Modeling Individual Reproductive Fitness using Resource Allocation leading to a Post-reproductive Life

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Two *Physa acuta* snails

Abstract:

Some species exhibit a post-reproductive period, where individuals stop reproducing before they die. This is often explained as kin interactions—individuals forego additional reproduction, in turn increasing the fitness of genetic relatives. Recent evidence suggests that post-reproductive periods are not restricted to species exhibiting kin interactions. We developed a fitness model to test the hypothesis that a post-reproductive period can evolve as a consequence of optimal resource allocation. In the model, resource allocation is plastic and divided into reproduction, growth, or inducible defenses. The survival function utilizes a modified Gompertz-Makeham law for mortality. The fecundity function is the product of the reproductive schedule and output. The schedule utilizes a gamma distribution and the output is modeled linearly. Optimizing the fitness model yields the optimal resource allocation and resulting reproductive schedule. This allows us to understand the effects of phenotypic plasticity in life-history traits on the evolution of a post-reproductive period.

Model:

We have modeled the fitness of Physa acuta, a species of freshwater snail. We adapt the standard model of fitness to include clutch size as follows:

$$R_o = \int_0^{\infty} l(x)f(x)c(x)dx$$

where l(x) is the probability of surviving till day x, f(x) is the reproductive schedule in clutches per day at day x, and c(x) is the reproductive output in eggs per clutch.[1]

This model begins at maturity and assumes a constant strategy throughout the organism's life.

Parameters:

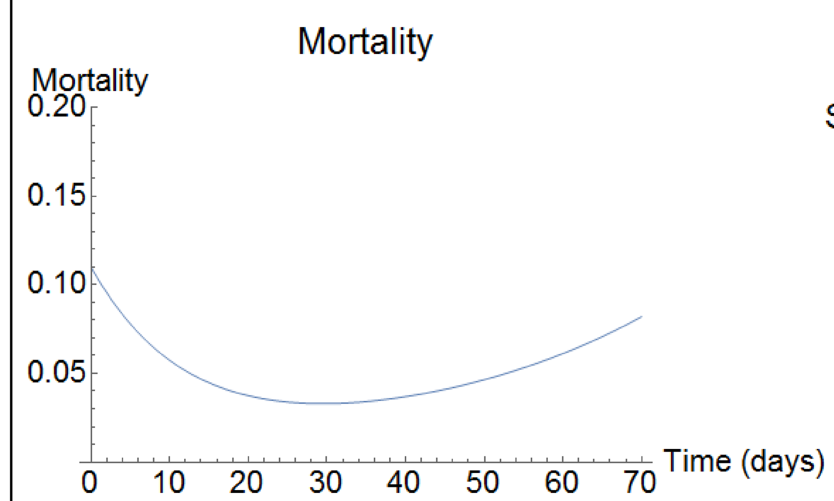
r:	Resource allocation to reproduction
s:	Resource allocated to size
d:	Resource allocated to inducible defenses
k_s:	Size Defense Efficiency
k_d:	Inducible Defense Efficiency
E:	Predation Rate
α:	Base age dependent mortality
β:	Rate of increase of age dependent mortality
a:	Age at which reproductive rate peaks when r=1
n:	Coefficient of variation of the reproductive schedule distribution
m_s:	Rate of increase of Clutch Size

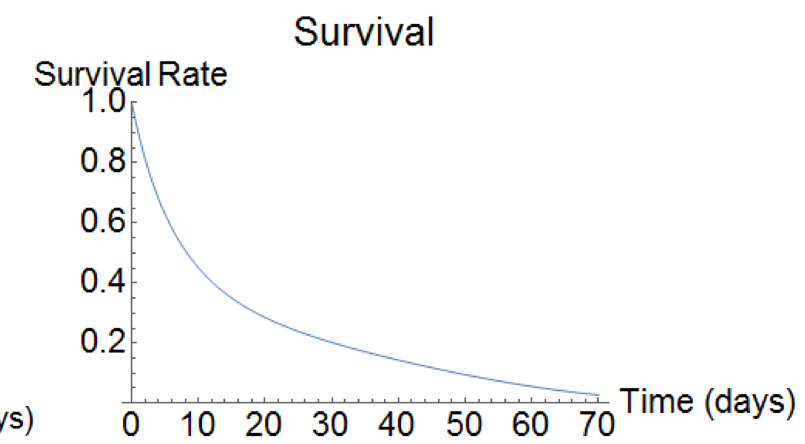
Survival Function: Modified Gompertz-Makeham Probability of Surviving until day t

$$h(t) = \alpha e^{\beta t} + E * e^{-(k_s * s + kd * d)t}$$

$$l(t) = e^{-\int_0^t h(x)dx}$$

There are two different types of mortality, age dependent and age independent. Age dependent mortality eventually become the dominant source of mortality as the species ages. Predation is the source of age independent mortality in this model. Instead of a modeling the age independent mortality as a constant as in a traditional Gompetz-Makeham distribution., the model allows predation to vary depending on the type of predator and resource allocation.





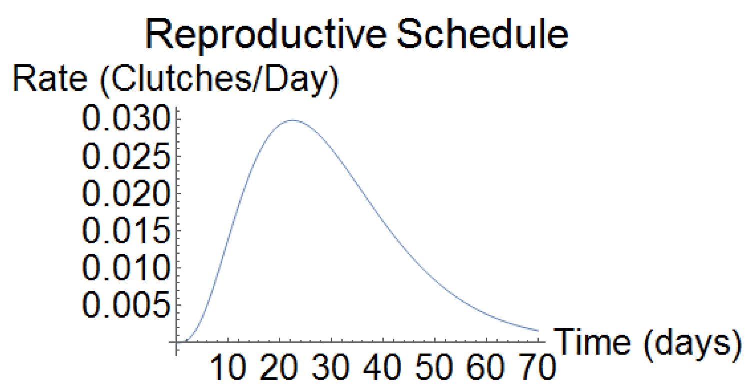
Reproductive Scheduling: Gamma Distribution Clutches per Day

$$f(t) = \frac{t^{k-1} e^{\frac{-t}{\theta}}}{\Gamma(k)\theta^k} \qquad Mean = \frac{a}{r} \qquad Std\ Dev = mean * n = \frac{a}{r} * n$$

The gamma distribution is a standard model for fecundity for species that experience reproductive senescence.[2]

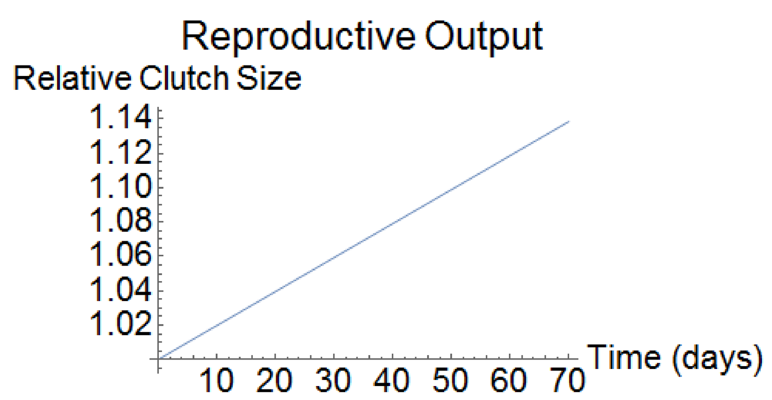
The mean and standard deviation are related to the shape parameter k, and the scale parameter θ of the gamma distribution as follows:

$$Mean = k\theta \qquad Variance = k\theta^2$$



Reproductive Output: Linear Eggs per Clutch

$$c(t) = 1 + m_s st$$



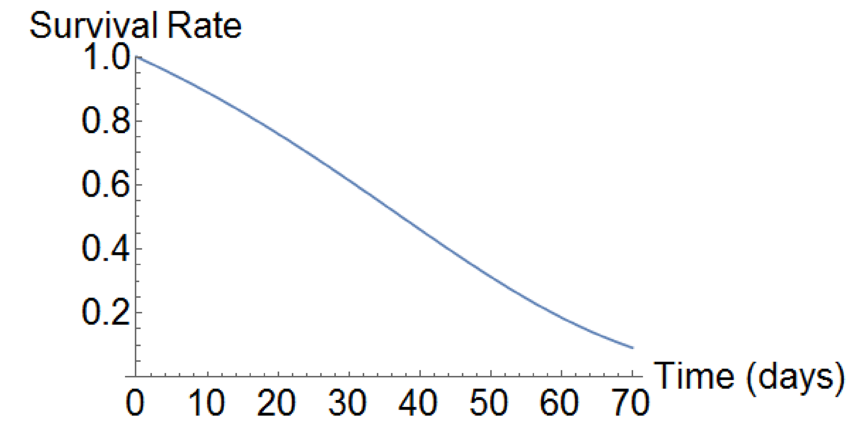
There is a positive correlation between size and clutch size and modeled linearly.

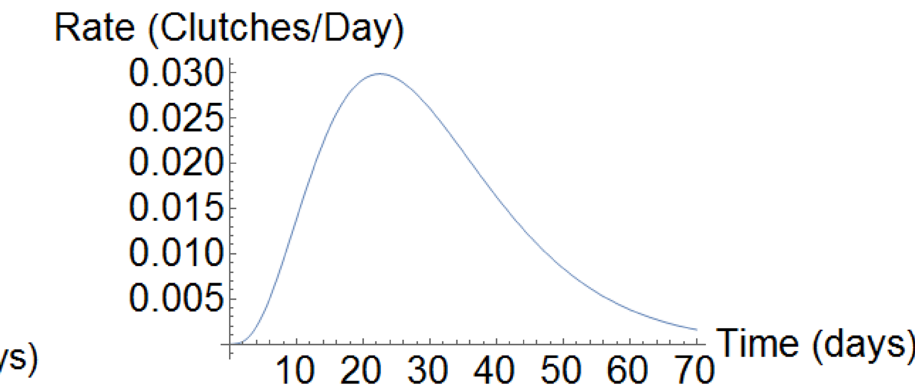
In each of the above plots:
k_s=.05, k_d=.20, E=.1, α=.01, β=.03, a=10, n=1/2, m_s=.006, r=.33, s=.33, d=.33

Model

There exists an unique optimal resource allocation over the $r + s + d = 1$ constraint that Mathematica's built in solver can calculate. This is used to plot the corresponding survival and reproductive schedule curves at the optimal allocation.

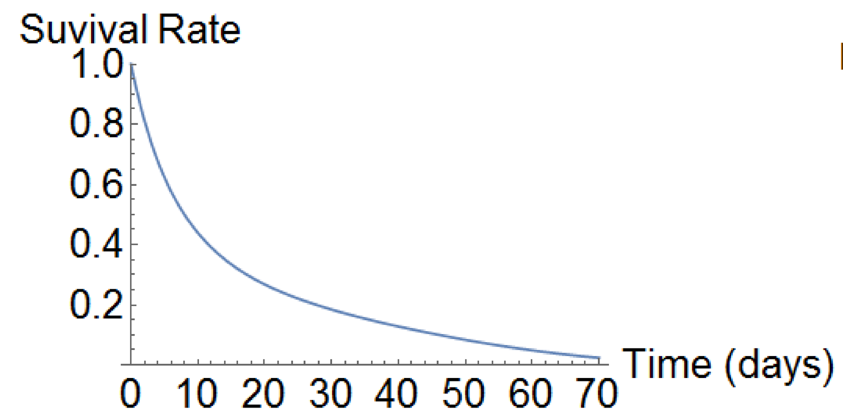
E=0: Optimal Output: r=1, s=0, d=0

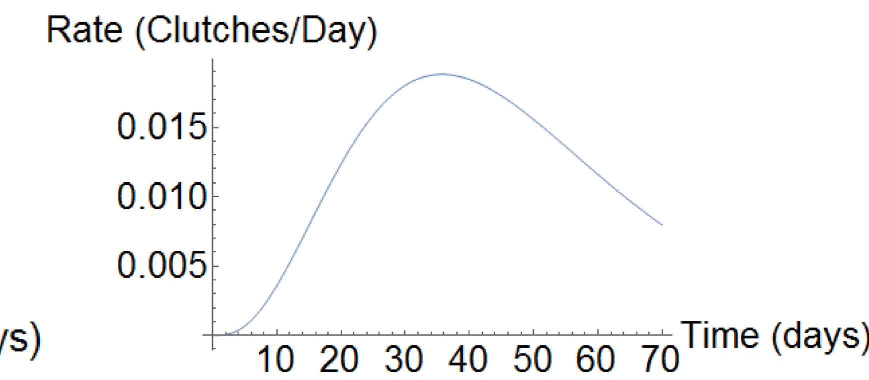




99% Reproduction ends at 76 days. 5.3% of snails survive until this day.

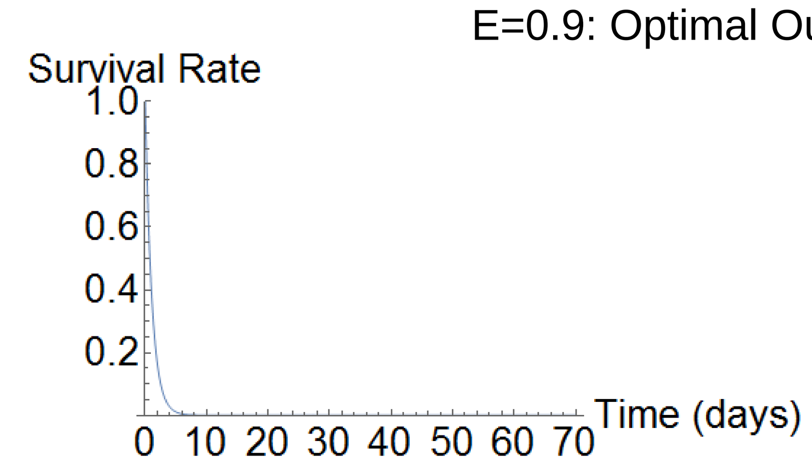
E=0.1: Optimal Output: r=.63, s=0, d=.37

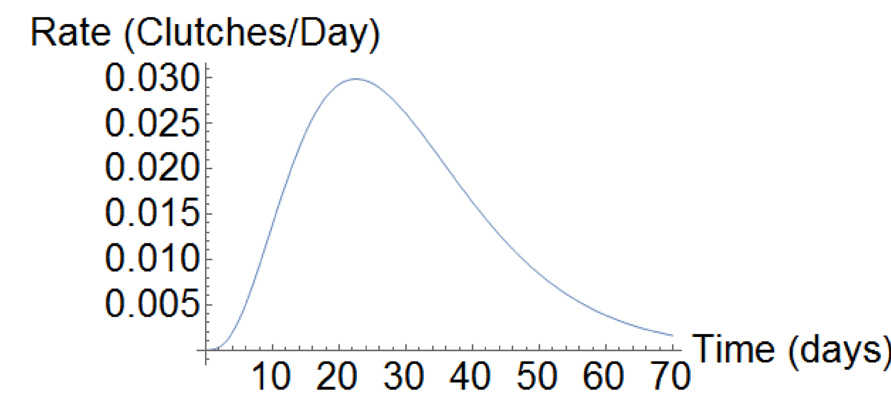




99% Reproduction ends at 120 days. 0.00018% of snails survive until this day

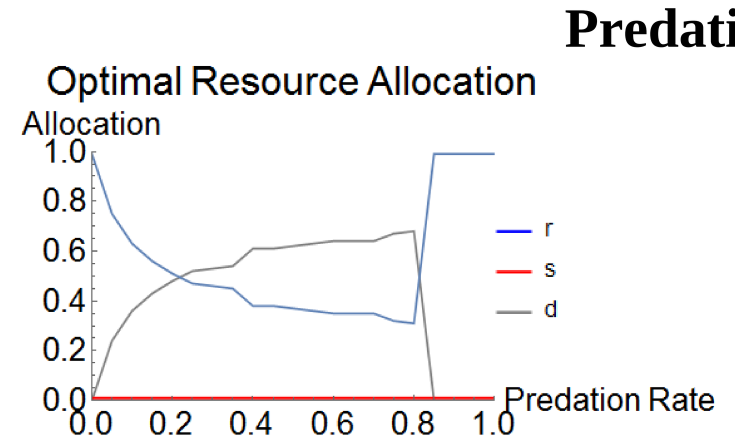
E=0.9: Optimal Output: r=1, s=0, d=0





99% Reproduction ends at 76 days. 1.11242*10^{-29}% of snails survive until this day.

Predation Parameter Sweep



As predation increases, more resources are allocated towards whichever defense is more valuable.

In this scenario, survival is shown to be more valuable as opposed to increasing the reproductive output and thus no resources are allocated towards size.

Conclusion

The optimal resource allocation varies with the environmental parameters. As predation increases, resources are allocated towards defenses and reproduction gets delayed. Once predation is sufficient large, resources are reallocated entirely towards reproduction once again.

Literature Cited

1. Stearns, S. C. *The evolution of life histories*. Oxford: Oxford University Press, 1992.
2. Gage, T. (2001). Age-specific fecundity of mammalian populations: A test of three mathematical models. *Zoo Biology*, *20*(6), 487–499. doi:10.1002/zoo.10029