Notes on Hamilton (1966)

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Video Notes

1. Fitness Sensitivities

Hamilton (1966)

If you read through Hamilton (1966) from end to end, good for you. Unfortunately, like Cole (1954) or (God forbid) Leslie (1945), most of this long paper is not actually that relevant for modern audiences. What you really need to know is really just contained in Hamilton's equation 8.

The rate of change in the so-called "Malthusian Parameter" (i.e., the intrinsic rate of increase from the characteristic equation) is given by

$$\frac{dm}{d\log p_a} = \frac{\sum_{a+1}^{\infty}\lambda^{-x}l_x F_x}{\sum_1^{\infty}x\lambda^{-x}l_x F_x},$$

where m is fitness (what we could probably call r), p_a is the survival probability from age a to $a+1$, $\lambda = e^m$ is fitness, l_x is the fraction ever born surviving to age x, and F_x is the age-specific fertility of females age x.

If we inspect the ratio on the right-hand side of this equation carefully, we see first that the denominator is the generation time. More precisely, it is the mean age of childbearing in the population. Note that $\lambda^{-x}l_x F_x$ is the probability that a randomly-chosen individual's mother was age x in a stable population. The denominator thus averages across all the ages of childbearing. The numerator is slightly more subtle. It is essentially the residual reproductive value for individuals of age a. Note that this paper came out in the same year that Williams formalized the concept of residual reproductive value (Williams, 1966), so that wasn't really a concept when Hamilton wrote this paper.

So the force of selection is essentially proportional to the remaining reproduction an individual has in their lifetime. If the organism in question has a long generation time, the force of selection on each age will be lower at each age since it needs to be spread out over a greater number of ages.

Hamilton, quoting Fisher (1958), gets something pretty spectacularly wrong: "As may be seen from the diagrams given in this paper [i.e., Fisher] a human curve of reproductive value (Fig. 3) rises to a maximum shortly after the attainment of reproductive maturity, while the curve of force of mortality (Fig. 2(a)) has a minimum at or slightly before it. Fisher argued that with an earlier age at marriage such as is very probable for our remote human and semi-human ancestry, the peak of reproductive value would have been earlier." (p. 13)

We now know that this is not, in fact, correct. Campbell and Wood (1988) note that the average age of menarche among hunter-gatherer populations was 19.5. With a couple of years of post-menarchial sub-fecundity, this suggests that women in "our remote ancestry" probably had ages of first reproduction not that different from those in modern nation states! What is really different in human history is the reproductive careers of agricultural peasants in the late 19th and the 20th centuries. We must seek another explanation for why the nadir of human mortality happens a full decade before the commencement of reproduction in most populations. Now, I should

note that Medawar (1952), whom Hamilton (1966) was criticizing in this passage, was also totally wrong. Medawar hypothesized that variants with deleterious age-specific effects early in life would be pushed by selection toward younger, pre-reproductive ages. Hamilton's results (and much subsequent research) shows that this is incorrect. In fact, the highest force of selection in an age-structured population falls on the pre-reproductive age classes.

The example that Hamilton (1966) uses is an interesting choice as well. He uses data from the Japanese colonial period of Taiwan (1906), a largely agrarian population with very high mortality and quite high fertility. Life expectancy was just under 30 in Taiwan in 1906, while the total fertility rate was greater than seven live births per woman. This is a pretty demographically extreme population. He also uses a fairly unconventional width of the age categories (2.5 years). Presumably, this required some interpolation from data that are typically reported by quinquennia (i.e., 5-year intervals).

Hamilton (1966) presents, almost as an afterthought, the sensitivity of fitness to changes in age-specific fertility. He is oddly reticent to discuss what the marginal benefits of a change in fertility would be because he is concerned about energy budgets: " it is not so plausible that a gene could simply add an element of fertility at a given age without affecting the rest of the schedule as it is that a gene might cause the elimination of a single element of mortality. Materials that went into the extra fertility would have to represent either materials 'saved' from potential earlier fertility or a subtraction from growth capital which would tend to cause all subsequent fertilities to be lowered." Nonetheless, he does, reluctantly provide an equation for the sensitivity of fitness to a change in age-specific fertility:

$$\frac{dm}{dF_a} = \frac{\lambda^{-a} l_x}{\sum_1^\infty x \lambda^{-x} l_x F_x}$$

Once again, the denominator is the mean age of childbearing. This time, the numerator is the proportional fraction of the stable age distribution in age-class a (see the notes on stable population theory). Note that unlike his equation 8 (for survival), this relationship is not a proper elasticity, since the change in $\log(\lambda)$ ($= m$) is not with respect to the natural logarithm of F_a.

A fair portion of Hamilton (1966) is dedicated to arguments about the validity of the fitness measure (it is; Charlesworth (1980) proved it) and about the mechanics for calculating numerical values for the derivatives. For example, he writes "Discussion in terms of the discrete treatment is here simpler on the whole: it not only steps off from the potentially available forms of schedule, but should be easier to follow. We shall therefore concentrate on this treatment and merely write the analogous expressions for the more ideal continuous one as we go along."

It turns out there is a much more straightforward and elegant way to calculate λ and its derivatives using demographic data from discrete age classes. This involves using projection matrices (e.g., the Leslie matrix), which the allow us to use the powerful and versatile tools of linear algebra. Caswell (1978) derived the formulae for calculating *fitness sensitivities* and *fitness elasticities* (which is what Hamilton's equation 8 are). The canonical reference for matrix population models is Caswell (2001).

Fitness Sensitivities and Fitness Elasticities

In a separate set of rather detailed notes, I lay out the derivation of fitness sensitivities and elasticities. Here, I will focus primarily on their calculation from demographic data.

Just remember the heuristic: the sensitivity of fitness with respect to a perturbation in some life-cycle transition (survival or otherwise) is the product of the reproductive value of the receiving

age/stage and the stable-population fraction of the sending age/stage (assuming that the right and left eigenvectors have been normalized so that their inner product is unity).

The R code for constructing demographic projection matrices and calculating fitness sensitivities is pretty simple. I have brought together a number of tools to facilitate this in the package demogR (Jones, 2007).

```r
library(demogR)
tw <- read.table("data/taiwan1906.txt", header=TRUE)
A <- leslie.matrix(tw$lx, tw$mx, L=FALSE, peryear=2.5, infant.class=FALSE)
## calculate a bunch of quantities
ea <- eigen.analysis(A)
## in case you wondered if Taiwan (1906) was unusual
## we can calculate the annual growth rate
log(ea$lam)/2.5
```

```
## [1] 0.03758702
```

```r
eee <- ea$elas
plot(eee,ylab="Elasticity")
legend("topright", c("survival","fertility"),lwd=2, col=c("black","grey"))
```
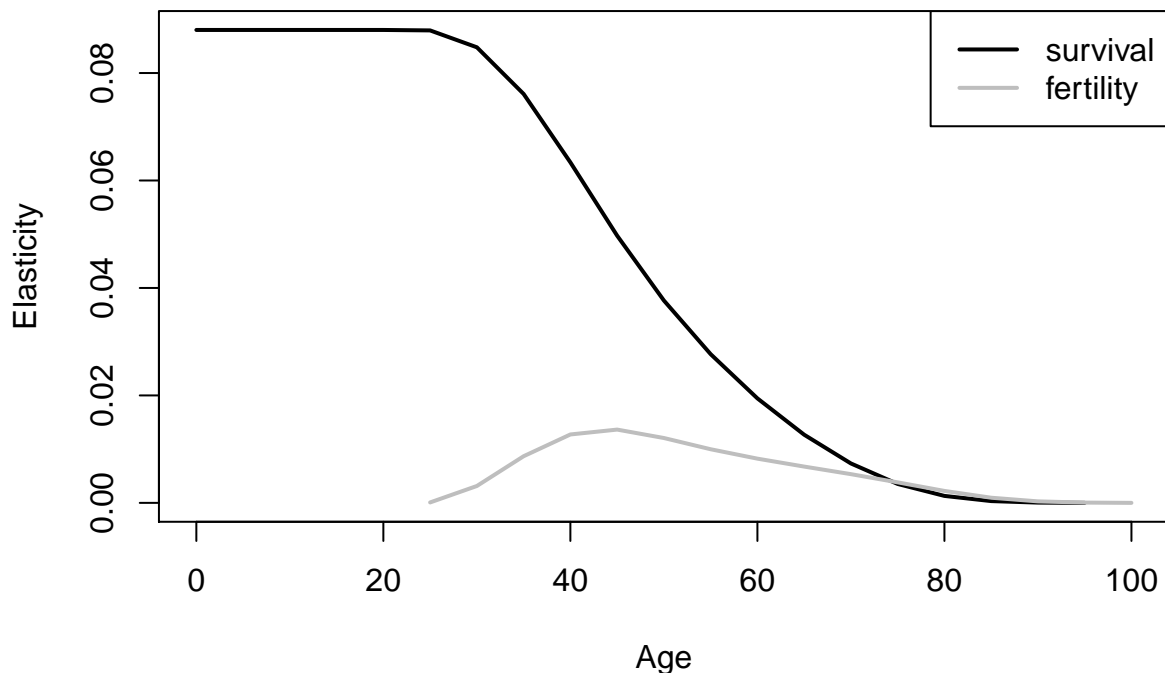

Note that this plot includes the elasticities of fitness with respect to both survival and fertility.

Check out that annual rate of increase. In 1906, the year of the first colonial census by the Japanese authorities, the annual rate of intrinsic increase was nearly 4%. This is *very* rapid growth. Note that our projection interval is 2.5 years. That means that the eigenvalue of our projection matrix, λ, is the multiplicative rate of increase per 2.5-year period. To get the annual rate of increase, we take the natural logarithm and divide by the projection interval.

We can plot famous "wall of death" that arises from Hamilton's theory (Charlesworth, 2001). As the force of selection approaches zero, the predicted mortality rate becomes infinite.

```r
## extract the subdiagonal
elas <- eee[row(eee)==col(eee)+1]
age <- cumsum(rep(2.5,20))
plot(age,1/elas, type="l", lwd=2, axes=FALSE, frame=TRUE,
     xlab="Age", ylab="Mortality Rate")
axis(1)
```
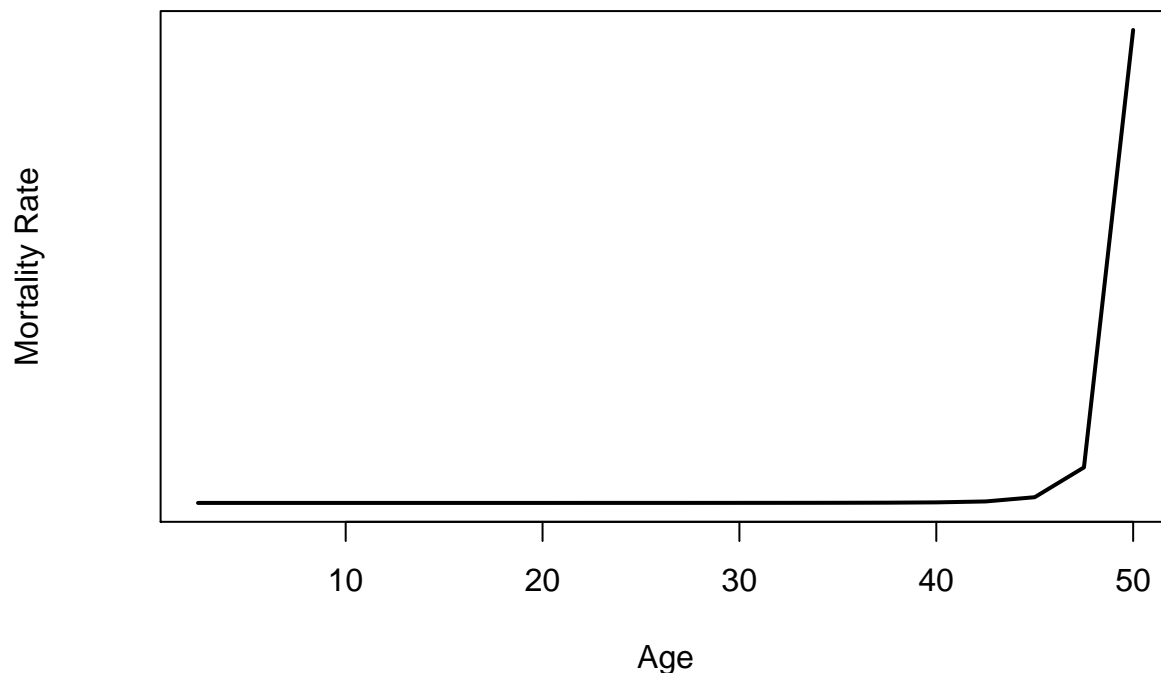

Remember that fitness sensitivities/elasticities are linearized estimates and that the actual fitness consequences of age-specific mutations are, in fact, quite nonlinear. Wachter et al. (2013) derive a nonlinear demographic model for mutation accumulation. Let's just say that they find things are a bit more complicated (it's a pretty challenging paper).

We used the function `eigen.analysis` from the `demogR` package to calculate and plot the elasticities. We can open up the black box, which is instructive. The construction of a Leslie matrix from demographic data is tedious, so we'll stick with the matrix we've already constructed. We'll just calculate the sensitivities more directly.

```r
# first, calculate eigenvalues/vectors of A
ev <- eigen(A)
# find the dominant eigenvalue and extract
# make sure only to take real part (since dominant eigenvalue is real)
lmax <- which(Re(ev$values)==max(Re(ev$values)))
lambda <- Re(ev$values[lmax])
# matrix of eigenvectors
U <- ev$vectors
# dominant eigenvector
u <- abs(Re(U[,lmax]))
# matrix of left eigenvectors (complex conjugate of the inverse of U)
V <- Conj(solve(U))
# dominant left eigenvector
```

```
v <- abs(Re(V[lmax,]))
# outer product of v and u
s <- v%o%u
# non-existent transitions -> 0
s[A == 0] <- 0
(ssurv <- s[row(s)==col(s)+1])
```

```
##   [1] 1.487877e-01 1.029903e-01 9.920296e-02 9.892871e-02 9.889502e-02
##   [6] 9.939245e-02 9.604344e-02 8.687920e-02 7.247216e-02 5.713744e-02
##  [11] 4.336106e-02 3.201452e-02 2.254900e-02 1.474489e-02 8.555541e-03
##  [16] 4.105204e-03 1.517160e-03 3.959903e-04 6.407484e-05 4.872607e-06
```

```
plot(age,ssurv, type="l", lwd=2, col="orange",
     xlab="Age", ylab="Fitness Sensitivity")
```
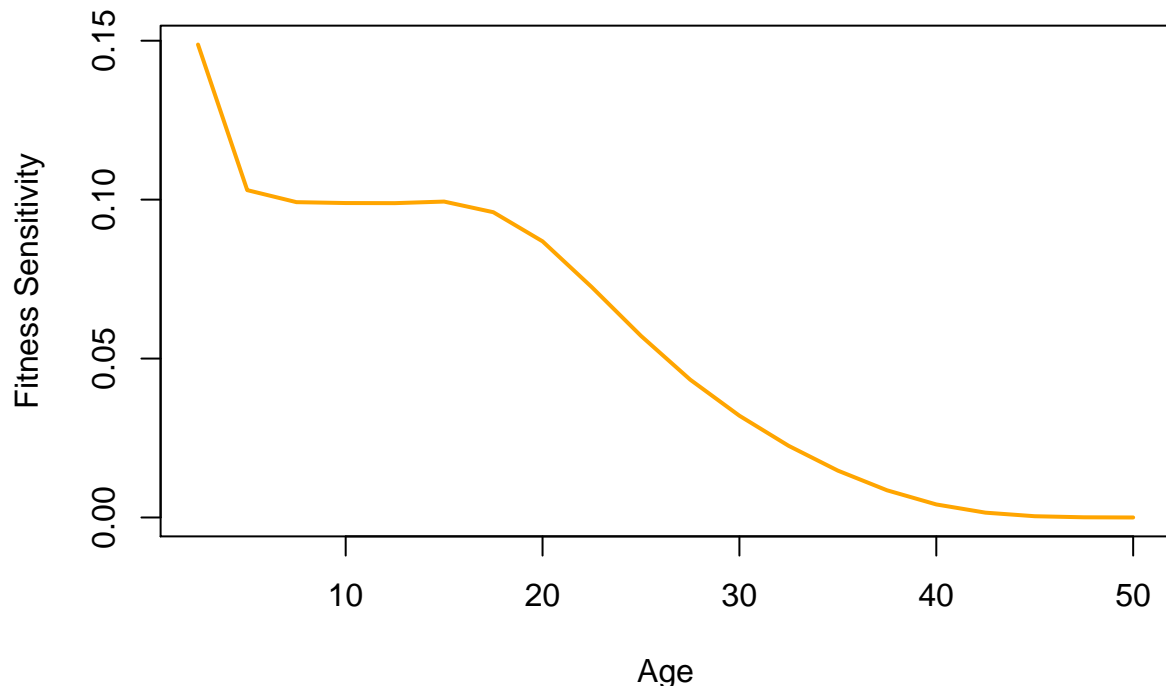


```
# weird
```

Elasticities are *proportional* sensitivities and are found simply by multiplying the sensitivities by a_{ij}/λ. Note that this is, in fact, what Hamilton (1966) calculated, since his equation 8 was for $dm/d\log p_a$. This is simply $e_{ij} = \partial \log \lambda / \partial \log a_{ij}$ for all $i = j + 1$ (i.e., the subdiagonal of the Leslie matrix).

```
e <- s*A/lambda
(esurv <- e[row(e)==col(e)+1])
```

```
##   [1] 8.801102e-02 8.801102e-02 8.801102e-02 8.801102e-02 8.801102e-02
##   [6] 8.792949e-02 8.478446e-02 7.610278e-02 6.337234e-02 4.973184e-02
##  [11] 3.766161e-02 2.767765e-02 1.944452e-02 1.268540e-02 7.335694e-03
##  [16] 3.518896e-03 1.295482e-03 3.356379e-04 5.401188e-05 4.058577e-06
```

```
## a neat trick
sum(e)
```

```
## [1] 1
```

```
plot(age,esurv, type="l", lwd=2, col="cornflowerblue",
     xlab="Age", ylab="Fitness Elasticity")
```
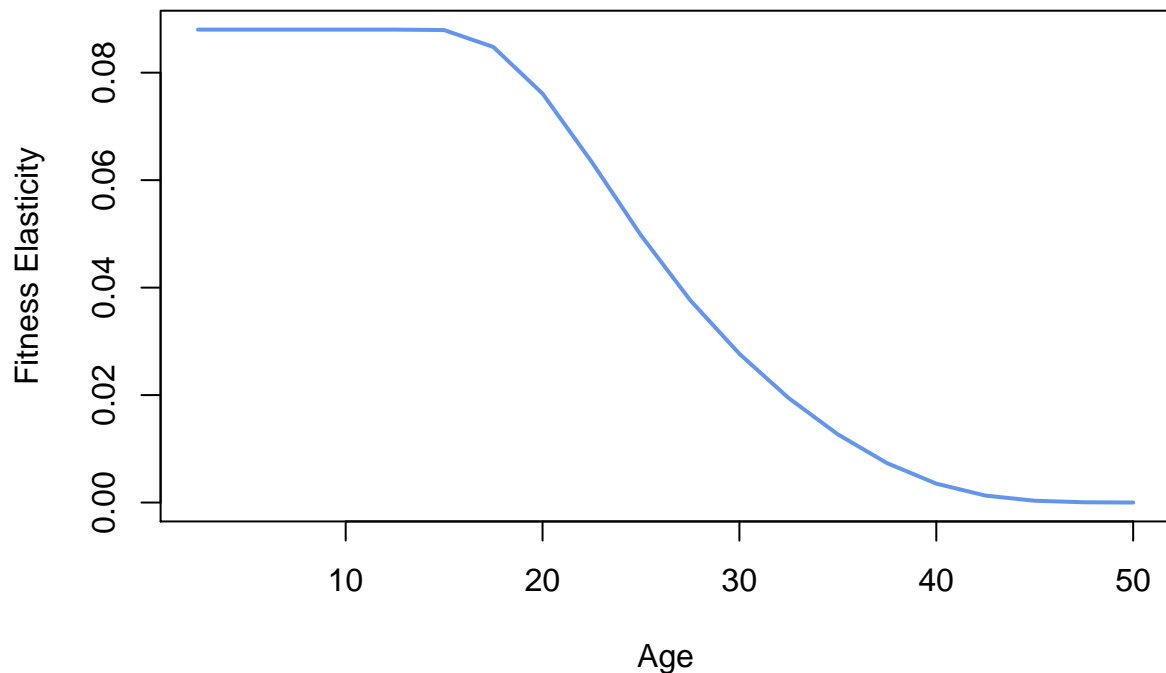
Note that the elasticities for all the pre-reproductive ages are identical. There are some very interesting results that help with the interpretation of elasticities with respect to the life-cycle graph in Van Groenendael et al. (1994). One of these results is that, for a given vertex in the life-cycle graph, the sum of the elasticities of all incoming arcs must equal the sum of the elasticities of all outgoing arcs. For the pre-reproductive ages, the only outgoing arcs are to the next age class, so they must all be equal. Going back to Hamilton's formula and the interpretation that the numerator of his equation 8 is equivalent to residual reproductive value, note that the elasticities of outgoing arcs essentially partition the incoming elasticity (i.e., the elasticity of survival from the previous age) between current reproduction (i.e., the elasticity of fertility at that age) and residual reproductive value (the elasticity of survival). Cool.

There are many applications for sensitivities and elasticities. The student of life history theory is well-advised to master their use. Three applications from my own work, that might be of interest to evolutionary anthropologists, include: (1) their contribution to stochastic measures of fitness (Jones, 2005), (2) the universality of the human life cycle (Jones, 2009), and (3) measuring constraints on selection on life histories (Jones and Tuljapurkar, 2015).

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