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

Lane D'Alessandro[1], Allison Kolpas[1], Josh Auld[2]
[1]Department of Mathematics, West Chester University,
[2]Department of Biology, West Chester University,
West Chester, PA

Two *Physa acuta* snails

Abstract:

Fitness is environment-specific, and many organisms have evolved the ability to alter resource allocation based on perceived environmental cues (e.g., food/mate availability, predation risk). We are developing an optimization model that examines relative resource allocation into growth, reproduction, and defensive morphology under varying conditions. Specifically, we are investigating how reproductive investment in terms of rate and amount changes as a function of predation risk. The survival function utilizes a modified Gompertz-Makeham law for mortality. The fecundity function is the product of the reproductive schedule and output. The reproductive schedule utilizes a gamma distribution and the output is modeled exponentially. 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 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. Resource allocation may change over time. Resources are modelled in the following manner.

$1 = s(t) + d(t) + r(t)$	Total Resource Allocation
$s(t) = i_s e^{-m_s * t}$	Allocation to Growth
$d(t) = i_d e^{-m_d * t}$	Allocation to Defenses
$r(t) = 1 - s(t) - d(t)$	Allocation to Reproduction

The model begins at maturity. Therefore we know the following:

$$r(0) = 0$$

$$i_s = 1 - i_d$$

Parameters:

i_s	Initial resource allocation to growth
m_s	Rate of change of resource allocation into growth
i_d	Initial resource allocation to inducible defenses
m_d	Rate of change of resource allocation into inducible defenses
k_s:	Growth Defense Efficiency
k_d:	Inducible Defense Efficiency
E:	Predation Rate
t_1:	Age at which age dependent mortality hits .1%
t_2:	Age at which age dependent mortality hits 100%
μ:	Age at which reproductive rate peaks when r=1
c_v	Coefficient of variation of the reproductive schedule distribution
r_s:	Clutch size growth efficiency
L	Maximum Clutch Size

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

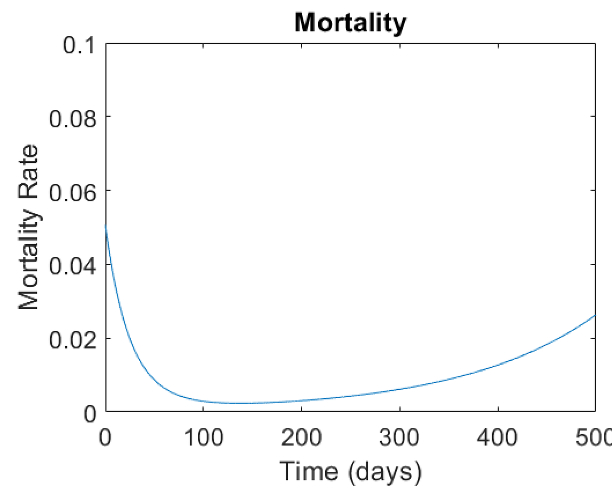
$$h(t) = \alpha e^{\beta t} + E * e^{-(k_s * s(t) + kd * d(t))t} \qquad l(t) = e^{-\int_0^t h(x)dx}$$

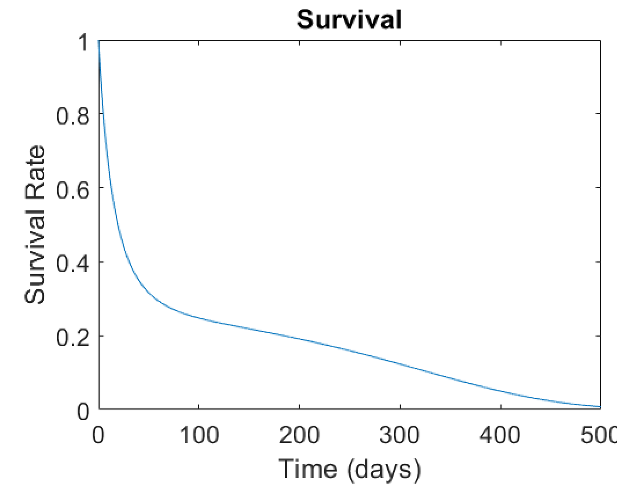
There are two different types of mortality, age dependent and age independent. Age dependent mortality eventually become the dominant source of mortality as the species ages. Predation is the source of age independent mortality in this model. Instead of a modeling the age independent mortality as a constant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

$\alpha e^{\beta t}$ is the age dependent component of the mortality function. α and β are computed by solving the following system.

$$\alpha e^{\beta\, t_1} = .001$$

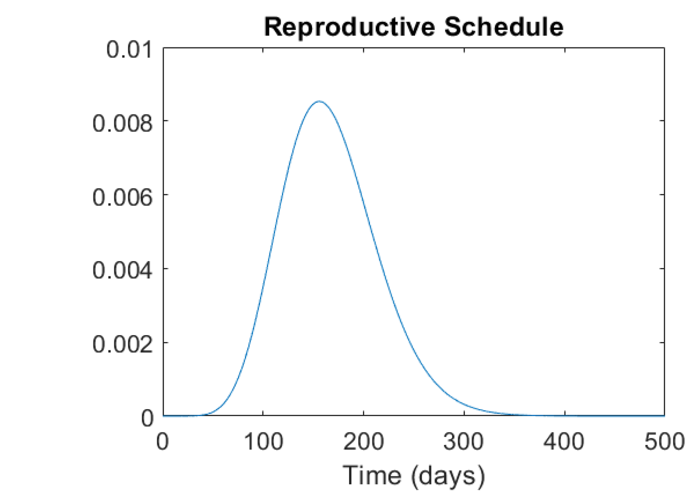
$$\alpha e^{\beta\, t_2} = 1.00$$





Reproductive Scheduling: Gamma Distribution
Clutches per Day

We model the reproductive schedule by modelling the mean of the schedule and the standard deviation of the schedule. The mean and standard deviation is used to determine the shape and scale parameter of the gamma distribution. The gamma distribution is then normalized.



$$Mean = \frac{\mu}{r(t)}$$

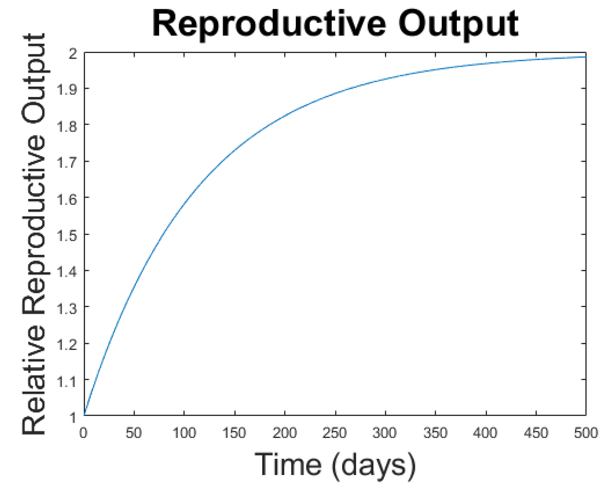
$$Std\ Dev = mean * c_v = \frac{\mu}{r(t)} * c_v$$

$$f(t) = gammapdf\left(\frac{1}{c_v}, \frac{\mu * c_v^2}{r(t)}\right)$$

Reproductive Output: Exponential
Eggs per Clutch

The reproductive output is modelled exponentially, using a differential equation. By placing more resources into growth, the organism may produce more offspring per clutch. The rate of increase for the clutch size decreases as it approaches the maximum size of *L*.

$$\frac{dc(t)}{dt} = r_s * s(t)(L - c(t))$$



In each of the above plots:
k_s=.0230, k_d=.0461, E=.1,t_1 = 50, t_1 = 1000, μ=50,c_v = .5, r_s=.0322, i_s = .272, m_s = .0001, m_d = .003

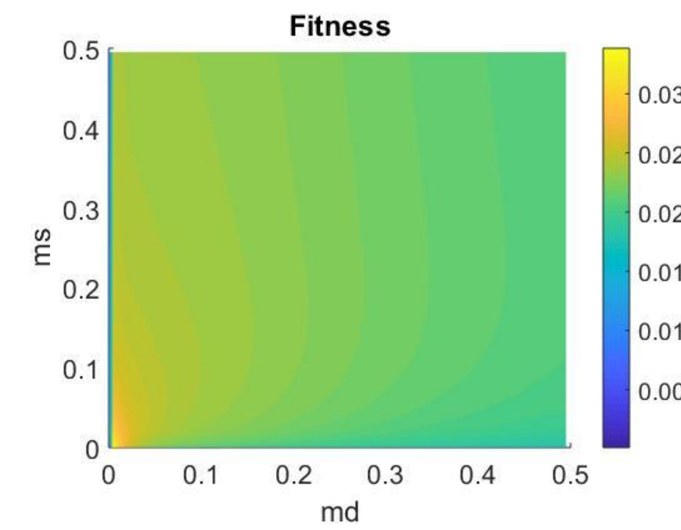
Optimization/Results

There exists an optimal allocation. We utilize Matlab to optimize over i_s, m_s, and m_d. We optimize the following function by finding the maximum R_o

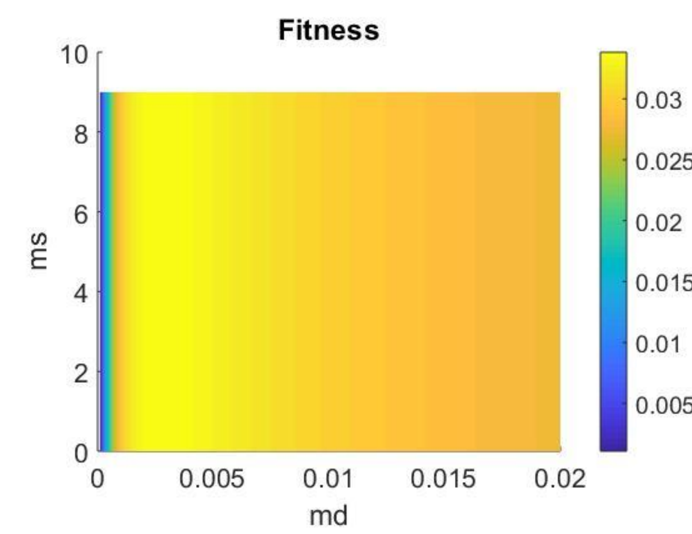
$$R_o = \int_0^{t_2} c(x)f(x)l(x)dx$$

E	i_s	m_s	i_d	m_d	Avg Reproductive Schedule	Std Dev of Reproductive Schedule
0	0.999998	0.006132	2.25E-06	24.9974	104.0173	30.78217
0.01	0.999999	0.007388	1.06E-06	24.98752	96.62654	29.11302
0.02	0.414693	1.22E-03	0.585307	0.005193	135.8719	39.80319
0.03	0.323286	0.000354	0.676714	0.004437	145.0509	42.63118
0.04	0.27229	7.94E-07	0.72771	0.003882	151.2478	44.22143
0.05	0.2413	1.67E-08	0.7587	0.00341	155.7441	44.93184
0.06	0.216701	1.41E-08	0.783299	0.003082	159.5707	45.6034
0.07	1.88E-06	24.98345	0.999998	0.004371	119.5538	34.42066
0.08	2.05E-06	24.93803	0.999998	0.003987	124.3015	35.55558
0.09	4.56E-07	24.9878	1	0.003682	128.5895	36.58711
0.1	2.06E-06	25.01828	0.999998	0.003434	132.4962	37.53171
0.11	1.46E-05	24.97842	0.999985	0.003229	136.0785	38.40176
0.12	3.36E-06	24.97989	0.999997	0.003054	139.4117	39.21292
0.13	3.88E-06	24.97132	0.999996	0.002904	142.5069	39.96865
0.14	0.114413	1.08E-06	0.885587	0.002046	178.0219	49.33293
0.15	5.27E-06	24.97553	0.999995	0.00266	148.1278	41.34548
0.16	0.10033	1.66E-06	0.89967	0.001936	180.8851	49.95585
0.17	7.34E-05	24.89056	0.999927	0.152274	51.1148	24.59103
0.18	9.98E-05	24.85727	0.9999	0.185566	50.72757	24.7062
0.19	1.14E-05	0.651983	0.999989	0.214193	50.52055	24.77556
0.2	0.000165	24.77366	0.999835	0.241085	50.38871	24.82368

We see there is an erratic behavior around predation rate of .14. We can examine the fitness landscape by producing a surface plot around that predation rate.



E = .14, i_s = .114413



E = .14, i_s = .00000108
(Optimal i_s at E = .141)

There are two local maximums. This presents two possible strategies that the organisms may take.

Conclusion

The optimal resource allocation varies with the environmental parameters. As predation increases, reproduction gets delayed in favor of defenses. Once predation hits a rate of 0.17, there is a complete shift in strategy, and the optimal strategy becomes to reproduce as quickly as possible.

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