Terminal investment equations

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Abstract

In this work we demonstrate the formation of a new type of polariton on the interface between a ....

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1. Introduction

1.1. Definition of terminal investment

I attempt here to use an approach considering that an individual not only varies is reproductive investment in terms of number of young produce but also in terms of young quality to see when an individual should terminally invest. Terminal investment is define here as an increase in reproduction decreasing survival to 0 for a discrete age (x). Continuous forms of terminal investment (*sensu* Pianka and Parker 1975) are not considered.

1.2. Classic terminal investment

Williams (1966) defined the reproductive value, RV_x, and the residual reproductive value, RV'_x, of an individual of age x in a stable population as:

$$\begin{aligned} RV_x &= m_x + RV'_x \\ &= m_x + \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} \cdot m_t \end{aligned} \tag{1}$$

in which m_x is the fecundity (*i.e.* number of offspring) of an individual of age x and l_x is the survival probability from age 0 to age x. This equation intuitively

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shows that the reproductive value of an individual of age x is the sum of its potential reproductions weighted by its survival probabilities from age x to each subsequent reproduction event. The residual reproductive value, RV'_x, is similar to the RV_x but excludes the reproduction at age x.

If we define Δm_x as the gain in fecundity obtained by terminally investing at age x, then following a "classic" terminal investment approach (Pianka and Parker, 1975; Williams, 1966), an individual should terminally invest when:

$$\Delta m_x > RV'_x. \tag{2}$$

Terminal investment predictions are thus based solely on the variation of the survival-reproduction trade-off curve with age. This limits terminal investment theory by restricting it to only consider increases in immediate fecundity and future reproductive output.

1.3. *Using expected fitness W_x instead of the reproductive value RV_x*

Hirshfield and Tinkle (1975) proposed a slightly modified version of the reproductive value equation (1) to define expected fitness. Because an individual's fitness depends on the quality of young produced, they weighed each reproductive event by the offspring survival probability to maturity, k_x. It should be noted that k_x is not fixed and is allowed to vary as a function of the age of the individual. Hirshfield and Tinkle (1975) expressed expected fitness as:

$$W_x = m_x \cdot k_x + \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} \cdot m_t \cdot k_t. \tag{3}$$

If k_x is unaffected by terminal investment, then the prediction for terminal investment using W_x is similar to inequality (2). However, if k_x is affected by terminal investment, then an individual should terminally invest when:

$$\underbrace{(m_x + \Delta m_x)}_{\text{Fecundity}} \cdot \underbrace{(k_x + \Delta k_x)}_{\text{Survival}} > \underbrace{m_x \cdot k_x}_{\text{Actual repr}} + \underbrace{\sum_{t=x+1}^{\infty} \frac{l_t}{l_x} \cdot m_t \cdot k_t}_{\text{Residual repr value}} \tag{4}$$

$$m_x \cdot \Delta k_x + \Delta m_x \cdot k_x + \Delta m_x \cdot \Delta k_x > \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} \cdot m_t \cdot k_t$$

In inequality 4, Δm_x and Δk_x are the increases in fecundity and juvenile survivorship to maturity due to terminal investment, respectively. If this estimation of expected fitness provides interesting new insights about terminal investment, we feel that that it is still too restrictive since it assumes that an effect only on survival of the offspring and not on their reproduction potential.

2. New terminal investment model

2.1. Reproductive value

We used the definition of reproductive value by Williams (1966).

$$RV_x = m_x + \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} \cdot m_t \qquad \text{(1, revisited)}$$

The reproductive value of an individual at birth is defined by RV_0. It is important to note that an individual may not be able to reproduce before a given age, in which case $m_t = 0$ until that age is reached.

2.2. The model

Here, to start and to keep things simple, we will consider only the direct parental effect on its offspring and no effect on other related kin. Therefore, the relatedness is 0.5, the reproductive value of the offspring could be expressed as RV_0, and the number of offspring produce is RV_x. We could thus rewrite:

$$\begin{aligned} I_x &= \frac{1}{2}\left(RV_x + \frac{1}{2}RV_x \cdot RV_0\right) \\ &= \frac{1}{2}\left(m_x + RV'_x\right) \cdot \left[1 + \frac{1}{2}RV_0\right] \end{aligned} \qquad (5)$$

Let us define Δm_x and ΔRV_0 to be the increase in an individual's fecundity and its offspring's reproductive value at age zero, respectively, due to terminal investment at age x. In this case, an individual's inclusive fitness given terminal investment (I'_x) will not include future reproductions because $RV'_x = 0$ when terminally investing. Again, an increase in current reproduction will be modelled with Δm_x. Likewise, in addition to producing more offspring, an individual may terminally invest by increasing the reproductive value (e.g., survival) of its offspring; to model this, we use ΔRV_0, which is added to RV_0. We could then write:

$$I'_x = \frac{1}{2}\left(m_x + \Delta m_x\right) \cdot \left[1 + \frac{1}{2}\left(RV_0 + \Delta RV_0\right)\right] \tag{6}$$

By substituting (5) and (6) in (**??**), we thus have terminal investment when,

$$\begin{gathered} \frac{1}{2}\left(m_x + \Delta m_x\right) \cdot \left[1 + \frac{1}{2}\left(RV_0 + \Delta RV_0\right)\right] > \frac{1}{2}\left(m_x + RV'_x\right) \cdot \left(1 + \frac{1}{2}RV_0\right) \\ \frac{1}{2}m_x \cdot \Delta RV_0 + \Delta m_x \left[1 + \frac{1}{2}\left(RV_0 + \Delta RV_0\right)\right] > RV'_x \left(1 + \frac{1}{2}RV_0\right) \end{gathered} \tag{7}$$

The above inequality is, unfortunately, not terribly elegant, but it is intuitively satisfying upon close examination. The first term on the left hand side of the inequality shows the inclusive fitness contribution from terminal investment on the baseline offspring production (i.e., for offspring that do not exist only because of the terminal investment, but would have anyway for an individual of age x). This inclusive fitness contribution includes the baseline offspring number itself (m_x), with an added increment of inclusive fitness caused by an increase in the reproductive value of those offspring (ΔRV_0), multiplied by the parent-offspring relation ($\frac{1}{2}$). The second term on the left hand side of the inequality shows the inclusive fitness contribution from the additional offspring produced through terminal investment (Δm_x). This contribution comes from the offspring themselves, plus the full reproductive value of those offspring ($RV_0 + \Delta RV_0$). The reason the full reproductive value is added, instead of just ΔRV_0 is because the inclusive fitness increment from terminal investment includes all of the reproductive value of these new individuals, not just the added increment to already existing individuals. There is an elegant way to consider just terminal investment in offspring production or offspring reproductive value (see below).

However before doing so, we can also rearrange inequality (7) on terminal investment into its direct and indirect fitness components.

$$\underbrace{\Delta m_x}_{W_{direct}} + \underbrace{\frac{1}{2} m_x \Delta RV_0 + \frac{1}{2} \Delta m_x \left(RV_0 + \Delta RV_0\right)}_{W_{indirect}} > \underbrace{RV'_x}_{W_{direct}} + \underbrace{\frac{1}{2} RV'_x \cdot RV_0}_{W_{indirect}} \tag{8}$$

$$\underbrace{\frac{1}{2}\left[RV_0 \left(\Delta m_x - RV'_x\right) + \Delta RV_0 \left(m_x + \Delta m_x\right)\right]}_{W_{indirect}} > \underbrace{RV'_x - \Delta m_x}_{W_{direct}} \tag{9}$$

Now, we can try to reorganise the equation by multiplying all terms by 2 and bring them all on the left side of the inequality.

$$\begin{aligned} RV_0 \left(\Delta m_x - RV'_x\right) + \Delta RV_0 \left(m_x + \Delta m_x\right) - 2\left(RV'_x - \Delta m_x\right) > 0 \\ \left(\Delta m_x - RV'_x\right)\left(2 + RV_0\right) + \Delta RV_0 \left(m_x + \Delta m_x\right) > 0 \end{aligned} \tag{10}$$

Now, if we divide the previous equation by $(2 + RV_0)$ and rearrange the terms, we obtain the much more elegant inequality predicting terminal investment:

$$\Delta m_x + \frac{\Delta RV_0 \left(m_x + \Delta m_x\right)}{2 + RV_0} > RV'_x \tag{11}$$

Terminal investment is beneficial when the in direct fitness plus the weighted gain in indirect fitness is higher than the residual reproductive value.

3. Simulations

4. Discussion

References

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