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Dustin J. Marshall, Selina S. Heppell, Stephan B. Munch, and Robert R. Warner. 2010. The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology* 91:2862–2873.

Appendix A. Do larger mothers contribute disproportionately more to recruitment? Details of model that explores the fitness benefits of mothers of various size producing suboptimal sized offspring.

If we assume that the probability of surviving a period of sibling competition depends on the number of siblings, $s_c(n)$, subsequent survival is a function of offspring quality $s_q(q)$, and that these effects act prior to any density-dependent recruitment, then the total number of surviving, pre-recruitment offspring produced by mother of age a, v_a, is given by $v_a = n_a s_c(n_a) s_q(q_a)$. Assuming that density-dependence acts on all of these surviving individuals in the same way, recruitment will be some function, *f*, of the total numbers produced over all ages, i.e.,

$$R = f\left(\sum_{a=1}^{\infty} v_a N_a\right)$$

where N_a is the number of mothers of age a.

Our interest is in determining the relative impact on recruitment of removing mothers of different ages. We can define the relative importance of mothers of age a, I_a, as the change in recruitment due to a change in the number of mothers of age a divided by the total change in recruitment resulting from an identical change in the number of mothers at all ages. That is,

$$I_a = \frac{\frac{\partial R}{\partial N_a}\Delta N_a}{\sum_{i=1}^{\infty}\frac{\partial R}{\partial N_i}\Delta N_i}$$

Since we are assuming the change in the number of mothers is the same at all ages, the ΔN terms cancel. Substituting the expression for recruitment, we find

$$I_a = \frac{f'\left(\sum_{i=1}^{\infty} v_i N_i\right) v_a}{\sum_{j=1}^{\infty} f'\left(\sum_{i=1}^{\infty} v_i N_i\right) v_j}$$

where $f'(x)$ indicates the derivative $\frac{df}{dx}$. Since this term is constant, it cancels, leaving behind the nicely simplified expression

$$I_a = \frac{v_a}{\sum_{j=1}^{\infty} v_j}$$

That is, regardless of the form of density dependence, the assumption that density dependence acts on all offspring the same way leads to the conclusion that the relative importance of mothers at age a depends only on their proportional contribution to the total offspring production prior to density-dependence. This result allows us to focus on the question of how the number of offspring that survive to density dependence varies with maternal age.

Assuming that energy allocated to reproduction, E, is the main thing that varies with age, we focus on how total pre-recruit production, v_a, varies with E and use the Lagrange multiplier theorem to show that

$$\frac{dv_a^*}{dE} = s_c(n^*)s'_q\left(\frac{E}{n^*}\right)$$

Since s_c is strictly positive, local changes in v_a are driven primarily by the shape of s_q. If s_q increases monotonically, the relative importance of females will always increase with age (i.e., E). However, it is certainly plausible that s_q flattens out at high values of q, allowing for the possibility that older mothers with higher E don't contribute substantially more than smaller mothers.

Specific example

We used specific forms for s_c and s_q that are biologically reasonable and allow exact analytical results. Specifically,

$$s_c(n) = e^{-kn}$$

and

$$s_q(q) = q^a e^{-bq}$$

where a>1. This last expression arises from asserting that the proportional change in survival for a proportional change in investment is initially high but decreases linearly with additional investment.

Under the constraint $nq=E$, we have the following condition for optimality (the arguments of each function are suppressed to save space):

$$s_c s_q + n s'_c s_q = q s_c s'_q$$

where the derivatives are given by $s'_c = -ks_c$ and $s'_q = (\frac{a}{q} - b)s_q$. After substituting the derivatives, the condition for optimality reduces to

$$1 - kn = a - bq$$

With the constraint, $y=E/n$, we have a quadratic equation for the optimal number of offspring, n^* with solution,

$$n^* = \frac{\sqrt{(a-1)^2 + 4kbE} - (a-1)}{2k}$$

Of course, we are interested in how the total surviving offspring, v_a, varies with age. Assuming that E is the main thing that varies with age, we can use the Lagrange multiplier theorem to show that

$$\frac{dv_a^*}{dE} = s_c(n^*)s'_q\left(\frac{E}{n^*}\right)$$

After substituting, we find that the optimal allocation changes with E such that

$$\frac{dv_a^*}{dE} = e^{-kn^*-b\frac{E}{n^*}}\left(\frac{E}{n^*}\right)^a(\frac{an^*}{E} - b)$$

Therefore, as long as $an^*>bE$ the maternal contribution to recruitment increases with E. Now, in this model, s_q attains a maximum at $q = a/b$, so it stands to reason that q^* must be less than or equal to a/b. Since $nq=E$, this implies that $\frac{E}{n^*} \leq \frac{a}{b}$. That is, an^* will *always* be greater than bE. The case where E is so large that it makes sense to over-invest in quality so as to avoid producing too many offspring must be regarded as anomalous; the energy would certainly be better spent on some other trait outside the scope of this analysis (e.g. maternal survival or growth). Substituting the equation for n^* into this condition and simplifying suggests that the maximum value E should attain is $E = a/kb$. Therefore, v_a^* always increases with increasing E. However, the increase becomes very slight as E approaches it's maximum value. The figures below provide some illustration of the above arguments.

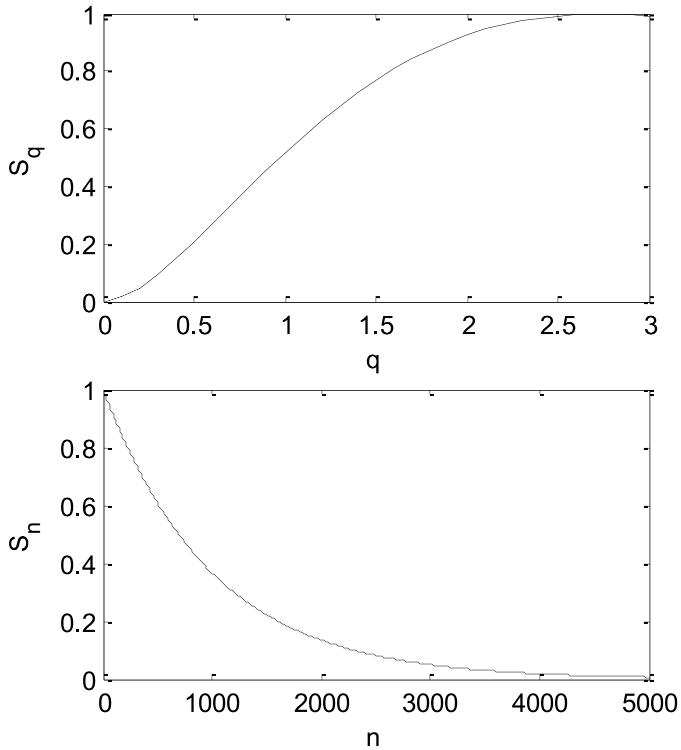

FIG. A1. Offspring survival as a function of (a) quality, q, and (b) density, n.

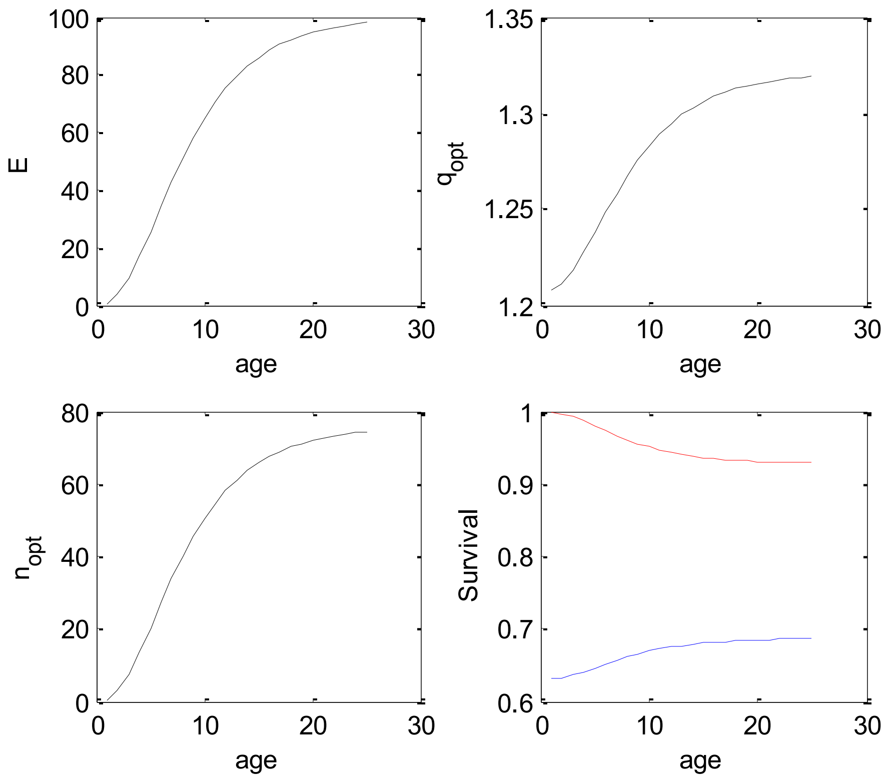

FIG. A2. Age patterns of energy, allocation, and offspring survival. (a) Available energy increases and levels off with age, E = 100(1-exp(-0.01*age)). (b) Optimal offspring quality with age, (c) optimal offspring numbers with age. (d) Blue line indicates the quality-dependent survival, S_q of mother of different ages, and the red line indicates the density-dependent survival, S_n.

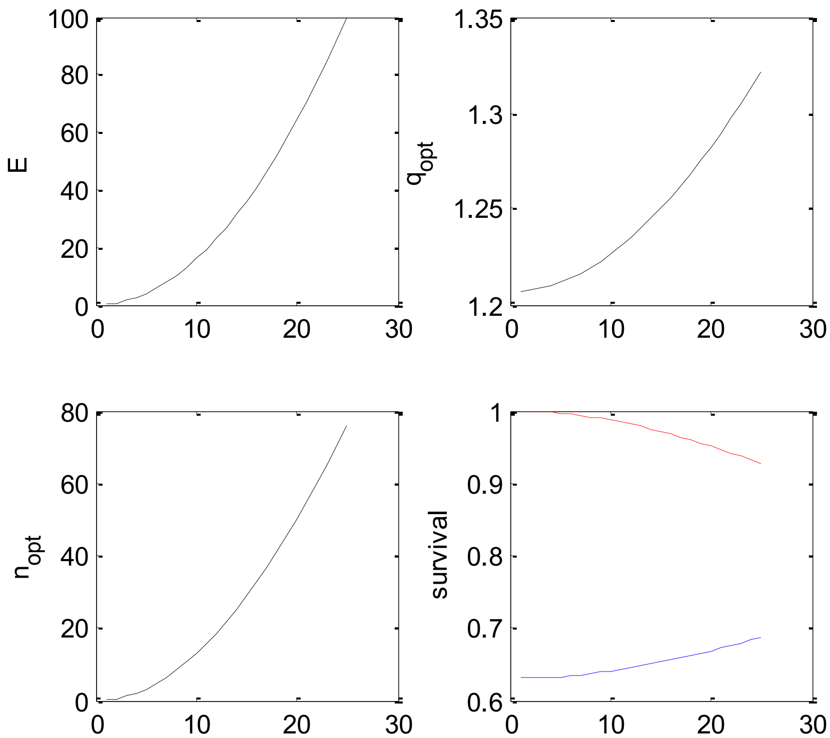

FIG. A3. (same as Fig. A2, but with different E schedule). Age patterns of energy, allocation, and offspring survival. (a) Available energy increases and levels off with age, $E = 100(age/25)^2$. (b) Optimal offspring quality with age, (c) optimal offspring numbers with age. (d) Blue line indicates the quality-dependent survival, S_q of mother of different ages, and the red line indicates the density-dependent survival, S_n.