Taylor 1997; app. A). However, because the mathematical concepts involved in control theory are unfamiliar to many biologists, we present a heuristic, intuitive argument in

the text and relegate the more careful formulation of the model and its analysis to the appendices.

Our heuristic argument is based on reproductive value, $V(t)$, which is simply an individual's expected future reproductive output at time t, given it has survived to time t (Fisher 1958). This is easily expressed using the integral in (2) as

$$V(t) = \frac{1}{l(t)} \int_t^T l(\tau) m(z(\tau), \bar{z}(\tau)) d\tau. \quad (4)$$

Now if we consider what happens in a small interval of time from t to $t + \Delta t$, we can decompose equation (4) into current plus expected future reproductive output (Williams 1966; Schaffer 1974; Taylor et al. 1974). The current output over the small time interval is $m(z(t), \bar{z}(t))\Delta t$. The expected future reproductive output is found by noting that, with probability $1 - \mu(\bar{z}(t))\Delta t$, the individual will survive from t to $t + \Delta t$ and then have a reproductive value of $V(t + \Delta t)$. Therefore, adding both terms gives

$$V(t) \cong m(z, \bar{z})\Delta t + (1 - \mu(\bar{z})\Delta t)V(t + \Delta t). \quad (5)$$

If the behavior of an individual does not affect the fitness of other individuals and there is no density-dependent population regulation, it is well known that choosing the entire function $z(t)$ that maximizes fitness is equivalent to choosing the value of z at each time that maximizes reproductive value (RV) at that time (Williams 1966; Taylor et al. 1974; Schaffer 1974, 1979). In other words, if we consider any time interval t to $t + \Delta t$ along the optimal strategy, it is not possible for an individual to increase its RV at that time by altering z within that time interval. Here, however, things are more complicated because fitness (eq. [2]) is frequency dependent, and the interacting individuals are related. We can proceed in analogy with the simple case, however (and get the correct answer!), by supposing that, for any time interval along the ESS strategy $z^*(t)$, it is not possible for an individual to increase its inclusive RV by altering z within that time interval. An expression for the inclusive RV effect of an individual altering its z value within the interval t to $t + \Delta t$ can be constructed in analogy with the construction of the standard inclusive fitness effect (see below; Hamilton 1964). To avoid the use of additional jargon, below we simply refer to the "inclusive RV effect" as the "inclusive fitness effect."

Proceeding, then, from equation (5) the inclusive fitness effect of a small increase in selfishness through current reproductive output is simply $(\partial m/\partial z + R\partial m/\partial \bar{z})\Delta t$. The inclusive fitness effect of a small increase in selfishness through expected future reproductive output is $-(Rd\mu/d\bar{z}V(t + \Delta t))\Delta t$; note that all par-

tial derivatives are evaluated at the population-wide strategy, $\hat{z}(t)$ (i.e., $z(t) = \bar{z}(t) = \hat{z}(t)$). Thus, dividing by Δt and considering the limiting case of small time steps, this suggests that the continuous-time inclusive fitness effect at time t, $\Delta W_{incl}(t)$, can be written

$$\Delta W_{incl}(t) = \left(\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}} - R\frac{d\mu}{d\bar{z}} V(t) \right)_{z=\bar{z}=\hat{z}}. \quad (6)$$

In other words, this is the inclusive fitness effect of an individual increasing its selfishness by a small amount at time t (given it has survived to time t), when in a monomorphic population using strategy $\hat{z}$. Provided the ESS is not $z^* = 0$ or $z^* = 1$, the inclusive fitness effect (6) evaluated at the ESS (i.e., $\hat{z} = z^*$) must equal 0 (Taylor and Frank 1996). Note, however, that (6) is a function of time so that this condition must hold at every time t between 0 and T. This is a dynamic (i.e., time-dependent) version of Hamilton's Rule (Day and Taylor 1997).

The inclusive fitness effect (6) captures an important trade-off. Since $\Delta W_{incl}(t) = 0$ at all times along $z^*(t)$ (except if $z^* = 0$ or 1), the ESS level of selfishness balances current and future inclusive fitness effects at all times. This suggests that the ESS level of selfishness will change through time whenever the nature of this trade-off changes through time. Since neither m nor μ is explicitly time dependent, consideration of equation (6) suggests that this should occur only when an individual's reproductive value, $V(t)$, changes through time.

At this stage we could choose specific functions for m and μ and characterize the ESS strategy by determining how the above trade-off changes through time. Instead, however, we show that some general qualitative predictions can be made by placing only mild restrictions on m and μ. Some of these are technical and of little biological consequence (table 1). Others, however, are motivated by what is biologically reasonable.

From equation (6) it is clear that the nature of the functions $(\partial m/\partial z + R\partial m/\partial \bar{z})_{z=\bar{z}=\hat{z}}$ and $d\mu/d\bar{z}|_{\bar{z}=\hat{z}}$ is what determines how current and future inclusive fitness effects trade off at any particular time. The restrictions we make are

$$\frac{d}{d\hat{z}} \left(\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}} \right)_{z=\bar{z}=\hat{z}} < 0 \quad (7a)$$

and

$$\frac{d}{d\hat{z}} \left(\frac{d\mu}{d\bar{z}} \right)_{\bar{z}=\hat{z}} \geq 0. \quad (7b)$$

To interpret these conditions, consider a monomorphic population at $\hat{z}$. Condition (7a) on m means that the inclusive fitness effect through current reproductive output

Table 1: Technical assumptions regarding the fecundity and mortality functions

Function	Assumption
$m(z, \bar{z})$	It has continuous derivatives up to second order on $(0, 1]$
	$m(z, \bar{z}) > 0$ and bounded for $\hat{z} \in [0, 1]$.
$\mu(\bar{z})$	It has continuous derivatives up to second order on $(0, 1]$
	$\mu(\hat{z}) > 0$ and bounded away from zero for $\hat{z} \in [0, 1]$
	$\mu_{\bar{z}}$ bounded on $[0, 1]$.

of an increase in selfishness is greater in an altruistic population (i.e., $\hat{z}$ near 0) than in a selfish population (i.e., $\hat{z}$ near 1). In others words, there are diminishing returns in this inclusive fitness effect as the background level of selfishness increases. We have already specified patch mortality rate as an increasing function of average selfishness, and therefore condition (7b) on μ means that patch mortality rate is either increasing linearly or increasing and concave up. That is, the effect of increased selfishness is higher when the level of selfishness is high. Both of these restrictions seem biologically reasonable.

Under these conditions it can be demonstrated that $z^*(t)$ is nondecreasing, and in fact it is strictly increasing as long as $0 < z^* < 1$. In particular, this implies that it is never possible for a constant, intermediate level of selfishness or altruism to be an ESS. The formal argument for this is presented in appendix B, but the idea behind the argument deserves mention. Recall that $z^*(t)$ will change only if an individual's RV, $V(t)$, changes through time. Since time is finite, $V(t)$ clearly decreases near the time horizon. It can also be easily shown, however, that $V(t)$ is strictly decreasing at all times (app. B, eq. [B9]). Now the ESS value of z must keep equation (6) equal to 0; therefore, if $V(t)$ decreases over time, then it follows easily from inequalities (7a) and (7b) that z^* must increase.

As an example, suppose our assumptions approximate reality for a population of annual bumblebee colonies. The model then predicts that as the end of the season draws near, the level of cooperation among individuals within a colony should decrease (selfishness should increase). When the colony first forms, the RV of an individual is large, and it is therefore important to keep mortality low so that this expected future fitness can be realized. This means having a high level of cooperation to keep colony mortality rate low. As the end of the season is approached, however, RV decreases until at $t = T$, $V(T) = 0$, and there is no future fitness remaining. The effect of having a high colony mortality rate therefore becomes unimportant, and, consequently, the optimal level of cooperation declines. Interestingly, this is exactly what

happens in *Bombus terrestris* colonies (van der Bloom 1985; Duchateau and Velthuis 1988).

The model also predicts that, if there is an upper and lower bound on the level of cooperation possible, then we never expect to see individuals within the colony exhibiting a constant, intermediate level of cooperation over time. All of these results hold for any m and μ satisfying the above restrictions (7a) and (7b), but other choices may generate the same predictions as well.

As an aside, we note that equation (6) also suggests that if the strategies of group members do not affect the expected life of the group, then the ESS level of selfishness is constant through time. In this case conditions (3b) and (3c) hold but condition (3a) does not ($d\mu/d\bar{z} = 0$). Therefore, equation (6) becomes

$$\Delta W_{\mathrm{incl}}(t) = \left(\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}} \right)_{z=\bar{z}=\hat{z}}. \tag{8}$$

Notice that an individual's RV is no longer relevant for determining the ESS. In the context of the bumblebee example, if the degree of cooperation within a colony did not affect the likelihood of realizing future reproductive success, then there would be no "reason" for individuals to alter their level of cooperation through time. Although an individual's RV still declines to 0, the likelihood of it obtaining future reproduction is not influenced by its strategy, and therefore there is no trade-off between the present and the future. This seems unlikely to be true for social insects, but it is possible that group mortality rate is independent of the group average selfishness in other cases.

Finally, to get a feeling for how the ESS level of selfishness is altered when other factors change, we consider a specific mathematical example: $m(z, \bar{z}) = z/\bar{z}$ and $\mu(\bar{z}) = \mu_0 + \beta\bar{z}$. These functions might be suitable when an individual using z in a $\bar{z}$ group gains a share $z/\bar{z}$ of local resources (per unit time), and a high average resource exploitation rate $\bar{z}$ results in a high group mortality (Frank 1995). It is easily checked that these choices satisfy our assumptions, and using the framework in ap-
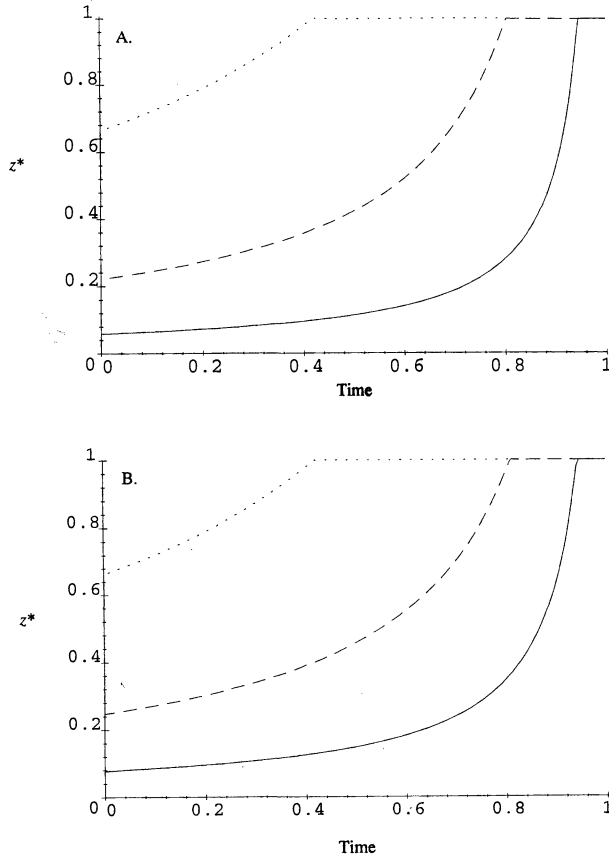
Figure 1: The ESS level of selfishness over time. Results are using the functions $m(z, \bar{z}) = z/\bar{z}$ and $\mu(\bar{z}) = \mu_0 + \beta\bar{z}$. Time units have been chosen so that $T = 1$, and $\mu_0 = 0.1$ for all results. *A,* The ESS level of selfishness through time for different degrees of relatedness and $\beta = 1$: *dotted line,* $R = 0.7$; *dashed line,* $R = 0.85$; and *solid line,* $R = 0.95$. *B,* The ESS level of selfishness through time for different values of β and $R = 0.7$. A large value means that an increase in the group average level of selfishness decreases the likelihood of future interactions by a large amount. *Dotted line,* $\beta = 1$; *dashed line,* $\beta = 3$; and *solid line,* $\beta = 5$.

pendix A (Day and Taylor 1997), the ESS strategy $z^*(t)$ is readily determined (fig. 1). Notice that, in this example, the ESS level of selfishness $z^*(t)$ increases through time and reaches the maximum level sometime before the group's time horizon T. Also, as expected, at any particular time the level of selfishness decreases as relatedness increases, although the qualitative temporal trend of increasing selfishness always remains. Figure 1*B* also demonstrates that when changes in average selfishness have large effects on group mortality rate, the ESS level of selfishness is, on the whole, lower. Again, however, selfishness always increases through time.

Variations of the Basic Model

What if T = ∞?

In some situations it might be reasonable to suppose that groups can persist indefinitely. In such cases we have $T = \infty$. Note, however, that this does not imply that groups persist forever because there is still mortality. Rather, it means that there is no fixed time horizon at which the group dissociates. Under this assumption the ESS level of selfishness, $z^*(t)$, is constant through time (app. B). This is intuitively reasonable as well. Since there is no time horizon, an individual's RV is constant. Regardless of the time t, the future always "looks the same." As a result, the trade-off between current and future inclusive fitness effects does not change through time and therefore neither does the level of selfishness.

What If All Reproductive Output Is Realized at t = T?

In some situations individuals' reproductive outputs might not be realized until the patch dissociates at time T. For example, perhaps all reproductive output is released at the end of a season, and if a patch happens to die before that time its members obtain zero output. Alternatively, suppose the development of a single viable offspring requires the investment of energy over a constant and nonnegligible development time and that offspring that obtain more nourishment over this period are more valuable. In this case the assumption of continuous reproductive output is not be acceptable, and this situation is equivalent to that where all output is released at the end of the season with T now representing development time. In either case, how does the ESS level of selfishness change during the existence of the group?

This problem can be handled using a control theoretic setup as well (app. C). Again, however, we present a heuristic argument here. The easiest way to visualize this problem is to imagine that each individual produces reproductive output continuously over the entire interval from 0 to T but that it is stored and not released until the time horizon is reached. Let $X(t) = \int_0^t m(z, \bar{z})d\tau$ denote the amount of reproductive output stored up by time t but not yet released. The fitness function in this case is then given by

$$W(z, \bar{z}) = l(T)X(T) \qquad (9)$$

since an individual must survive to the time horizon to realize any fitness (and this occurs with probability $l(T)$), and in this event it realizes a total reproductive output of $X(T)$.

We can proceed in the same way as previously and define an individual's reproductive value at time t. This is

simply the probability of surviving from time t to the time horizon, multiplied by $X(T)$:

$$V(t) = \frac{l(T)}{l(t)} X(T) \tag{10a}$$

$$= \frac{l(T)}{l(t)} \left(X(t) + \int_t^T m(z(\tau), \bar{z}(\tau)) d\tau \right). \tag{10b}$$

We have split $X(T)$ in equation (10b) into two pieces, the output stored before and after time t, to emphasize that in order to specify an individual's reproductive value at time t we now need to know $X(t)$ as well as t. For example, two individuals, both at time t, might nevertheless differ in expected future reproductive output because they differ in the amount of reproductive output stored by time t. Now, again we are interested in calculating the inclusive fitness effect of an individual increasing z within a small time interval. Thus, considering the interval t to $t + \Delta t$, we can approximate (10b) as

$$V(t) = \frac{l(t + \Delta t)}{l(t)} \frac{l(T)}{l(t + \Delta t)}$$
$$\times \left(X(t) + \int_t^{t+\Delta t} m(z, \bar{z}) d\tau + \int_{t+\Delta t}^T m(z, \bar{z}) d\tau \right) \tag{11a}$$

$$\cong (1 - \mu(\bar{z}) \Delta t) \frac{l(T)}{l(t + \Delta T)}$$
$$\times \left(X(t) + m(z, \bar{z}) \Delta t + \int_{t+\Delta t}^T m(z, \bar{z}) d\tau \right). \tag{11b}$$

Expression (11b) highlights the components of $V(t)$ that will change when z is changed within the interval t to $t + \Delta t$. The inclusive fitness effect of a small increase in z in this interval is then (Taylor and Frank 1996)

$$(1 - \mu(\bar{z}) \Delta t) \frac{l(T)}{l(t + \Delta t)} \left(\frac{\partial m}{\partial z} + R \frac{\partial m}{\partial \bar{z}} \right) \Delta t$$

$$- R \frac{d\mu}{d\bar{z}} \Delta t \frac{l(T)}{l(t + \Delta t)} \left(X(t) + m(z, \bar{z}) \Delta t + \int_{t+\Delta t}^T m(z, \bar{z}) d\tau \right),$$

or, dividing by Δt and taking the limit as Δt becomes small,

$$\Delta W_{\text{incl}}(t) = \left[\frac{l(T)}{l(t)} \left(\frac{\partial m}{\partial z} + R \frac{\partial m}{\partial \bar{z}} \right) - R \frac{d\mu}{d\bar{z}} V(t) \right]_{z = \bar{z} = \hat{z}}. \tag{12}$$

Notice the similarity between equations (12) and (6). The only difference is that the inclusive fitness effect through current reproduction in (6) is now multiplied by $l(T)/l(t)$. The factor $l(T)/l(t)$ is the probability of survival from time t until the time horizon and gives the "value" of a unit of current output stored at time t in terms of

realized reproductive output. With continuously released reproduction, a unit of current output is worth an entire unit of realized reproduction. When reproduction is released at the time horizon, however, this is no longer true. Because there is the possibility of death prior to the time horizon (which results in zero realized reproductive success), a unit of current output must be weighted by the probability of actually surviving to realize it.

To determine the ESS strategy, we need to know how changes in both V and $l(T)/l(t)$ through time affect the trade-off in (12). From equation (10), $V(t) = X(T) l(T) / l(t)$ at all times; the expected future reproductive success at time t is the product of the probability of survival from t until the time horizon and the expected output at the time horizon, $X(T)$. Therefore, both $l(T)/l(t)$ and $V(t)$ change through time in the same way, and this causes the trade-off in (12) to remain constant. This means that $z^*(t)$ remains constant as well (app. C).

Discussion

General Conclusions

Most models of intrademic selection treat the stage of the life cycle when individuals associate into groups as a point in time. In most situations, however, groups actually exist over a period of time, and therefore individuals have the opportunity to interact with other group members continuously for some duration. The results presented here demonstrate that if this temporal nature of groups is explicitly incorporated into intrademic selection models, some general predictions can be made with regard to how we expect the level of selfishness and altruism to change systematically during this period.

If groups persist indefinitely after they are formed, then the ESS level of selfishness is constant over this period. However, if there is a finite time horizon for a group's existence, as would occur for annual organisms, for example, the situation changes. In this case, when more selfish strategies result in greater group mortality, the ESS level of selfishness can never decrease over time and can remain at a constant level only if it has attained some maximum value beyond which it cannot increase. This result applies to situations in which reproductive output is realized continuously as it is produced. However, if all reproductive output is realized only at the end of the group's existence, then a constant level of selfishness or altruism is the ESS.

There are several ways in which the present model might be extended to consider other, more sophisticated biological scenarios. For example, the fecundity and mortality functions can be made to vary with time to model phenomena such as senescence or growth. With senes-

cence, m will decrease and/or μ will increase with time. In this case we would expect predictions to be qualitatively similar to the above results for finite T, even if groups persist indefinitely, because a finite group time horizon is really an extreme form of senescence that occurs at a point in time.

The present model assumes that within-patch mortality is absent or it is low and group size is large so that group size remains approximately constant (Day and Taylor 1997). It would be interesting to incorporate within-patch mortality by allowing patch size to change through time. The additional complexity that this introduces makes it likely that only some special cases could be handled. In some situations it seems plausible that the temporal decrease in patch size that results will increase average patch relatedness and thereby favor an increase in altruism through time. Alternatively, if individual mortality is positively related to an individual's level of altruism, we might expect groups to contain a smaller proportion of altruists as time progresses as a result of differential culling. It is unclear, however, how this would affect the level of altruism exhibited by the surviving members of the group (we thank R. Holt for this suggestion). In fact, in this case it would be useful to distinguish between the temporal trend in altruism at two levels: temporal changes in altruism at the group level and temporal changes in altruism at the level of surviving individuals since these need not be the same. Clearly, a more careful treatment is required to answer these questions, and as of yet we have not managed to obtain any results. Future work in this direction is ongoing, however, and we are considering the effects of allowing forms of class structure (e.g., male/female, dominant/subordinate, etc.) among individuals as well.

Very little data are yet available to test the model adequately, but there is some suggestive evidence from different sources. As already mentioned, in some annual bumblebee colonies there is a breakdown in cooperation near the end of the season, and individuals become increasingly aggressive (van der Bloom 1985; Duchateau and Velthuis 1988). The situation is more complicated than in the present model, however, in that there are different classes of individuals and colony size changes. Another example involves trisomy in humans. It has been hypothesized that the increase in frequency of trisomic pregnancies in humans with increasing maternal age results from increased chromosomal drive (Axelrod and Hamilton 1981; Kloss and Nesse 1992; Day and Taylor 1998). Here, a female is thought of as a patch and individual chromosomes exhibit an increasingly aggressive "drive" strategy as the female ages.

Other evidence might be sought in viral infections. If multiple strains of virus infect a host we might expect an increasing level of virulence as the host ages (Eshel 1977; Axelrod and Hamilton 1981; Sasaki and Iwasa 1991; Frank 1992). Also, studies of the annual plant *Impatiens capensis* have suggested that individual plants may sacrifice personal size to increase the survival of their group (Stevens et al. 1995). An examination of this species for seasonal trends in such "altruistic" behavior might prove interesting as well. Aside from looking for temporal trends in selfishness and altruism, the present model might be tested by examining whether its assumptions are valid. In particular, for our model to explain temporal declines in altruism, group mortality rate must increase as the average level of altruism decreases. If a temporal decline in altruism is observed when this assumption is not met, then other explanations must be sought. Similarly, it must also be true that reproductive output is realized continuously during the existence of the group for our results to explain such temporal trends.

Repeated Interactions Can Promote the Evolution of Altruism through a Mechanism Other Than Reciprocity

At least three factors have been identified that can promote the evolution of altruism and cooperation (Dugatkin et al. 1992; Mesterton-Gibbons and Dugatkin 1992; Connor 1995): reciprocity—this is the effect at the core of models based on IPD; group selection—this is the effect at the core of the present model; and by-product mutualism—this is the effect whereby cooperative behavior is an incidental by-product of individual selfishness. These three factors have been proposed in addition to that of kin selection, but our model effectively treats kin selection and group selection as a single factor, which we term *intrademic selection*.

The vast majority of the literature on models that involve repeated interactions is based on the game of iterated prisoner's dilemma. In this game, opponents meet repeatedly with a fixed probability. Because individuals can learn, they can condition their behavior at any time on the past behavior of their opponent. In this way the behavior exhibited by an individual at any time not only affects its current fitness but its future fitness as well because it affects the future strategy of its opponent. If it is likely that the opponents meet again, then each individual may be more likely to cooperate in the hope of enticing future cooperation by their opponent. As Axelrod (1984, p. 126) has stated, "Mutual cooperation can be stable if the future is sufficiently important relative to the present." Thus, in models of IPD, the ability to learn allows repeated interactions to enhance the evolution of altruism through reciprocity.

The present results demonstrate that repeated interactions can promote the evolution of altruism through a

different mechanism as well. The primary factor responsible for the evolution of altruism in our model is intrademic selection, and this effect is present even in the absence of repeated interactions. For example, at the time horizon there are no future interactions, yet a certain degree of altruism might still be favored through intrademic selection. This is represented by the balance being struck between the first two terms of equation (6) at $t = T$ (the third term is 0 because $V(T) = 0$). Thus we can determine how repeated interactions among group members affect the ESS level of altruism here by comparing the level of altruism at the time horizon with that at earlier times.

In general, altruism will be greater at earlier times than at the time horizon because $z^\star(t)$ is nondecreasing. As with reciprocity, greater altruism is favored when future reproductive output is sufficiently important relative to current reproductive output. Note, however, that under reciprocity the balance between current and future reproduction is mediated indirectly through the future behavior of opponents. Here such reciprocity is not possible, and the balance between current and future reproduction is mediated through the effect that current behavior has on the probability that the group remains intact. This mechanism is another route through which repeated interactions can promote the evolution of altruism.

Acknowledgments

APPENDIX A

An Outline of the Inclusive Fitness-Control Theoretic Approach

The following is a brief synopsis of the modeling methodology presented by us elsewhere (Day and Taylor 1997), customized for the present purposes.

Suppose the fitness of strategy z in a patch with an average of $\bar{z}$ is given by a function of the form

$$W(z, \bar{z}) = \int_0^T l(t) m(z, \bar{z}) dt + G(l(T), X(T)). \quad (A1)$$

In the terminology of economic control theory, $z(t)$ is a control variable and $l(t)$ and $X(t)$ are state variables, the integral is an intermediate reward, and the function G is

a terminal reward. For the model with continuous reproductive output (app. B), $G(l(T), X(T)) = 0$ and there is only one state variable required (i.e., $l(t)$). When all reproductive output is realized at $t = T$ (app. C), both state variables are required, and we have $G(l(T), X(T)) = l(T)X(T)$ with the integral in (A1) set to 0. The state variables change through time according to differential equations specific to the model.

The first step in characterizing the ESS strategy, $z^\star(t)$, is to construct the Hamiltonian function. (Note that this is named after the mathematician William R. Hamilton, not the evolutionary biologist William D. Hamilton.) This is done by taking the integrand of (A1) and adding to it the equations for the state variable dynamics, each multiplied by a so-called costate variable:

$$H = lm + \lambda^x \frac{dX}{dt} + \lambda^l \frac{dl}{dt}. \quad (A2)$$

The costate variables have interesting biological interpretations (León 1976; Iwasa and Roughgarden 1984; Perrin and Sibly 1993; Day and Taylor 1997). In particular, for the present article, λ^l represents an individual's reproductive value, V (app. B), and λ^X represents $l(T)/l(t)$, the probability of surviving from time t until the time horizon (app. C). The inclusive fitness effect of an individual increasing its strategy slightly at time t, when in a population monomorphic at $\hat{z}$, is given by

$$\left(\frac{\partial H}{\partial z} + R \frac{\partial H}{\partial \bar{z}} \right)_{z(t) = \bar{z}(t) = \hat{z}(t)}. \quad (A3)$$

With these definitions, $z^\star(t)$ can then be characterized as follows: if $z^\star(t)$ is an ESS, then

$$\text{(i)} \begin{cases} -d\lambda^l/dt = \partial H/\partial l & \lambda^l(T) = \partial G/\partial l(T), \quad \text{(A4a)} \\ -d\lambda^X/dt = \partial H/\partial X & \lambda^X(T) = \partial G/\partial X(T), \quad \text{(A4b)} \end{cases}$$

$$\text{(ii)} \begin{cases} \text{if } 0 < z^\star(t) < 1 & \text{then } \Delta W_{\text{incl}}|_{\hat{z} = z^\star} = 0, \\ \text{if } z^\star(t) = 0 & \text{then } \Delta W_{\text{incl}}|_{\hat{z} = z^\star} \leq 0, \quad \text{(A4c)} \\ \text{if } z^\star(t) = 1 & \text{then } \Delta W_{\text{incl}}|_{\hat{z} = z^\star} \geq 0, \end{cases}$$

where everything is evaluated at the ESS strategy, $z^\star(t)$. To connect this approach to the heuristic argument based on reproductive value presented in the text, it is necessary to redefine the inclusive fitness effect (A3) by conditioning it on the probability of survival to time t (i.e., by dividing [A3] by $l(t)$).

APPENDIX B

Results for Continuous Reproductive Output

We begin by setting up the model of the text within the framework outlined in appendix A and then go on to prove the main results for continuous reproductive output.

The control variable here is the level of selfishness over time, $z(t)$, and the single state variable is the probability of survival to time t, $l(t)$. From definition (1) the state variable dynamics are governed by the differential equation

$$dl/dt = -\mu l \quad l(0) = 1, \tag{B1}$$

and we construct the Hamiltonian by introducing the costate variable $V(t)$:

$$H = lm - V\mu l. \tag{B2}$$

From equation (A4a) the costate variable dynamics in a monomorphic population (i.e., $z = \bar{z} = \hat{z}$) is governed by the differential equation

$$dV/dt = \mu(\hat{z})V - m(\hat{z}, \hat{z}) \quad V(T) = 0. \tag{B3}$$

This is the continuous-time analogue of equation (5). The inclusive fitness effect of an individual increasing its selfishness at time t, given it has survived to time t, is found by dividing (A3) by $l(t)$:

$$\Delta W_{incl} = \frac{1}{l}\left(\frac{\partial H}{\partial z} + R\frac{\partial H}{\partial \bar{z}}\right)_{z(t)=\bar{z}(t)=\hat{z}(t)}, \tag{B4}$$

which gives equation (6) of the text.

We now obtain four preliminary results that are applicable when T is finite and that simplify the analysis. To begin, note that although ΔW_{incl} is treated as a function of time in the text, it should really be treated as a function with two arguments, $\hat{z}$ and V, each of which are functions of time; that is, $\Delta W_{incl}(\hat{z}(t), V(t))$.

(i) $\qquad\qquad V$ is nonnegative. $\qquad$ (B5)

The proof is by contradiction. Suppose that V were negative at some time between 0 and T. Because m and μ are both positive, this would imply that $dV/dt < 0$ for all future time from equation (B3), and therefore the terminal condition $V(T) = 0$ could never be satisfied. Thus V must be nonnegative.

(ii) $\Delta W_{incl}(\hat{z}, V)$ is a strictly decreasing function of $\hat{z}$. $\quad$ (B6)

Calculating $\partial \Delta W_{incl}/\partial \hat{z}$ using equation (B4) gives

$$\frac{\Delta W_{incl}}{\partial \hat{z}} = \frac{d}{d\hat{z}}\left(\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}}\right)_{z=\bar{z}=\hat{z}} - VR\frac{d}{d\hat{z}}\left(\frac{d\mu}{d\bar{z}}\right)_{\bar{z}=\hat{z}}. \tag{B7}$$

From conditions (7a) and (7b) and result (B5), it can be seen that (B7) is strictly negative.

(iii) $\quad$ Hamilton's Rule implicitly defines z^*
$\qquad\qquad$ as a function of V. $\qquad$ (B8)

Hamilton's Rule for this model is given by conditions (A4c) (Day and Taylor 1997). Conditions (A4c) implic-

itly define z^* as a function of V as follows. For any fixed value of V, ΔW_{incl} is a strictly decreasing function of $\hat{z}$ from result (B6); therefore, there are three possibilities. If $\Delta W_{incl} > 0$ at $\hat{z} = 0$ and $\Delta W_{incl} < 0$ at $\hat{z} = 1$, then by (A4c) z^* cannot be 0 or 1; therefore $z^* \in (0, 1)$. As a result, we also have $\Delta W_{incl}|_{z=z^*} = 0$, and by the implicit function theorem (Rudin 1976), $\Delta W_{incl}|_{\hat{z}=z^*} = 0$ implicitly defines z^* as a function of V. If $\Delta W_{incl} \leq 0$ for all $\hat{z}$, then, because ΔW_{incl} is strictly decreasing, $\Delta W_{incl} < 0$ for all $\hat{z} > 0$. Therefore, by (A4c), $z^* = 0$. Finally, if $\Delta W_{incl} \geq 0$ for all z, then, because ΔW_{incl} is strictly decreasing, $\Delta W_{incl} > 0$ for all $z < 1$. Therefore, by (A4c), $z^* = 1$. Thus there is a unique value of z^* for every value of V. As a useful aside we note that this result also immediately implies that z^* is constant if V is constant.

(iv) $\quad V$ is strictly decreasing in time if T is finite. $\quad$ (B9)

The proof is by contradiction. From result (B8) we can write differential equation (B3) as a nonlinear, autonomous differential equation:

$$dV/dt = U(V)V - M(V) \quad V(T) = 0. \tag{B10}$$

Equation (B10) has a unique solution because the vector field (the left-hand side of [B10]) satisfies a Lipshitz condition (Perko 1991). Now suppose V was increasing at some time. Because $dV/dt < 0$ at $t = T$, there must be some time at which $dV/dt = 0$ for the solution to "turn around" and decrease to 0. Setting $dV/dt = 0$, however, defines a (nonzero) equilibrium solution of (B10), and therefore, if V were ever to increase it must then intersect this equilibrium solution. By uniqueness this is not possible.

With these preliminary results we can now prove the following:

Result: $z^*(t)$ is nondecreasing at all times $t \in [0, T]$.

Proof: First consider the time dynamics of $\Delta W_{incl}(\hat{z}(t), V(t))|_{\hat{z}=z^*}$;

$$\frac{d\Delta W_{incl}|_{\hat{z}=z^*}}{dt} = \frac{\partial \Delta W_{incl}}{\partial \hat{z}}\frac{dz^*}{dt} + \frac{\partial \Delta W_{incl}}{\partial V}\frac{dV}{dt}. \tag{B11}$$

The partial derivatives of ΔW_{incl} are given by (B7) and

$$\frac{\partial \Delta W_{incl}}{\partial V} = -R\frac{d\mu}{d\bar{z}}\Big|_{\bar{z}=\hat{z}}. \tag{B12}$$

To prove the desired result, it is enough to show that if $z^* \in (0, 1)$, then z^* is increasing and if $z^* = 1$, then z^* remains at 1 for all future time. If $z^* \in (0, 1)$ at any time, then Hamilton's Rule (A4c) implies that $\Delta W_{incl}|_{\hat{z}=z^*} = 0$, and therefore (B11) equals 0 as well. Now dV/dt is negative by result (B9), as are expressions (B7) and (B12) from conditions (3a) and (7a) and (7b). Therefore, setting (B11) equal to 0, we can conclude that $dz^*/dt > 0$.

The ESS level of selfishness, z^*, is therefore strictly increasing if it is not 0 or 1. If z^* is constant through time at $z^* = 1$, then Hamilton's Rule (A4c) implies that $\Delta W_{\text{incl}}|_{\hat{z}=z^*} \geq 0$. Noting that $dz^*/dt = 0$ and that both dV/dt and expression (B12) are negative, we can conclude from (B11) that $\Delta W_{\text{incl}}|_{z=z^*}$ is increasing through time. Thus, from Hamilton's Rule (A4c), $z^* \equiv 1$ for all remaining time.

Result: It is never possible for a constant, intermediate level of selfishness or altruism to be an ESS.

Proof: This follows immediately from the previous proof, where we have shown that if $z^* \in (0, 1)$, then z^* is strictly increasing through time.

Result: If $T = \infty$, then z^* is constant.

Proof: When there is no time horizon, we need to look for solutions of differential equation (B10) (neglecting the terminal condition) that are bounded for all time, $t \in (0, \infty)$. The only solution with this property is the equilibrium solution $V \equiv M(V)/U(V)$. Therefore, because V is constant in time, z^* is constant as well (from result [B8]).

APPENDIX C

Results for When All Reproductive Output Is Realized at $t = T$

For this case fitness is simply $X(T)$ multiplied by the probability of surviving to time T:

$$W = l(T)X(T). \tag{C1}$$

Using the setup in appendix A, there are now two state variables, l and X. The dynamics of $l(t)$ are again given by (B1) and the dynamics of $X(t)$ are

$$dX/dt = m(z(t), \bar{z}(t)) \quad X(0) = 0. \tag{C2}$$

The Hamiltonian is

$$H = \lambda^X m - V\mu l, \tag{C3}$$

where λ^X and V are costate variables corresponding to the state variables X and l, respectively. The temporal dynamics of V and λ^X are given by (A4a) and (A4b):

$$\frac{dV}{dt} = \mu V \quad V(T) = X(T) \tag{C4}$$

and

$$\frac{d\lambda^X}{dt} = 0 \quad \lambda^X(T) = l(T). \tag{C5}$$

The inclusive fitness effect of an individual increasing its selfishness at time t, given it has survived to time t, is again calculated as in (B4):

$$\Delta W_{\text{incl}}(t) = \left[\frac{\lambda^X}{l} \left(\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}} \right) - R\frac{d\mu}{d\bar{z}} V \right]_{z=\hat{z}=\dot{z}}. \tag{C6}$$

From equation (C5) we can see that $\lambda^X/l = l(T)/l(t)$, and therefore (C6) is equation (12) of the text. We can rewrite (C6) as

$$\Delta W_{\text{incl}}(t) = \frac{l(T)}{l(t)} \left[\frac{\partial m}{\partial z} + R\frac{\partial m}{\partial \bar{z}} - R\frac{d\mu}{d\bar{z}} X(T) \right]_{z=\hat{z}=\dot{z}}, \tag{C7}$$

and therefore the sign of $\Delta W_{\text{incl}}(t)$ is determined by the sign of the expression in the parentheses of (C7). Since this is not explicitly time dependent, the ESS strategy is therefore constant.

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