

Notes on Smith and Fretwell (1974)

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Video Notes

1. [Smith & Fretwell's \(1974\) Graphical Model for Quantity-Quality Trade-Offs](#)

Smith & Fretwell (1974)

This is a pretty disappointing paper on re-read. The model is quite poorly described and terms are quite vague. It is honestly quite surprising that this paper is such a mainstay of human behavioral ecology because the authors specifically note that it probably applies organisms with clutch sizes substantially greater than one – and that is not humans!

[Hill and Kaplan \(1999\)](#) may be part of the reason this paper has remained so relevant. They describe models where fertility and offspring quality as *The Smith-Fretwell Model*. The elements that [Hill and Kaplan \(1999\)](#) attribute to the Smith-Fretwell model include:

1. Parental investment increases juvenile survival up to some asymptotic.
2. Total number of offspring produced is the total resources available to the parent for reproduction divided by the resources invested per offspring.
3. Amount of investment per offspring is independent of parental income – i.e., all parents produce offspring of the same quality; better-off parents just produce more offspring.

Following the approach of [Levins \(1962\)](#) and [Levins \(1968\)](#), [Smith and Fretwell \(1974\)](#) define the *fitness set* as the curve that relates what they (confusingly) call “offspring fitness” to the average parental effort per offspring. “Offspring fitness” presumably refers to viability of an individual offspring. It's a sloppy use of the term since it confuses the technical definition with the colloquial meaning. The fitness set represents the possible phenotypes achievable by a species in a fitness space ([Levins, 1962](#)). Now, again, this is slightly sloppy usage, at least by my reading since neither of the axes of their figure 1 actually represent fitness. Rather, they represent some sort of proxy for two fitness components (parental investment per offspring and offspring viability).

In Levins's fitness-set approach, the optimal phenotype is found by the intersection of the fitness set with the *Adaptive Function*, $A(W_1, W_2)$, which is a function that maps the two (or more) fitnesses to a single value. We normally think of the adaptive function as being something like a budget constraint, showing the locus of allowable combinations of two phenotypes, but it doesn't necessarily need to be that way. [Levins \(1968\)](#) has a number of examples more like the present usage. What matters for the analysis is that the Adaptive Function relates the allowable combinations of the variables depicted on the axes. For Smith & Fretwell, the adaptive function is a line that connects equal combinations of parental investment and offspring viability, i.e., $W_y/I_p = k$ for some constant k . They assume that these are straight lines.

The Model

I will change the notation used by [Smith and Fretwell \(1974\)](#) because I don't think it is illuminating and is actually a bit confusing. Bertrand Russell famously commented that good notation can permit material to almost teach itself. In contrast, poor (or, worse, sloppy) notation can muddle even

simple things. In particular, they use W_y for offspring “fitness” (W is the conventional notation for fitness in population genetics). The thing is, they don’t mean fitness in the technical sense, they really just mean juvenile recruitment. We will call this P_j . Similarly, they refer to the investment required per offspring as I_y , while they denote the investment that a parent makes as I_p . These seem like different biological phenomena when analyzed from the perspective of the parent. So we will denote the investment required per offspring as I_j and, because in their model I_p is fixed and represents the total available energy for reproduction, we will let this be Δ . The parameter α appears out of nowhere on p. 502 (full paragraph after equation 2). Presumably, this is the angle of the Adaptive Function since W_y/I_y would be the tangent of that angle.

The fundamental assumption of [Smith and Fretwell \(1974\)](#) is that the number of offspring will simply be the ratio of the total available resources for reproduction and the cost per offspring:

$$N_j = \frac{\Delta}{I_j}.$$

The parental fitness for a given litter size will thus be the product of this and the average juvenile recruitment, P_j :

$$W_p = P_j N_j = \frac{P_j \Delta}{I_j}.$$

Assume that there are no costs to future reproduction. That is, the litter size now does not affect future litter size or juvenile recruitment. This means that we simply maximize W_p . [Smith and Fretwell \(1974\)](#) use a graphical argument for the optimum I_j , assuming a concave function relating juvenile survival to parental investment (i.e., $P_j'' < 0$; diminishing marginal returns to parental investment).

Lines rooted at the origin of different slopes, $P_j/I_j = k$, represent investment/clutch-size combinations of equal fitness for different values of k . The highest allowable intersection with the constraint curve will be where an equal-fitness line is tangent to that curve.

A confusing aspect of the plots in figure 2 is that the abscissa (x-axis) represents two different things: it’s both the parental investment per offspring *and* the number of offspring. Remember that offspring number is just the inverse of investment (multiplied by a constant, Δ).

The bottom panel of their figure 2 is constructed from the following observation: “The ratio of the slope of a fitness function through another point on the curve to the slope of the fitness function tangent to the curve gives the fitness to the parent of expending the amount of energy per offspring represented by that other point.” Note that the maximum value for this function is $W_p = 1$, indicating this is the ratio of the slope of the tangent line to itself.

We can recreate a plot like the top panel of figure 2. We’ll use the (arbitrary) classic form for diminishing marginal returns, a negative exponential, and offset it by one from the origin (hence the $x-1$ in the exponential). We’ll also use a somewhat obscure trick for making illustrative/schematic/theoretical figures like this. R will typically leave padding on the axes beyond the range of your data. For a figure like this, we don’t want that; we want the axes to meet at the origin, etc. To force the plot to do this, we use the parameters `xaxs="i"` and `yaxs="i"`. Because of the offset, we need to specify that the origin is included, hence `ylim=c(0,1)`; otherwise the x-axis would start at 1 rather than the origin.

In addition, we will solve for the optimal investment so we can draw a tangent line to the curve¹ To find the tangent point we want the point where the difference between the function and

¹Thanks to Mike Price for helping me figure this one out.

a first-order Taylor-series approximation of the function is zero. This is, by definition a point of tangency. We further specify the constraint that this line must pass through the origin. We then use the R function `uniroot()` to find the solution. Let f be our constraint function (i.e., the negative exponential) and f' be it's derivative. We want:

$$f - f'(z - x) = 0,$$

where z is the point of tangency. Solve for z and find the value of z that satisfies our equation.

```
x <- seq(0,20,length=500)
# constraint function
f <- function(x) {
  1 - exp(-0.2*(x-1))
}
# derivative of the constraint function
fprime <- function(x) {
  0.2*exp(-0.2*x)*exp(0.2)
}

# f + fp*(z-x) = 0
# z = x - (f/fp)
# solve for tangency; find the root of this
xinter <- function(x) {
  return(x - f(x)/fprime(x))
}

soln <- uniroot(xinter,c(0,10))

plot(x,f(x), type="l", lwd=2, xaxs="i", yaxs="i",
      xlab="Clutch Size (Parental Investment)",
      ylab="Offspring Survival",
      ylim=c(0,1))
lines(x,(f(soln$root)/soln$root)*x,col="red")
## some non-optimal adaptive functions
lines(x,(f(2)/2)*x,col=grey(0.85))
lines(x,(f(1.5)/1.5)*x,col=grey(0.85))
lines(x,(f(11)/11)*x,col=grey(0.85))
```

What happens to the optimal investment if the constraint curve is shifted down? For example if the exponential rate parameter were 0.1 rather than 0.2? What is the interpretation of such a shift?

Applicability to Human Life Histories

It's remarkable that the Smith-Fretwell model has been so influential in anthropology since they note that their model probably only works for organisms with a clutch size greater than one: "We consider in detail curves sufficiently convex for the intercept of the derivative to pass through zero for at least one point on the curve. Apparently this case applies to most of nature, as most clutches are greater than one, but we cannot prove this."

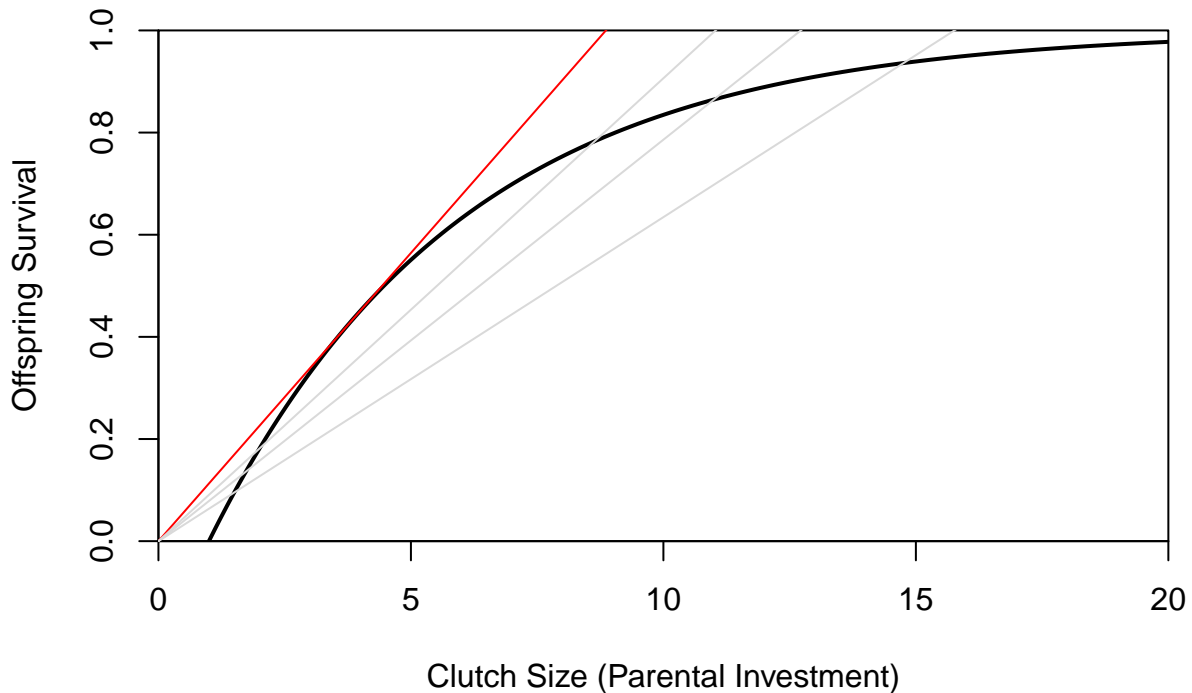


Figure 1: Fitness-set approach to optimal clutch size

Of course, there's nothing that says that the I_j -intercept can't be 1 or that the slope of P_j/I_j can't be quite steep.

However, the application of the Smith-Fretwell model to humans is clearly more about total fertility than it is about litter size per reproductive bout per se. Does it make sense to think of lifetime total fertility as "litter size"? Honest question.

A clear violation of the assumptions of the Smith-Fretwell model happens when people become richer and subsequently reduce their fertility. This phenomenon is often referred to as "the demographic transition," but the terminology is sloppy since there have actually been numerous demographic transitions throughout human history. This suggests that the simple framework laid out in [Smith and Fretwell \(1974\)](#) is insufficient to understand human decisions about reproductive investment. In all fairness, the model was never designed to do that, so we shouldn't be surprised!

I think that an approach like that of [Kaplan \(1996\)](#) or, even better, a dynamic optimization approach like that used by Ruth Mace in the early 90s (e.g., [Mace, 1993, 1996](#)), is the best approach. Unfortunately, students of human evolutionary ecology has not shown much taste for formulating models since the 1990s (I would love to be proven wrong on this). The problem is that we need students interested in the ecology and evolution of human life histories who are willing and able to learn the theory and the tools needed to extend and test that theory. This, in turn, means we need to be able to teach these methods, even if demand for courses that teach such methods is low. Hopefully, this course and these notes will help move us in that direction, even if only slightly.

References

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