

Notes on Gadgil and Bossert (1970)

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Video Notes

1. [Concavity and Convexity](#)
2. [Residual Reproductive Value](#)
3. [Deriving Reproductive Value](#)

Reproductive Effort

The big innovation of [Gadgil and Bossert \(1970\)](#) is to recognize (and formalize) the fact that both survival and fertility are likely to be functions of reproductive effort (RE). The greater RE is, the greater fertility will be. However, because of trade-offs, greater RE should also lead to lower survival.

While it's quite technical, there aren't really any new mathematical results in this paper. One aspect of the paper that was highly innovative in 1970 was the use of "an automatic computer," which they programmed to numerically solve the optimization problems of finding schedules of reproductive effort that maximize fitness. They use a discrete-time characteristic equation:

$$1 = \sum_x e^{-rx} l_x b_x$$

The schedules of age-specific survival (l_x) and fertility (b_x) are made to be functions of reproductive effort, θ (increasing for fertility; decreasing for survival). They then search the space of different solutions to the characteristic equation for values of θ that maximize r .

Survival is a function of both RE (θ) and "satisfaction" (ψ). This latter term indicates "the fraction of the resources actually available to the individual that is maximally utilizable." Gadgil and Bossert distinguish intrinsic interval survival probabilities (which they denote as α_i but I change to P_i here) from escape from predation, which is given by parameter η . All of these parameters (θ , ψ , η) are indexed by age (i.e., are age-specific). Thus survival to age x is given by:

$$l_x = \prod_0^{x-1} P_i f_1(\theta_i) g_1(\psi_i) \eta_i,$$

where P_i is the interval survival probability, $f_1(\theta_i)$ is a monotonically decreasing penalty on survival that is a function of reproductive effort θ_i , $g_1(\psi_i)$ is a monotonically increasing premium function on satisfaction ψ_i , and η_i is the probability of escaping death from predation.

[Gadgil and Bossert \(1970\)](#) also include a feature they call "reproductive potential," by which they basically mean size, if we want to be concrete about it. On p. 7 and thereafter, they actually equate reproductive potential with size: "The latter [fertility] depends on size at that age, w_j ..." It turns out that the size interpretation is problematic for homeothermic organisms (see below). They provide an equation that specifies the growth of organisms. Like survival, growth is a function of both RE (θ) and satisfaction (ψ):

$$w_x = w_0 + \sum_0^{x-1} \delta_i f_2(\theta_i) g_2(\psi_i)$$

where δ_i is the interval growth increment, $f_2(\theta_i)$ is a monotonically decreasing penalty on growth that is a function of reproductive effort θ_i , and $g_2(\psi_i)$ is a monotonically increasing premium function on satisfaction ψ_i .

Finally, fertility is also a function of both RE (θ) and satisfaction (ψ). Note that in Gadgil and Bossert's formalism, fertility is proportional to body size. This works for poikilotherms, but it certainly is not true for mammals, for whom annual fertility shows a pronounced negative allometry. The age-schedule of fertility is given by:

$$b_x = w_x f_3(\theta_x) g_3(\psi_x)$$

where w_x is the reproductive potential at age x , $f_2(\theta_i)$ is a monotonically increasing premium on fertility that is a function of reproductive effort θ_i , and $g_3(\psi_i)$ is a monotonically increasing premium function on satisfaction ψ_i .

Substitute appropriate values into the discrete-time characteristic equation:

$$1 = \sum_{x=0}^n e^{-rx} l_x b_x$$

where, as usual, r denotes the intrinsic rate of increase, sometimes called "the Malthusian parameter" (following Fisher).

This paper pre-dates the controversy over how to index ages in a discrete-time version of the Euler-Lotka equation. We should note that it is more appropriate to index from $x = 1$ than from $x = 0$ (Goodman, 1982; Caswell, 2001).

The objective of their analysis is to maximize r . The parameters α_i , δ_i , and w_0 are biological constraints on the life history, while ψ_i and η_i describe the environment.

Gadgil and Bossert invert the terms *concave* and *convex* from our contemporary usage. For a continuous function $f(x)$ in \mathbb{R} on the interval $[a, b]$, a necessary and sufficient condition for a convex function is that $f''(x) \geq 0$ for all $x \in [a, b]$. This is clearly the opposite of what Gadgil and Bossert say when they conclude that repeated reproduction can only be optimal when the profit function $P(\theta_j)$ is "concave" or the cost function $C(\theta_j)$ is "convex."

One perhaps confusing statement is that "Since θ_j affects neither l_j nor w_j , P_j will be a monotonically increasing function of θ_j for any given l_j and w_j ." We noted in the equations for survival and growth that both were functions of effort, so how can this be? The key is to look at the limits on the sums/products that define these schedules. The survival probability to age j does not depend on RE expended in age j ; it depends on the reproductive effort expended in previous ages. The situation with growth is similar.

It's unclear how important "satisfaction" is for the model. It seems likely that these were left constant across different parameter combinations. Similarly, it seems that specifying predation mortality is superfluous for the main results of the paper. Satisfaction does get used for the results in their table 2. Comparing their life histories 5 and 7, which are identical except that satisfaction declines in the last two age classes for LH7, LH7 shows greater RE early in life. This result, which is not discussed, anticipates the results of Schaffer (1974). Presumably, lower satisfaction leads to lower survival and fertility of the oldest age classes – it's effectively senescence. This makes the value of older adults less relative to the value of younger individuals, favoring greater RE.

There are two broad outcomes: (1) "big-bang" reproduction, or (2) repeated reproduction – in other words, semelparity vs. iteroparity. In the former case, the optimal RE is zero until an age is reached at which the profit exceeds the cost. At this point, maximal RE is optimal. In the case of repeated breeding, the optimal RE is $1 > \theta > 0$. This can only happen if the profit function is

concave or the cost function is convex. Think about this geometrically. Only when one of these two cases obtains can we have an intermediate difference between the benefits and costs be maximum.

In line with [Williams \(1966\)](#), Gadgil and Bossert find that reproductive effort always increases with age. Interestingly, they refer to Williams's argument as "deficient" since he fails to consider the possibility that the profit function could decrease with age. Gadgil and Bossert seem to have beef with Williams, as there are a number of put-downs aimed at him throughout the paper.

Gadgil and Bossert show that an iteroparous life history (i.e., $0 < \theta_j < 1$ for any age j) will only be favored when (1) the profit function is concave or (2) the cost function is convex.

Cost is essentially residual reproductive value ([Williams, 1966](#)): "For any given life history, the cost function C_j will decrease as the age j increases. This is because the cost is determined by the contribution to fitness of reproductive effort at ages $> j$ " ([Gadgil and Bossert, 1970, 12](#)).

[Gadgil and Bossert \(1970\)](#) suggest that cessation of growth before age at first reproduction should be rare. They write, "The rare instances of cessation of growth before maturity, as in the case of the albatross, may be explained by an increase in reproductive potential through learning after the growth has ceased." (p. 17). This sounds rather like the human-capital model proposed by [Kaplan and Robson \(2002\)](#) for humans. "Growth" is thus not simply about somatic tissue, but about a broader class of embodied capital.

There are six main take-aways from this fundamental paper:

1. Only when the profit function is concave or the cost function is convex can repeated breeding be optimal.
2. Reproductive effort increases with age in repeated breeders.
3. When mortality increases following some age j , reproductive effort increases for ages less than j .
4. When reproductive potential increases slowly with size, RE will be lower at maturity, rise with age, and growth will continue beyond maturity.
5. A uniform change in mortality – affecting all ages equally – will have no direct impact on RE.
6. If the population is resource-limited, such a uniform change will increase satisfaction ψ_j with its consequent effects, including a lowering of age at first breeding and increase in RE.

Profit-Cost Curves

This is the code for making the Gadgil-Bossert-inspired figure 2 in [Jones \(2011\)](#). I've commented out the legends because they don't look good with the small figure. Cost functions indicated in red; profit functions in black. When the profit function is concave, intermediate effort is optimal. When the profit function is convex, the optimal effort is maximal. When the cost is greater than the profit for all values of effort, optimal effort is zero (i.e., delay reproduction).

```
x <- seq(1,11,length=110)
y <- 4*log(x)
y1 <- 0.1*exp(x/2)
y2 <- 0.1*exp(x/1.5)
# maxima
d1 <- y-y1
d2 <- y-y2
max1 <- x[which(d1==max(d1))]
max2 <- x[which(d2==max(d2))]
```

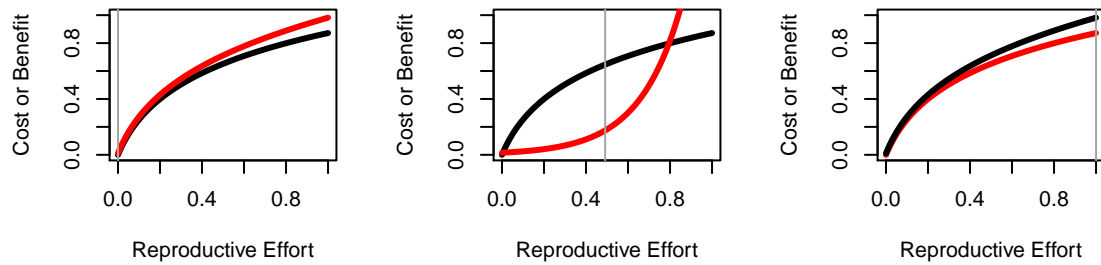


Figure 1: Three combinations of profit/cost functions leading to (a) zero effort, (b) intermediate effort, (c) full effort.

```
par(mfrow=c(1,3))
### concave benefits/concave costs
plot((x-1)/10,y/11, type="l", lwd=3,
      xlab="Reproductive Effort",
      ylab="Cost or Benefit",
      xlim=c(0,1), ylim=c(0,1))
lines((x-1)/10, y/11 + 0.01*x, lwd=3, col="red")
#legend(0.05,1, c("Benefit","Cost"), lwd=3, lty=1, col=c("black","red"))
abline(v=0, col=grey(0.65))

### concave benefits/convex costs
plot((x-1)/10,y/11, type="l", lwd=3,
      xlab="Reproductive Effort",
      ylab="Cost or Benefit",
      xlim=c(0,1), ylim=c(0,1))
lines((x-1)/10,y1/11, lwd=3, col="red")
abline(v=max1/11, col=grey(0.65))
#legend(0.05,1, c("Benefit","Cost"), lwd=3, lty=1, col=c("black","red"))

### concave benefits/concave costs, full RE
plot((x-1)/10,y/11, type="l", lwd=3, col="red",
      xlab="Reproductive Effort",
      ylab="Cost or Benefit",
      xlim=c(0,1), ylim=c(0,1))
lines((x-1)/10, y/11 + 0.01*x, lwd=3, col="black")
#legend(0.05,1, c("Benefit","Cost"), lwd=3, lty=1, col=c("black","red"))
abline(v=1, col=grey(0.65))
```

References

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