# A Dynamic Model of Size-Dependent Reproductive Effort in a Sequential Hermaphrodite: A Counterexample to Williams's Conjecture

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ABSTRACT: In 1966, G. C. Williams showed that for iteroparous organisms, the level of reproductive effort that maximizes fitness is that which balances the marginal gains through current reproduction against the marginal losses to expected future reproduction. When, over an organism's lifetime, the value of future reproduction declines relative to the value of current reproduction, the level of effort allocated to current reproduction should always increase with increasing age. Conversely, when the value of future reproduction increases relative to the value of current reproduction, the level of effort allocated to current reproduction should decrease or remain at zero. While this latter pattern occurs commonly in species that exhibit a delayed age at first reproduction, it may also occur following an initial period of reproduction in some sex-changing organisms that experience a dramatic increase in reproductive potential as they grow larger. Indeed, this schedule of reproductive effort is predicted by models of "early" sex change; however, these models may arrive at this result incidentally because they consider only two reproductive states: on and off. In order to examine the schedule of reproductive effort in greater detail in a system where the potential reproductive rate increases sharply, we adapt the logic and methods of time-dependent dynamic-programming models to develop a size-dependent model of reproductive effort for an example species that experiences a dramatic increase in reproductive potential at large sizes: the bluehead wrasse, *Thalassoma bifasciatum*. Our model shows that the optimal level of reproductive effort will decline with increasing size or age when increases to the residual reproductive value outpace the increases to current reproductive potential. This result confirms the logic of Williams's analysis of optimal life histories, while offering a realistic counterexample to his conjecture of ever-increasing allocation to current reproduction.

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The goal of life-history theory is to explain the evolution of the schedules of reproduction and survival over an organism's lifetime (Fisher [1930] 1958; Williams 1966a, 1966b; Gadgil and Bossert 1970; Schaffer 1974, 1979, 1983; Pianka and Parker 1975). The importance of these schedules in an evolutionary context is clear because these two fitness components jointly determine an organism's expected lifetime reproductive success ($R_0$), which in stationary populations is equivalent to fitness (Fisher [1930] 1958; Schaffer 1979; Roff 1992). Related to $R_0$ is Fisher's concept of reproductive value. Reproductive value($V_x$) is the expected contribution of an individual of age $x$ to the growth of the population (Fisher [1930] 1958). At age 0, $R_0$ is equivalent to $V_0$ in stationary populations (Stearns 1992), and the schedules of survival and fecundity that maximize reproductive value at each age $x$ also maximize $R_0$ and consequently fitness (Fisher [1930] 1958; Williams 1966b; Schaffer 1979).

Although these schedules may be viewed as separate characters, in reality they are bound together by the fact that organisms have limited resources. This forces the investments toward reproduction and survival to be traded off against one another (Bell 1980; Reznick 1983; Warner 1984a; Partridge and Harvey 1985; Schluter et al. 1991; Roff 1992; Stearns 1992), and a single schedule of allocation to current versus future reproduction can therefore be considered. The optimal solution to this trade-off was examined by Williams (1966a, 1966b), who modified the concept of reproductive value by splitting it into two elements: one representing the contribution to fitness through current reproduction and another representing the contribution to fitness through expected reproduction in the future. This latter element is termed the "residual reproductive value" (RRV). Williams's (1966a, 1966b) analysis shows that the allocation to current reproduction ($E$) maximizing $V_x$ is that which balances the marginal
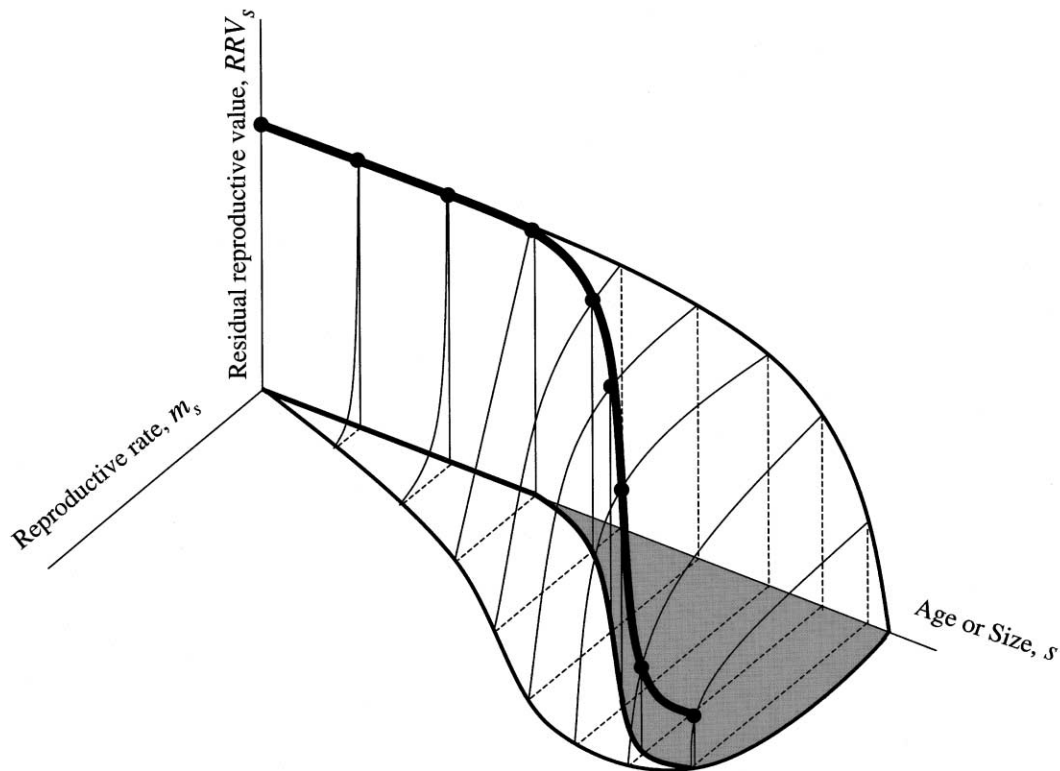
**Figure 1:** Modified from Pianka and Parker (1975). Plot shows the trade-offs between the contributions to reproductive value (or fitness) through current and future expected reproduction over the lifetime of an iteroparous organism. The dots and the heavy line on the curved surface of the three-dimensional solid trace the optimal life history balancing the allocation to current reproduction ($E_{\mathrm{opt}}$) versus future reproduction ($1 - E_{\mathrm{opt}}$). The drop lines and the shaded area on the floor of the surface trace the realized reproductive rate that is a function of the potential (maximal) reproductive rate and the allocation of effort toward reproduction. Note that as the residual reproductive value ($\mathrm{RRV}_s$) declines with increasing age/size, the proportional allocation of effort toward current reproduction is predicted to increase. This is Williams's (1966a) conjecture.

fitness benefits of increased current reproduction against the marginal fitness costs of decreased expected future reproduction resulting from increases in $E$.

Over a lifetime, an organism's reproductive value may change in a predictable manner when increasing age or increasing size affect current reproductive potential, future reproductive expectations, or both. As a result, the optimal investment to current versus future reproduction will change in a similarly predictable way. The classic example of this is Williams's (1966a) conjecture that for iteroparous organisms, the optimal level of reproductive effort ($E_{\mathrm{opt}}$) is always expected to increase with age. This prediction is founded on the assumption that as an individual ages, its RRV declines. Such a decline may result from senescence (i.e., an age-specific reduction in either survival or reproductive capacity) but could also result from changes in the environment (e.g., the onset of winter) that similarly affect future fitness but are independent of an organism's condition. In either case, as the value of current reproduction

increases relative to RRV, the optimal level of effort allocated to current reproduction increases (see fig. 1 for a graphical presentation taken from Pianka and Parker 1975).

Although theoretical and empirical studies have generally supported Williams's (1966a) prediction (see Roff 1992 and Stearns 1992 for reviews), three counterexamples in which the optimal level of reproductive effort is expected to decrease as age increases have been described (Fagen 1972; Charlesworth and León 1976; Roff 1992). Here, we briefly review and discuss these before focusing on a fourth counterexample. Fagen (1972) showed that $E_{\mathrm{opt}}$ can decline with age when the functions describing the age-specific patterns of growth, reproduction, or survival are not monotonic. Specifically, the example described by Fagen (1972) outlines a four-age (0, 1, 2, and 3) life history in which reproduction is possible at ages 1, 2, and 3 and growth is possible at ages 0, 2, and 3. In this case, because the maximum growth increment from age

1 to age 2 is 0, the function describing the growth rate is not monotonic but rather concave. The resulting optimal allocation schedule is a relatively high investment to current reproduction at age 1 because any negative effect of high levels of $E$ on fitness is eliminated by the fact that individual size at future ages is independent of $E$ at this age; $E_{opt}$ then falls at age 2 because size, and therefore future fecundity, is a function of $E$ at this age. Finally, $E_{opt}$ increases to the maximum at age 3 because there is no future reproduction for which to withhold some investment (i.e., $RRV_{age\,3} = 0$).

In Roff's (1992) counterexample, the probability of survival to the next age is a declining step function of $E$, and growth is determinate. Let $E_{crit}$ equal some critical level of reproductive effort. Levels of allocation in excess of $E_{crit}$ result in zero survival, while levels less than $E_{crit}$ result in a high probability of survival. Under these circumstances, the optimal solution at each point in the life history is for $E$ to be the maximal value that still results in high survivorship ($E_{opt} < E_{crit}$). If $E_{crit}$ decreases as a function of age, the $E_{opt}$ will likewise decrease over age. Although this model assumes that survival is a nonlinear step function of reproductive effort, a sigmoidal approximation of this step function would have the same effect and yet would formally be a monotone function. Thus, in theory, $E_{opt}$ can decrease with age in life histories where survival is either a monotone or a nonmonotone function of age.

A third set of circumstances leading to an age-specific decrease in $E_{opt}$ was identified by Charlesworth and León (1976), who show that under density independence, when the intrinsic rate of increase for the population ($r$) is high and the cost of reproduction is low (i.e., survival and growth rates do not drop sharply with increasing $E$), the optimal schedule of reproductive effort can decline with age (Charlesworth 1994). In this case, the decline in $E_{opt}$ is driven by the fact that early life reproduction has a greater contribution to fitness than late life reproduction when $r$ is high and is permitted by the fact that RRV is not greatly reduced by relatively high levels of allocation to current reproduction.

While these three counterexamples show that the optimal schedule of reproductive effort will not inevitably increase with age, they are each somewhat artificial (Roff [1992, p. 261] in reference to Fagen's [1972] model and his own but not that of Charlesworth and León [1976]). Nonmonotone vital-rate functions of the form described by Fagen (1972) are conceivable, but it is difficult to imagine a realistic system that would fit his model. Fagen (1972) does note that certain large mammal species (specifically male African elephants, some seals, and toothed whales) exhibit a pattern of growth that matches the predictions of the nonmonotone model (size increases until puberty, remains constant for some period, then increases again

following the latent period). However, it is not readily apparent that such a latent period results from incapacity for growth, as suggested by Fagen (1972), or from an allocation of resources to other components of the life history (i.e., survival and reproduction). The model suggested by Charlesworth and León (1976) is more realistic; however, its key condition, that the intrinsic rate of increase is relatively high due to density independence, is unlikely to be sustained for long in natural populations. Thus, the Charlesworth and León (1976) model can explain why reproductive effort might decline over size or age for some interval; however, it cannot explain why this pattern should hold for populations at equilibrium densities.

## Sex Change as a Counterexample: When Gains to RRV Outpace the Gains in Current Reproduction

Here we suggest that iteroparous organisms that experience a dramatic increase in potential reproductive success as they grow larger (a pattern observed in some species of sex-changing fishes) constitute an unrecognized and biologically realistic counterexample to Williams's (1966*a*) conjecture. In such species, as some critical point in the life history is approached, the size-specific gains in expected future reproduction can outpace the size-specific gains to current reproductive potential, which drives the predicted optimal level of reproductive effort down. This case is then simply the converse of the conditions outlined by Williams (1966*a*), who assumed that RRV generally declines with age or size and simply makes the opposite prediction (see fig. 2 for a graphical presentation of this adapted from Pianka and Parker 1975).

This pattern of size-specific reproductive potential is observed in some species of protogynous (i.e., female first, male second) sex-changing fish, such as the bluehead wrasse, *Thalassoma bifasciatum* (Labridae). In this species, small, initial-phase females spawn once a day, while very large, terminal-phase males spawn with an average of 20–30 females per day (Warner and Schultz 1992). Furthermore, individuals in this species exhibit what is termed "early" sex change. Early sex change occurs when, after reproducing for some period in the initial sex, an individual changes sex but immediately enters a protracted nonreproductive period (i.e., $E$ falls to 0) before eventually resuming reproduction in the second sex. This observed nonreproductive period is predicted by existing life-history models of early sex change developed by Hoffman et al. (1985) and Iwasa (1991). However, we suggest that these models may arrive at this prediction inadvertently. In support of this perspective, we caution that the model of early sex change by Hoffman et al. (1985) explicitly considers only two reproductive states (off [$E = 0$] and on [$E =$
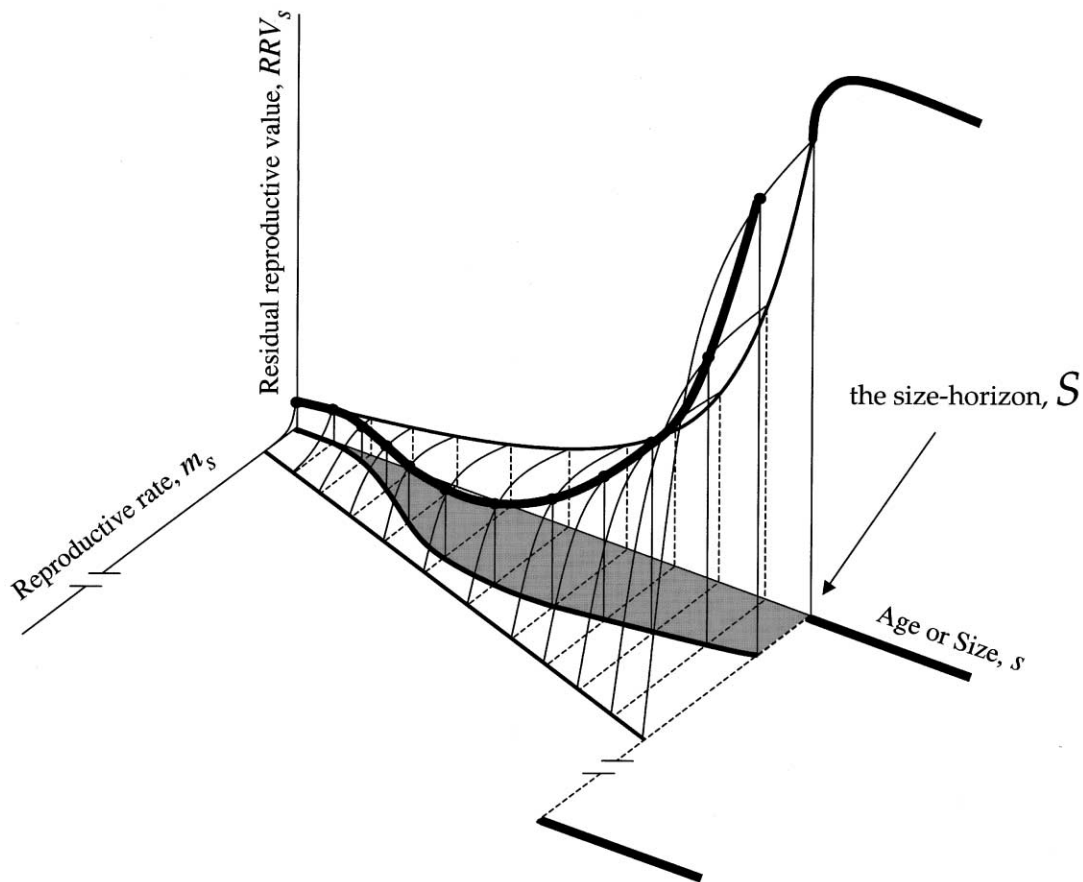
**Figure 2:** Adapted from Pianka and Parker (1975). As in figure 1, plot shows the trade-offs between current and future expected reproduction in an iteroparous organism. The dots and heavy line on the surface of the three-dimensional solid trace the optimal life history. Here, there is a dramatic increase in the potential reproductive rate at the size horizon (*S*). In species such as the bluehead wrasse, *Thalassoma bifasciatum*, the size-specific potential reproductive rate increases at sex/color-phase change to 20–30 times the average rate before this point. This increase in reproductive potential at *S* (size at sex/color-phase change) generates an increase in the residual reproductive value at sizes leading up to *S*. When the size-specific gains to $RRV_s$ outpace the size-specific increase in the potential reproductive rate, the optimal allocation to current reproduction will fall. This provides a counterexample to Williams's (1966*a*) conjecture while reinforcing the logic underlying his prediction.

1]), and therefore any reduction in $E_{opt}$ can only be a reduction to 0. In a similar vein, we note that, under the assumptions made by Iwasa (1991) concerning the trade-off between current and future reproduction, the optimal reproductive effort is effectively restricted to be 0 or 1 (T. Day, personal communication). We also note that data from a field study by Warner (1984*a*) measuring growth and survival rates in *T. bifasciatum* do not appear to support the assumptions of the early-sex-change models. Finally, we argue that alternative explanations for early sex change exist (e.g., Aldenhoven 1986; Rogers 1998; L. Rogers, unpublished manuscript), and thus trade-offs between life-history components may not be a selective force behind the evolution of early sex change.

Below, we briefly review sex-change models, their ev-

olution, and their explicit and implicit restrictions. Motivated by the models of Hoffman et al. (1985) and Iwasa (1991), we then develop a new model applying dynamic-programming methods (Bellman 1957; Mangel and Clark 1988) that permits *E* to vary between 0 and 1.

### Sex-Change Theory

Sex change is a taxonomically widespread, albeit uncommon, pattern of sexual expression (Policansky 1982; Warner 1984*b*) in which individuals reproduce first as one sex and later as the other sex. Models of sex change have historically examined the adaptive significance of two aspects of this pattern. First, these models sought to understand the conditions under which sex change may be

favored. Second, given that sex change is indeed favored, these models explored the factors affecting the timing of the shift from the initial to the terminal sex.

The principal model of sex change, the size-advantage hypothesis (Ghiselin 1969), proposes simply that selection will favor sex change when an organism can reproduce at a higher rate as one sex when small or young and at a higher rate as the other sex when large or old, while all other aspects of the life history (e.g., growth and survival) are equal between the sexes. Analytical models by Warner and his colleagues (Warner 1975; Warner et al. 1975; Leigh et al. 1976; Charnov 1982) confirm the selective advantage of sex change under these circumstances and show that this advantage is maximized when sex change occurs at the point where the curves describing the age- or size-dependent male and female reproductive rates intersect.

For mathematical tractability, these original formulations of the size-advantage model (Warner 1975; Warner et al. 1975; Leigh et al. 1976) adopt the convention of assuming the sex-specific reproductive rates and survival probabilities to be functions of age (e.g., Pianka and Parker 1975). Thus, as in demographic studies, the reproductive rate at age $x$ is denoted $m_x$ and the probability of survival from age 0 to age $x$ is denoted $l_x$. While this assumption greatly simplifies the models and does not change their fundamental results (Warner 1975, 1988), this formulation can implicitly restrict such models in two interrelated ways. The first restriction results from the fact that, while it is logical to treat survival ($l_x$) as a function of age, the reproductive rate ($m_x$) is often more appropriately a function of size. Although treating $m_x$ as a function of age may be justifiable because size and age are correlated in organisms with indeterminate growth, this assumption implicitly forces size and age into synonymity. This becomes a problem when, for mathematical tractability, $l_x$ and $m_x$ are assumed to be simple functions of age (for example, $l_x = e^{-ax}$ and $m_x = bx + c$) because growth rate cannot vary over $x$. That is, the result of this fusion of size and age is that models adopting this formulation are incapable of addressing trade-offs between growth and other components of the life history, such as survival and reproduction. Related to this is the fact that $l_x$ and $m_x$ are the realized outcomes of age- and size-specific potential survival and reproductive rates and the level of effort directed toward these potentials. Thus, while models using these terms allow the conceptual illustration and investigation of ideas such as the size-advantage model (Warner 1975; Warner et al. 1975; Leigh et al. 1976; Hoffman et al. 1985; Charnov 1986; Iwasa 1991), because $l_x$ and $m_x$ are measures of output and not input, they are inadequate when the goal is to model the pattern of allocation to growth, reproduction, and survival across an organism's lifetime.

The first limitation, the implicit fusion of size with age,

was recognized and to a certain extent corrected by Hoffman et al. (1985) and Iwasa (1991). Hoffman et al. (1985) and Iwasa (1991) recast the size-advantage model to permit examination of the effect of trade-offs between life-history components on sex-change timing. These authors note that when reproduction imposes a sufficiently high cost to survival or growth, both of which increase future reproductive potential, selection may favor a nonreproductive period. While such a nonreproductive period could hypothetically occur at any point in an organism's lifetime, both Hoffman et al. (1985) and Iwasa (1991) assume that it intervenes between reproduction in the initial and terminal sexes. Thus, the phenomenon referred to as "early" sex change, in which individuals of many species of sex-changing fish appear to change sex "too early" (i.e., before they are capable of reproducing in the second sex), may be an adaptive life-history strategy (see also Thresher 1979; Jones 1981; Moyer and Zaiser 1984; Aldenhoven 1986).

Although the models of Hoffman et al. (1985) and Iwasa (1991) are improvements over the simplest treatments of the size-advantage model (e.g., Warner 1975; Warner et al. 1975; Leigh et al. 1976), there are theoretical and empirical problems with these models of early sex change as well. First, despite its ability to explain the basic pattern of reproductive effort (i.e., reproduce as the initial sex, cease reproduction for some period, and finally begin reproduction again in the terminal sex) across a sex-changing individual's lifetime, the model by Hoffman et al. (1985) artificially dichotomizes reproduction as either on or off. The functions describing the reproductive effort at age $x$ in this model are oversimplified because they do not include a term describing the level of allocation to reproductive effort at $x$. Second, the model by Iwasa (1991) assumes the trade-off between future and current reproduction to be linear. If this function is not convex but rather linear or concave, there can be no intermediate optimum (Pianka and Parker 1975), and the optimal life history will be a so-called bang-bang transition from one reproductive state to another (e.g., fully reproductive to fully nonreproductive).

Empirically, if the nonreproductive period exists as the result of a shift in allocation from current to future reproduction, then life-history components correlated to future reproduction (e.g., growth and survival rates) are predicted to increase at this point. In agreement with this prediction, Warner (1984a) found that growth rates of terminal-phase male *Thalassoma bifasciatum* that were newly sex-changed but not yet territorial (i.e., early sex-changed) were approximately 50% higher than comparably sized initial-phase females. While this is a substantial increase, Warner (1984a) also shows that mortality rates among terminal-phase males are two to three times higher

than males and females in the initial phase. Thus, it is not obvious that the early sex-change strategy does in fact result in an increase in future expected reproduction sufficient to balance the cost of a nonreproductive period.

## Reproductive Effort Model

### *Methods*

In order to determine the optimal schedule of effort invested toward current reproduction ($E_{opt}$) across an organism's lifetime, one must be able to determine the effect of a given level of effort on the expected contributions to fitness through both current and future reproduction. The difficulty here is that, while determining the effect of some level of effort on current reproduction is relatively straightforward, establishing its effect on future reproduction can be very complicated.

One method used to solve such problems is dynamic programming (Bellman 1957; Mangel and Clark 1988). Dynamic programming (DP) is an optimization technique used to find the optimal sequence of decisions (e.g., patch choice, allocations to a physical structure or to reproduction, foraging decisions, etc.) along a time axis (see Mangel and Clark 1988 for a more complete description of these methods). The dynamic-programming equation applied to life histories can take the general form

$$V(x, t, T) =$$

$$\max_i \Big( m(x, i, t) + \{p(x, i, t)V[x + g(x, i, t), t + 1, T]\}\Big),$$

(1)

where $V(x, t, T)$ is the current reproductive value of an individual of condition $x$ at time $t$ adopting the optimal decision or behavior $i$ ($\max_i$) given a time horizon of $T$ (see Sargent 1990; Ydenberg et al. 1995; St. Mary 1997 for similar treatments of the DP equation). The terms $m(x, i, t)$, $g(x, i, t)$, and $p(x, i, t)$ are, respectively, the contribution to fitness through current reproduction, the increment to condition (e.g., size), and the probability of survival to the next time ($t + 1$). The second term on the right-hand side (within braces) represents the residual reproductive value (i.e., the expected contribution to fitness through future reproduction). It is interesting to note that by partitioning reproductive value into two elements representing current and future expected reproduction, Williams (1966*b*) and Bellman (1957) independently derived solutions that have the same logical form (Schaffer 1974; Rogers 1998). A DP model is solved by backward iteration beginning at the last time step to yield the optimal trajectory over time (Bellman 1957; Mangel and Clark 1988).

The critical feature of a dynamic program is the time horizon ($T$) that serves as a temporal benchmark for terminal-fitness determination (e.g., the time of occurrence of dominant life-history events such as maturation, the end of reproductive season, the date on which an ephemeral pond will dry up, etc.). It is the time horizon, or rather an organism's proximity to it, coupled with the fitness expectation of a given condition level at $T$ (the terminal-fitness function) that drives the dynamics of DP models. When the time horizon represents something like the point in a season at which maturation occurs, the terminal-fitness function may be set such that expected fitness at $T$ is an increasing function of condition. Alternatively, when the time horizon represents something like a killing freeze, the terminal-fitness function may be set to 0, regardless of condition.

In the model developed here, we assume that there is no important point-in-season effect imposed by the environment and that individual reproductive, growth, and mortality rates are not functions of time (or therefore age) but of size. Thus, while time would exist coincidentally in such a model, a critical point in time, such as a time horizon, has no meaning but a critical size does. In this case, logical replacement of the time horizon with a size horizon ($S$) representing the size at sex change permits solution for the optimal decision trajectory by backward iteration across size. Because this model has a single axis, the terminal-fitness function can also be replaced by a terminal-fitness value; the reproductive value at the size at sex change, $V_S$.

Dropping the variable time ($t$) and the time horizon ($T$) from the DP equation above yields

$$V(s) = \max_E \Big( m(s, E) + \{p(s, E)V[s + g(s, E), S]\}\Big), \quad (2)$$

where $E$ (proportion of total effort [e.g., resources or energy] allocated to current reproduction) replaces $i$ from equation (1). The terms $V(s)$, $m(s, E)$, $g(s, E)$, and $p(s, E)$ represent, respectively, the size-specific reproductive value, reproductive contribution, growth increment, and survival probability for an individual of size $s$, allocating a level of effort $E$ to current reproduction. The reproductive value in the next size given a size horizon of $S$ is $V[s + g(s, E), S]$; the product of this future reproductive value and the probability of survival to the next size ($p(s, E)$), is the residual reproductive value (within braces).

In this model, we assume that reproductive output at size $s$ is an increasing linear function of both size and reproductive effort. Conversely, we assume that somatic output (i.e., growth) is a linearly increasing function of size and a linearly decreasing function of reproductive effort. The rationale for these functions is that it seems

simplest to assume that somatic and reproductive output will be the product of size-specific physiological potentials as well as the levels of allocation ($E$) dedicated toward each. We assume that the probability of survival ($p(s, E)$) is a nonlinear, decreasing power function of reproductive effort ($p(s, E) \propto 1 - E^d$, where $d > 1$ and $0 < E < 1$). This assumption is made to force the model to exhibit an intermediate optimum over $E$ (Gadgil and Bossert 1970). When there is no intermediate optimum, there are two local optima: $E_{opt} = 0$ (a complete allocation to future reproduction) and $E_{opt} = 1$ (a complete allocation to current reproduction at a suicidally high level [i.e., semelparous reproduction]). As a biological example justifying this assumption, imagine a fish making a slight overinvestment in current reproduction resulting in its being slightly slower than its schoolmates. Here, a linear increase in $E$, resulting in a linear decrease in escape speed, will result in a nonlinear increase in the probability of mortality to the slowest member of the school.

## *Results*

The results of this model show that the optimal schedule of reproductive effort in an iteroparous organism will initially increase, plateau, and eventually decline over some range when the size-specific increase in residual reproductive value outpaces the size-specific increase in current reproductive potential (here, when the reproductive value at $S$, $V_S$ is sufficiently high [fig. 3, *curve c*]). Thus, this model confirms the intuition that inverting Williams's (1996*a*) assumption concerning a size-specific (or age-

specific) decline in RRV results in the inversion of the predicted schedule of allocation to current reproduction. In such cases, the effect of very high reproductive value at the size horizon is that the residual reproductive value increases dramatically relative to the value of current reproduction (i.e., the fitness contribution through current reproduction) as $S$ is approached, favoring an increased proportional investment to RRV. In contrast to this result, when $V_S$ is low, RRV declines with increasing size, and the schedule of reproductive effort increases monotonically (fig. 3, *curve a*). This corresponds to the circumstance envisioned by Williams (1966*a*) and is included here for the sake of comparison. At intermediate values of $V_S$, the allocation of reproductive effort may remain more or less constant over size because the contributions to fitness through current and expected future reproduction remain in balance (fig. 3, *curve b*). Significantly, we note that in none of our simulations were we able to generate a pattern in which the optimal allocation of effort drops to 0 as predicted by Hoffman et al. (1985) and Iwasa (1991).

Another pattern that emerges from this model is that, despite the differences in the schedule of reproductive effort as $V_S$ varies, the effect of $V_S$ on the predicted schedule is generally restricted to the larger sizes and has very little effect on the pattern at small sizes. Intuitively, although it is the size (or time) horizon that drives the behavior of a DP model, the influence of this point-in-size diminishes with distance. In standard DP models, this commonly observed phenomenon is referred to as "stationarity" (McNamara and Houston 1982; Mangel and Clark 1988; Sargent 1990).
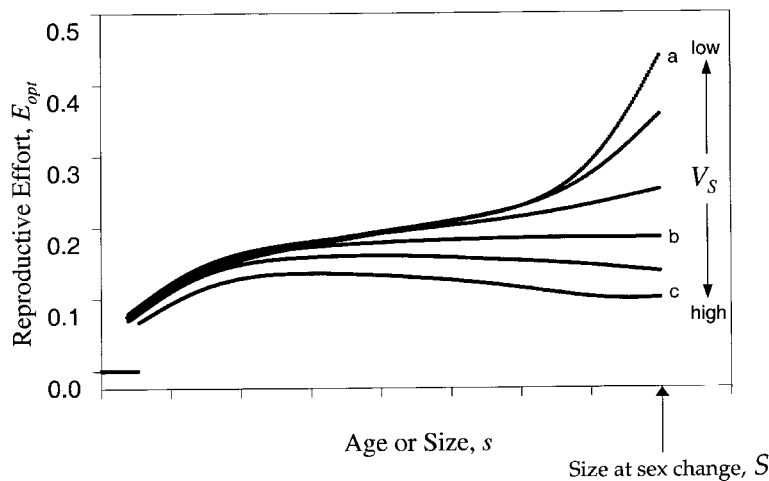


**Figure 3:** The schedule of optimal reproductive effort ($E$) over size for six levels of reproductive value at sex/phase change ($V_S$). If the reproductive value at the size at sex/phase change ($S$), approximately 80 mm (in standard length) in *Thalassoma bifasciatum*, is sufficiently high (e.g., *curve c*), the optimal level of reproductive effort will decline as $S$ is approached. If not, $E_{opt}$ is predicted to increase with size (*curve a*).

A sensitivity analysis was performed to examine the effects of three key parameters on the results of the model. The first of these is the background probability of survival, which, in conjunction with the schedule of reproductive effort, determines the schedule of survival and thus an organism's eventual probability of reaching the size horizon. The second parameter is the value of the exponent describing the decrease in survival as a function of increasing $E$. Changes in both of these parameters subtly affect the curves describing the optimal levels of reproductive effort over size. However, the fundamental result (that the optimal level of reproductive effort is predicted to decline when $V_S$ is sufficiently high) is unaffected by changes in these parameters. The third parameter examined is the shape of the function describing the availability of resources over size. This effectively sets the size-specific physiological upper limit for growth and reproduction. Specifically, in addition to the default case in which resource income increases as a linear function of size, we considered the cases where resource income increases exponentially over size and where it remains constant over size. We found that as in the two previous cases, the shape of the schedule of resource income does not qualitatively affect the optimal schedules of effort (i.e., input) over the lifetime. Moreover, although the schedules of growth and reproduction (i.e., output) are strongly affected by this schedule, their basic shape (e.g., linear, convex, or concave) is only affected by resource levels when the resource income rate is strongly curvilinear. For example, if the resource income increases at an accelerating rate over size, a decreasing proportional allocation of effort toward reproduction can still result in an increasing level of reproductive output.

## Discussion and Predictions

Our model illustrates that the optimal level of reproductive effort ($E_{opt}$) is predicted to decline with increasing size (or age) when the value of future reproduction increases relative to the value of current reproduction (figs. 2, 3). As such, this result simply mirrors Williams's (1966*a*) conjecture of ever-increasing levels of $E_{opt}$ when RRV falls relative to the value of current reproduction with age or size (fig. 1). The biological example we point to is that of protogynous sex-changing fishes in which the residual reproductive value increases dramatically relative to current reproductive potential as the critical size at sex (or phase) change is approached.

This model contrasts with previous models of early sex change in which reproduction is effectively an on/off decision (Hoffman et al. 1985; Iwasa 1991). In Hoffman et al. (1985), this restriction results from the explicit consideration of only two reproductive states: active and inactive.

Iwasa (1991), on the other hand, does allow for a full range of allocation from a total investment to current reproduction at one extreme ($E = 1$) to a total investment in future reproduction at the other ($E = 0$). However, Iwasa's (1991) assumption of a linear trade-off between the two components of reproductive value results in the optimal reproductive effort being functionally restricted to the active and inactive states as well (see Gadgil and Bossert 1970; Pianka and Parker 1975).

The model we present permits the proportional allocation to current reproduction to vary semicontinuously between 0 and 1 over size (i.e., discretely but in greater detail). It also follows earlier optimal life-history models in assuming that the trade-off between current and future reproduction is concave (Williams 1966*a*, 1966*b*; Gadgil and Bossert 1970; Pianka and Parker 1975; Schaffer 1983).

This difference in the structure of the models results in distinct differences in the predictions. The results of both Hoffman et al. (1985) and Iwasa (1991) predict that when the value of future reproduction is sufficiently high, current reproductive output will fall to 0 for some period between bouts of reproduction in the initial and in the terminal sex. The model we develop here does not predict a nonreproductive period under any circumstances (fig. 3). It is for this reason that we suggest that the complete cessation of reproduction leading to a protracted nonreproductive period exhibited in such species is not due to trade-offs between current and future reproduction. In further support of this perspective, we note that at least in *Thalassoma bifasciatum*, individuals in the physically male but nonreproductive interval produce sperm and thus have some nonzero allocation to both current and future reproduction (K. Clifton, personal communication).

The size-horizon model makes very specific predictions about the pattern of reproductive effort over size in a hypothetical iteroparous organism that experiences indeterminate growth and a step function increase in reproductive potential with increasing size. For all levels of reproductive value at the size horizon ($V_S$), the model predicts an initial period of immaturity. That is, even though reproduction at very small sizes is permitted in the model, the optimal sequence of reproductive effort includes a juvenile period. Likewise, at all levels of $V_S$, small reproductive individuals are predicted to have a low investment to current reproduction, while intermediate-sized individuals over a broad range of sizes are predicted to have higher, and relatively constant, levels of reproductive effort. This is in contrast to the predicted pattern of $E_{opt}$ at very large sizes, which is strongly dependent on the reproductive value at sex/phase change (i.e., at the size horizon). If $V_S$ is sufficiently high, the value of this future reproduction may push the current level of reproductive

effort down as the size at sex/phase change is approached, which results in either accelerated growth, increased survival, or both. In this case, the predicted relationship between reproductive rate and size should be curvilinear and convex and bend down at large sizes (i.e., the slope of the first derivative is negative). Correspondingly, the predicted relationship between growth rate and size should also be curvilinear but concave and bend up at large sizes.

## Conclusions

In 1966, Williams showed that reproductive value is maximized at the level of reproductive effort that balances the marginal gain in fitness through current reproduction against the marginal losses in fitness through expected reproduction in the future. Based on this conclusion, Williams (1966*a*) speculated that because the expected contribution to total lifetime fitness through future reproduction generally declines with increasing age, the optimal proportion of effort allocated to current reproduction ($E_{\mathrm{opt}}$) should always increase. Fagen (1972), Charlesworth and León (1976), and Roff (1992) offer three counterexamples in which $E_{\mathrm{opt}}$ decreases with age, but these are biologically unrealistic (see Roff 1992). In this article, we develop a life-history model based on the natural history of the sex/phase-changing bluehead wrasse, *Thalassoma bifasciatum*, that illustrates that Williams's (1966*a*) conjecture can be reversed to predict that when the potential contribution to fitness through future reproduction increases relative to the potential through current reproduction, the optimal level of *E* should decrease.

In many ways, the model we develop resembles previous ones addressing the phenomenon of early sex change (Hoffman et al. 1985; Iwasa 1991). These models show that a nonreproductive period can be favored when the fitness benefits in the future outweigh fitness costs in the present. However, we propose that because both of the models of early sex change effectively treat reproduction as an on/off decision, the predicted nonreproductive period results from implicit restrictions in these models. That is, any reduction in $E_{\mathrm{opt}}$ with age or size can only be a reduction to 0 in these models. Our model permits *E* to vary semicontinuously and therefore contrasts with the predictions of Hoffman et al. (1985) and Iwasa (1991). We interpret this inconsistency to suggest that the observed nonreproductive period is not a result of trade-offs between life-history components. In support of this perspective, we note that despite the fact that growth rates increase in *T. bifasciatum* at sex/phase change, there is a concomitant decrease in survival rates at this transition (data in Warner 1984*a*). Finally, we note that an alternative explanation for early sex change is that environmental uncertainty in the timing of successful acquisition of a mating territory in the terminal phase drives early sex change (Moyer and Zaiser 1984; Hoffman et al. 1985; Aldenhoven 1986; Rogers 1998; L. Rogers, in review).

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