BET-HEDGING AND PERSISTENCE AS ADAPTATIONS OF COLONIZERS

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ABSTRACT

Colonizers have traditionally been viewed as short-lived, early-maturing, highly fe-
cund invaders of disturbed sites. Forest-canopy trees also invade disturbed sites,
light-gaps in the canopy, which open up at random in space and time. We explored the
evolution of the life-history traits of gap-colonizers with optimality models, explicit-
ly contrasting the consequences of using one or the other of two definitions of fitness,
bet-hedging (growth rate) and persistence (probability of extinction). We assumed a
cost of reproduction to the adult in the form of increased mortality, and a negative ex-
ponential seed distribution. First, the two fitness definitions lead to different pre-
dictions. Second, at the optimum for either fitness definition, the trees were always
iteroparous; for bet-hedging, however, the trees had shorter lives as a consequence of
their higher seed output. Third, a tree could have a seed output that optimized one
fitness measure without suffering a significant decrease in the other. Fourth, both
fitness measures were most sensitive to juvenile mortality and the slope of the seed
distribution. This emphasizes that gap-colonizers are under strong selection to produce
high-quality offspring that disperse great distances.

INTRODUCTION

The traditional view of a colonizing
species held that its life-history has
been shaped by natural selection towards
early maturity, many small offspring, and
a short life (Lewontin 1965; MacArthur &
Wilson 1967; Pianka 1970). The models
generating those predictions contained
two important assumptions: (i) that the
environment colonized deteriorated equally
rapidly for juveniles and adults, and (ii)
that fitness is defined as rate of popu-
lation increase for a stable age distri-
bution.

We have examined the consequences of
relaxing both assumptions by analyzing
life-histories of forest-canopy trees,
which here serve as a model for all spe-
cies for whom the environment is largely
hostile with scattered pockets where ju-
venile survival is high. Such species
must get seeds into spots in the forest
which either are currently open light-
gaps (for early successional species), or
will become such gaps before the seedlings
mature (for late successional species).
Note that we do not identify gaps with
tree-falls, although they may be identical
for some trees. Gaps are simply discrete
spots where the probability of survival to

maturity is high, for whatever reasons.
Hubbell's (1979) elegant field work sug-
gests that such spots are located at ran-
dom in space, and that the seed distribu-
tion away from the parent tree is a nega-
tive exponential.

Forest-canopy trees are gap-colonizers,
and for them the environment is much more
risky for seeds, seedlings, and juveniles
than it is for adults that have reached
the canopy. Gaps open up in the forest at
random in space and in time, introducing
a strong element of the unpredictable to
the life of trees. Because of this unpre-
dictability, the life-history consequences
of selection for maximizing growth rate
may differ from the life-history conseq-
uences of selection for minimizing proba-
bility of extinction. We have therefore
treated both fitness definitions explicit-
ly, for one cannot decide a priori whether
natural selection operates according to
one, the other, or a combination of the
two.

Because we have used optimality models
in our analysis of alternative fitness de-
finitions, the next section discusses the
assumptions implicit to and the limitations
inherent in such models and such defini-
tions.

BACKGROUND

Optimality models have become controversial within the last five years (Stearns 1977; Oster & Wilson 1978; Maynard Smith 1978a; Lewontin 1979; Levin 1981). They give the appearance of violating the mechanistic constraints of morphology and genetics, while providing more tractable mathematics than the alternatives explored to date. Although the criticisms of optimality models have been powerful, three considerations blunt their force (Stearns 1980): (1) most optimality models contain a hidden genetic component and are not the phenotypic, organism-level models they appear to be; (2) polygenic traits-- the most important traits in ecology and the traits normally modeled with optimization techniques--do not evolve under the genetic constraints that can hold phenotypes away from the optimum in few-locus systems; and (3) canalization, developmental plasticity, and the evolution of the developmental system in general should release the phenotype from many of the genetic constraints suggested by the visualization of one gene producing one character. Because opinion remains divided on the value of optimality models, we here list the assumptions contained in them to make clear what we are doing.

Most optimization procedures in evolutionary ecology contain at least these assumptions. First, the population is conceived of as a set of asexual, haploid clones, asexual because heritability is assumed to be perfect, haploid because there is no allowance for dominance or other diploid complications. Second, each clone is then mentally endowed with different traits--in our models, life-history traits--which determine the contrasts of interest. Third, the optimization procedure tells us which clone will win the intraspecific competition for numerical dominance. Fourth, these clones adequately model the fate of diploid alleles with marginal effects on the traits of interest in an outcrossing population. Fifth, it is sufficient to perform an analysis of the near-equilibrium maintenance of traits. Thus most optimization arguments deal with the maintenance, not the evolutionary origin, of traits.

There are objections to optimality models in life-history theory that use r-- population growth rate--as the definition of fitness. The argument is, first, that r is a characteristic of populations, not of individuals and much less of genes, and, second, that most populations are not growing exponentially in stable age distribution but spend most of their time near equilibrium. If the definition of

fitness in fact were r then these objections would have great force, but in fact the definition of fitness is not the rate of growth of a population, but the rate of growth of a haploid clone into a population that could be stable, increasing, or decreasing. In using r this way, one assumes that such a set of haploid clones adequately represents the dynamics of diploid alleles. To the extent that that is reasonable, the force of the objection is reduced, but we cannot yet say that it has been entirely eliminated.

With these caveats as background, we now can give the two definitions of fitness that we used in these models:

Bet-hedging: Maximizing the rate at which a clone increases in an unpredictable environment. In our models, finding that set of life-history traits that result in the solution r to the Euler-Lotka equation with the highest value.

Persistence: Minimizing the probability that a clone will disappear from the population. In our models, finding that set of life-history traits that results in the smallest chance that the individual will die without leaving progeny that survive to maturity.

Both definitions are couched at the level of the gene, for we conceive these haploid clones as adequate representatives of diploid alleles with marginal effects on life-history traits and, through those effects, on fitness. Even though individuals, not genes, have life-histories, an allelic substitution at one of the many loci affecting life-history traits will have marginal effects on those traits. The optimization procedure--for either bet-hedging or for persistence--tells us which allele or clone will win out given one or the other fitness definition.

THE MODEL

Assumptions.--Our background assumption is that we are dealing with the maintenance and fine-tuning of the life-history traits of a forest-canopy tree species in a mature, diverse forest. The tree delays maturity until it reaches the canopy, and for present purposes we take canopy height as a given characteristic of the forest community. The tree is not conceived as having the option of changing height or age at maturity. The critical resource to the tree is the set of colonizable patches, either open at the time the tree sends out seed or opening up between that time and

the time one of the seeds, growing under the canopy, attains canopy height and matures. We make no allowance for juveniles remaining in a holding pattern for years, just below the canopy, until a gap opens. Thus there is no provision for developmental plasticity--either the seedling makes it to canopy height and matures at a fixed age, or it dies.

Patches--or light-gaps--open up at random in space and time according to a two dimensional poisson distribution. The distribution of seeds along a transect away from the parent tree is taken to be a negative exponential with a slope consistent with Hubbell's (1979) data on the distribution of seedlings away from trees --about 0.01 to 0.02/m. We have assumed that no matter how many seeds land in a patch, at most one survives to maturity, thus introducing a form of density-dependence to the model. The adult death rate climbs as seed output rises, slowly at first but then very rapidly as the seed output approaches a maximum that is an independent variable in the model. This assumption introduces the cost of reproduction to the model in a specific and plausible way. Finally, we have assumed that the juvenile death rate does not vary with seed output, and we have not made provisions for a tradeoff between a few large seeds and many small seeds.

We do not keep track of all seeds, but only of seeds that hit patches. The juvenile death rate we use models the death of seedlings in patches; all other seeds are assumed lost. Thus to move from the model to the real world requires a scaling of seed output and juvenile mortality by a factor equal to the inverse of the patch frequency.

Mathematical Interlude.--A full treatment of the model will appear elsewhere (Stearns & Crandall, in prep.), but a few details will make precise the meaning of some of the assumptions just listed.

The models are patch-oriented, and deal with a finite number of patches of finite area. Consider a region of area A with n disjoint patches each of area a. Distribute a total of m seeds at random uniformly over A (the negative exponential enters later), and denote by ne the number of empty patches and by ns the number of seeded patches.

$$n = ne + ns$$

We want to know the expected value of the number of seeded patches given m total seeds. For m total seeds, denote by $p(j)$ the probability that we encounter j empty

patches ($j = 1 \ldots n$). If there are q empty patches then an additional seed will remove one of them with probability qa/A, and

$$p_{m+1}(j) = p_m(j)(1-ja/A) + p_m(j+1)ja/A$$

i.e., the probability that we will get j empty patches with $m+1$ seeds in the sum of the probabilities that we had $j+1$ empty patches with m seeds and the next seed hit a patch, plus the probability that we had j empty patches with m seeds and the next seed did not hit a patch. By noting that the expected number of empty patches for 0 seeds is n, the total number of patches, and then applying the recursion formula, we get the expectation of seeded patches given m seeds as

$$<ns>_m = n[1-(1-a/A)^m]$$
$$= n[1-\exp(mc)]; \quad c = log(1-a/A).$$

This relation can be used to get an expression for the number of patches seeded by a tree that emanates S seeds distributed with a probability $f(\rho)$ per unit area where ρ is the distance from the tree.

Consider an annulus with area $A = 2\pi\rho\Delta\rho$ over which $f(\rho)$ is relatively constant, but with $A \gg a$. The expected number of seeds which fall in the annulus is

$$m = Af(\rho)S,$$

and the expected number of patches in the annulus is

$$n = Ag/a,$$

where g is the fraction of area taken up by patches. The expected number of patches seeded in the annulus is

$$<ns> = n(1-\exp[-aSf(\rho)])$$

to first order in a/A. Thus the expected number of patches seeded by the tree in one season is

$$\beta(S) = (2\pi g/a) \int_0^\infty \rho d\rho[1-\exp(-aSf(\rho))]$$

It is evident from this expression that for any $f(\rho)$ we assume, the limit of zero patch area (a approaches 0) just gives $\beta(S) = gS$. This is intuitively plausible because a single seed will fertilize a patch with probability g in this case. In the present treatment we take $f(\rho)$ to be the negative exponential density:

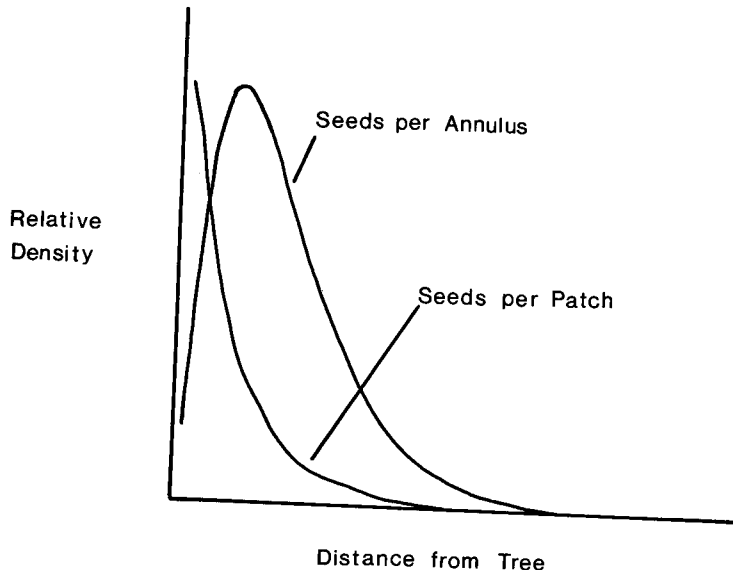$$f(\rho) = (k^2/2\pi)\exp(-k\rho), \quad (cf. \text{ fig. 1})$$

then

Fig. 1. The expected number of seeds per patch falls of exponentially with distance from the tree. The expected number of seeds per annulus--per ring at a fixed distance from the tree--first climbs and then falls because of the interaction between area increasing as the square of distance and seed density falling exponentially with distance.

$$\beta(S) = (2\pi g/ak^2) I(Sak^2/2\pi)$$

where I is given by

$$I(z) = \int_0^z du (log(1+u)/u).$$

Although all this appears to be quite complex, in fact the behavior of $\beta(S)$, the expected number of patches seeded, is related to S, the total number of seeds produced, in a plausible and straightforward way (fig. 2): $\beta(S)$ increases as s increases, but less and less rapidly. One would expect this because the increase in seeds produced means that a few additional seeds reach areas further and further from the tree. The number of patches encountered rises with the square of the distance from the tree, but the number of seeds reaching that distance falls exponentially. The result is that $\beta(S)$ is asymptotic to $g[log(S)]^2$.

To get the equations for clonal growth rate and probability of extinction, we define the death function as

$$d(S,x)=\begin{cases} do; & x<\propto \\ d(S); & x>\propto \end{cases}$$

and the birth function as

$$b(S,x)=\begin{cases} 0; & x<\propto \\ \beta(S); & x>\propto \end{cases}$$

where $\propto$ denotes age, s denotes age at maturity, x denotes age, S denotes seed output, d_o denotes juvenile mortality rate (assumed constant), $d(S)$ denotes the expected number of patches seeded by the tree in one season. Thus we are counting as births only those seeds which hit patches. We also impose that condition that

$$d(0) = d_a,$$

corresponding to no cost of reproduction for no seed output. In general, d_a, the basal adult mortality with no reproduction, does not equal d_o, the juvenile mortality, because seedlings and adults encounter dramatically different environments.

The clonal growth rate r is completely determined by these assumptions and the Euler-Lotka equation as

$$1= [exp(-d_o\propto)exp(-r\propto)\beta(S)]/[r+d(S)]$$
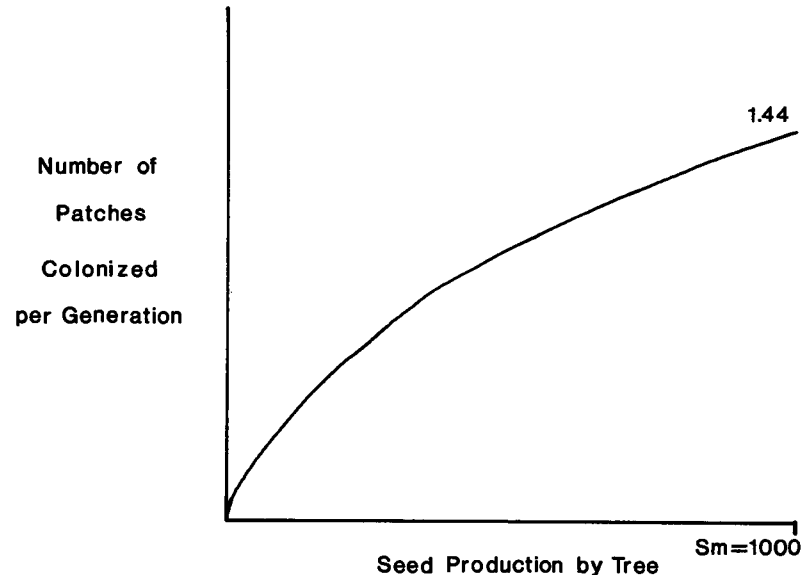
while the probability of extinction, pe,

Fig. 2. The number of patches colonized per generation, $\beta(S)$, increases monotonically as the number of seed produced, S, increases, but at an ever slower rate.

is

$$pe= 1-exp(-d_o\propto)+[d(S) exp(-d_o\propto-\beta(S)\propto)]/ [d(S)+\beta(S)]$$

We assumed that the adult death rate, $d(S)$, has a simple pole at some maximum seed output, Sm, which we envision as the seed output which would kill the tree:

$$d(S)= d_aSm/(SmS) \quad (cf.\ fig.\ 3)$$

Because the equations for r and pe are not analytically tractable, at this point we had to resort to numerical analysis on a computer. However, we did know when to expect solutions, given negative exponential seed distributions, from two theorems that are consequences of these assumptions and the results of Crandall and Stearns (in prep.):

(1) If

$$\lim_{S \to \infty} log(S)/\sqrt{d(S)} = 0$$

then there is a locally optimal seed output s for which r is a local maximum.

(2) If $d(S)$ is defined as above, and if

$$\beta'(Sm)/\beta(Sm) < 1/\propto daSm,$$

then pe has a maximum for some s: $0<S<Sm$.

These results reduced the amount of trial and error searching for solutions, for they told us when to expect solutions only at $S= 0$ or at $s= Sm$ if at all, and they provided us with useful analytical checks on the computational results.

Computation Methods.--The equations for r and pe contain eight independent variables: g and a for gap frequency and area, S and Sm for actual and maximum possible seed output, d_o and d_a for juvenile and basal adult mortality, $\propto$ for age at maturity, and k for the slope of the negative exponential seed distribution. Because it would require burdensome calculations to explore the 10-dimensional space of the problem, and because the results would be complex, hard to interpret, and difficult to report concisely, we adopted the strategy used by Lewontin (1965) in his analysis of r-selection. We first found what we thought would be a reasonable life-history for a forest-canopy tree, and a reasonable environment for it to live in. For example, if average longevity in the whole forest-canopy guild is 200 years, then gaps open with frequency $g= 0.005$ per year
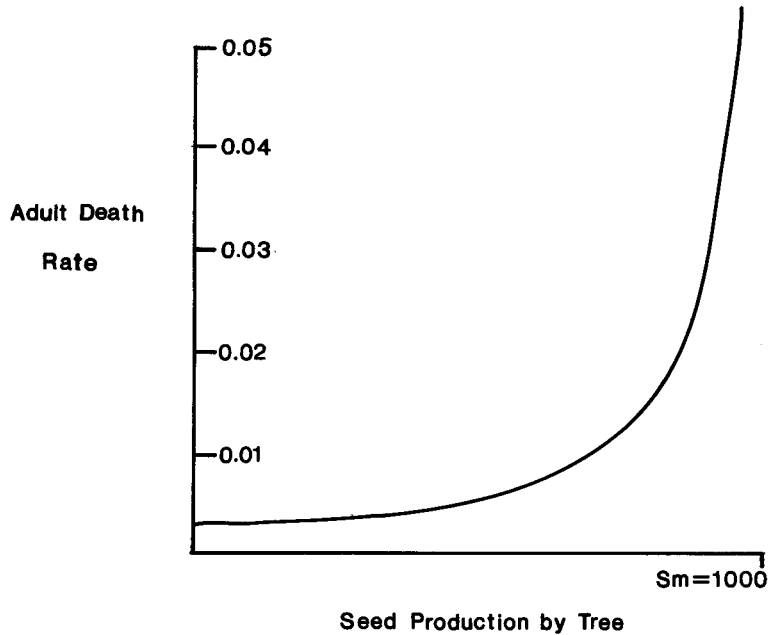
Seed Production by Tree

Fig. 3. The adult death rate rises as seed output increases, slowly at first but then rapidly, and diverges to infinity at some maximum seed output which would kill the tree.
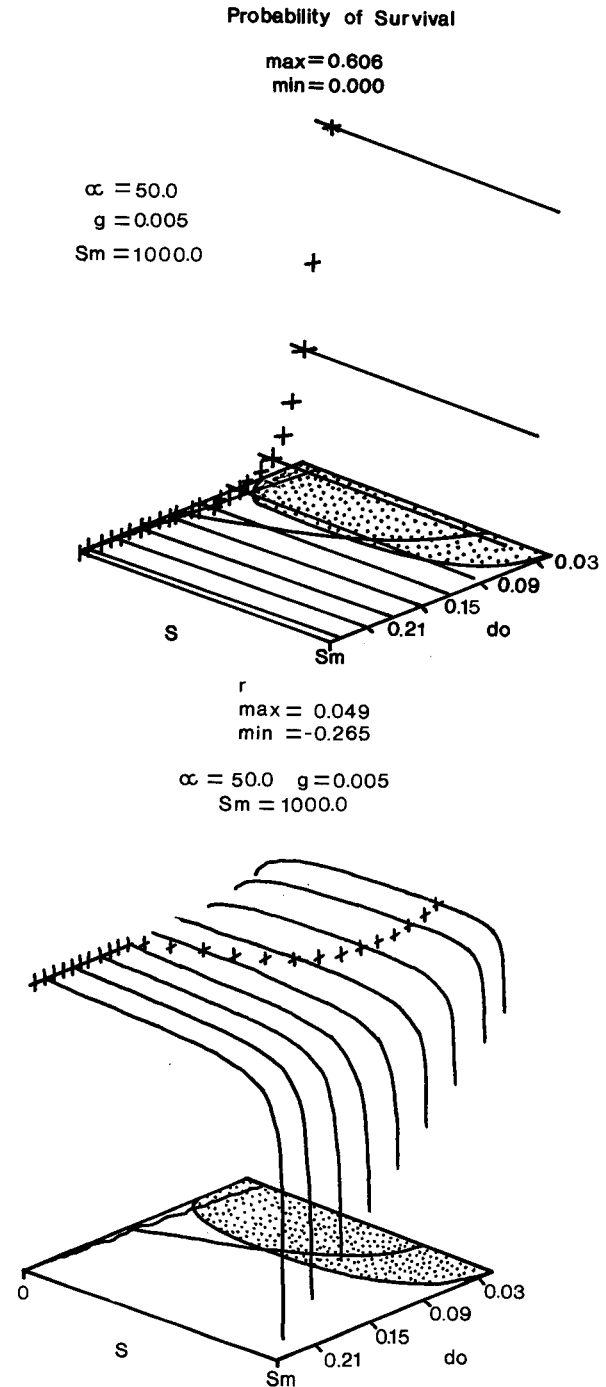
Probability of Survival

max=0.606
min=0.000

$\alpha = 50.0$
$g = 0.005$
$Sm = 1000.0$

r
max = 0.049
min =-0.265

$\alpha = 50.0$ $g = 0.005$
$Sm = 1000.0$

per gap, and if canopy area can be approximated by a square 25 m x 25 m, then gap area is 625 m. We chose an age at maturity α= 50 years, a juvenile mortality d_o= 0.05, a basal adult mortality d_a= 0.0033, a maximum seed output S_m= 1000, and an actual seed output s= 250. We took the slope of the negative exponential seed distribution, k= 0.015, as the midpoint of the range of values reported in Hubbell (1979) for seedling distribution.

These values of the eight independent variables formed the focal point of our calculations. We then varied the values around the focal point in both directions for each variable, and produced three-dimensional graphs that depicted the fitness surfaces as functions of two independent variables, e.g., actual seed output, s, and juvenile death rate, d_o. We also printed out the results so that we could

quantify the sensitivity of the fitness measures to changes in the independent variables.

RESULTS

Because the number of graphs produced would be inconvenient to publish, we summarize the results with examples of two combinations of independent variables and a table of sensitivities. In the first case, with juvenile mortality and seed output as independent variables, probability of survival *(ps= lpe)* increases sharply as juvenile mortality drops (because of the $exp(-\alpha d_o)$ term in the expression for *pe*), but it is insensitive to changes in seed output (fig. 4a). Clonal growth rate, *r*, also rises as juvenile mortality drops, but less dramatically, and optimal *r* is sensitive to changes in seed output. For positive *r*, on the other hand, decreases in

→ Fig. 4. (a) Probability of survival, d_o, declines exponentially as juvenile mortality rises, but is insensitive to changes in seed output, *s*, over a broad range of juvenile mortalities. (b) As juvenile death rate, d_o, rises, *r* declines and the seed output, *s*, that maximizes *r* declines. Stippled area: region where *r>0*. +: location of optimal *s* for that value of d_o. The two lines projected onto the *r, ps= 0* plane trace the location of the *s* and d_o that optimize *r* and *ps*.

juvenile mortality favor increased seed output--and with it higher adult mortality and a shorter life span (fig. 4b). Moreover, in the region of phase space where r is positive, the seed output that optimizes r is much greater than the seed output that optimizes pe.

In the second case, with juvenile mortality and the slope of the seed distribution as control variables, we see more dramatic behavior. Probability of survival increases sharply, as before, as juvenile mortality drops, and it is insensitive to changes in the slope of the seed distribution at higher values of juvenile mortality (fig. 5a). Over the region of phase space spanned by high juvenile mortality r is negative throughout and probability of extinction is high. As juvenile mortality drops past 0.06, the sensitivity of pe to k, the slope of the seed distribution, appears, and becomes prominent at low juvenile mortality rates. Clonal growth rate shows a similar but more pronounced pattern (fig. 5b); quite low and insensitive to changes in both juvenile mortality and the slope of the seed distribution when juvenile mortality is high, but rising steeply in both variables as juvenile mortality drops into regions where r is positive.

These two examples illustrate the general procedure. Other similar graphs indicate that r and pe are most sensitive to changes in juvenile mortality and next most sensitive to changes in the slope of the seed distribution (but only for pe at juvenile mortalities below those of the focal point, cf. Table I, but compare with fig. 5a). Increases in the rate at which gaps open up and in the maximum seed production level result in significant increases in r but little change in pe, and both measures are relatively insensitive to changes in adult mortality and actual seed output (Table I).

Four general results emerge from a survey of all cases analyzed. (1) The seed output that maximizes clonal growth rate is always different from, and nearly always much greater than, the seed output that minimizes probability of extinction. Thus the predictions that result from using a bet-hedging definition of fitness differ from those that result from using

a persistence definition. (2) All combinations of variables explored yield a prediction of iteroparity no matter what the fitness definition, but use of the persistence definition yields predictions of greater longevity: For bet-hedging, optimal seed output= 40-80% of the maximum, and 0.03% to 37% of trees that mature live another 200 years, whereas for persistence, optimal seed output= 1-10% of the maximum, and 2-82% of trees that mature live another 200 years. (3) This result must be qualified by noting that over much of phase space the sensitivity of r and pe to changes in seed output, s, is slight, and the tree could have a seed output that optimized one fitness measure without suffering a very significant decrease in the other. (4) The traits to which both r and pe are consistently most sensitive are juvenile mortality, d_o, and the slope of the negative exponential seed distribution, k. Both r and ps increase as k and d_o drop, and their sensitivity increases as well, underlining the point that a low k associated with greater seed dispersal becomes more important as juvenile mortality drops, and vice versa.

DISCUSSION

We must begin the discussion with two qualifications. Many of the results we report are computational rather than analytic and therefore carry no guarantee of generality, and we do not yet know how robust our conclusions are to the relaxation of certain critical assumptions, such as replacing the negative exponential seed distribution by a gaussian seed distribution centered on the tree.

Nevertheless, we feel that our major conclusion is robust for all gap-oriented models in which seed density falls off with distance from the tree. The combination of life-history traits that maximizes clonal growth rate differs significantly from the combination of life-history traits that minimizes probability of extinction, and in the direction of greater seed production, increased cost of reproduction, and decreased longevity. We also think that other gap-oriented models of forest-canopy trees will yield consistent predictions of iteroparity no matter which of the two definitions of fitness is employed.

→ Fig. 5. (a) At high values of juvenile mortality, d_o, probability of survival is insensitive to changes in the slope of the seed distribution, but as juvenile mortality drops, probability of survival rises and becomes sensitive to k. (b) At high values of juvenile mortality, d_o, clonal growth rate, r, is also insensitive to changes in k, but as juvenile mortality drops, r rises and is even more sensitive to k at low values of d_o than is ps. +, stippled area, and projected lines as in fig. 4 (p. 377).

Probability of Survival

max=0.606
min=0.000

k 0.006   0.03   0.21   0.16   0.11   0.06   0.01 do

r
max=0.046
min=0.004

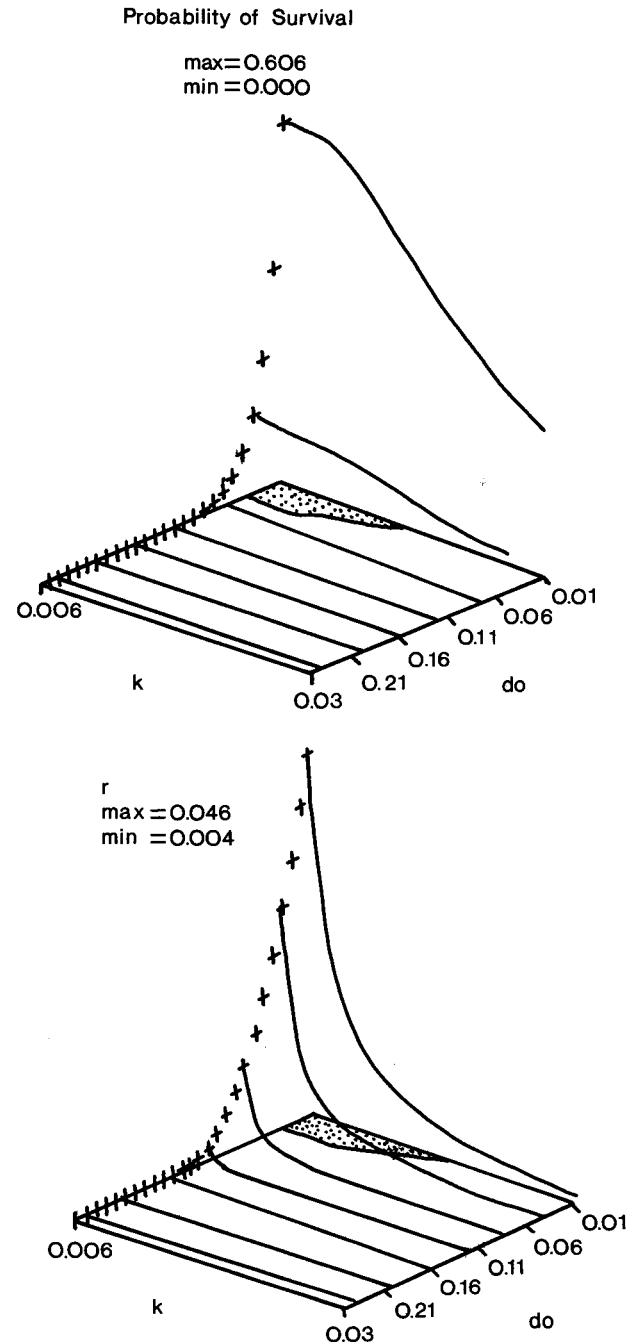k 0.006   0.03   0.21   0.16   0.11   0.06   0.01 do

TABLE I

Sensitivity of the fitness measures to changes in the
life-history traits at the focal point

Trait	Change	Response in r	Response in ps
Juvenile mortality	0.05→0.10	-99%	-92%
Adult mortality	0.003→0:006	-13%	0%
Slope of the seed distribution	0.015→0.030	-37%	0%[1]
Proportion of forest in gaps	0.005→0.010	+40%	0%[1]
Maximum seed output	1000→2000	+20%	+1%
Actual seed output	250→500	+1%	-1%[1]

[1] Greater sensitivity observed elsewhere in phase space.

These results open up the possibility of performing an empirical test in the field to see which, if either, fitness definition is in use, or to see if in fact some combination of the two (maxi-min or mini-max) is operating on natural populations. If work proceeds in this direction, it will have to focus on measuring the spatial and temporal distribution of open space as an environmental resource, as Levin and Paine (1974) have emphasized for the sessile organisms of rocky intertidal. Because of the effort involved in such a test--measuring gap distributions, seed dispersal, reproductive effort, mortality rates, and the cost of reproduction --we feel that more theoretical work must be completed before the empirical work begins, for we cannot yet be sure of the robustness of our conclusions.

Of the other results, the most interesting is the critical importance of juvenile mortality rate and the slope of the seed distribution. A tree could decrease juvenile mortality and gain in both definitions of fitness by making its seeds larger and more costly, with more energy reserves and protective chemicals. It could also decrease the slope of the seed dispersal function, and thus send its seeds farther away, but only by making its seeds smaller if they are passively dispersed. Thus at first sight the two most important selection forces in the model affect seed size strongly and in opposite directions. However, if we envision reponses having more to do with seed design and dis-

persal mode than with mathematical demography, a solution appears: Make the seed large, but use a bird or bat to carry it directly to an open patch, or at least far from the parent tree. Hubbell's (1979) paper provides evidence that this route has been taken, resulting in seed-distribution slopes for bird-bat dispersed seed of about 0.01, lower than those for wind-dispersed (0.02) or non-bat mammal-dispersed seeds (0.03). What our model does not explain is the trees that have not evolved large seeds and taken advantage of birds and bats.

This model suggests applications broader than just forest-canopy trees. The patch assumption bears no necessary relation to open space; all it really assumes is that most of the environment is extremely hostile to dispersing juveniles, but that there are local areas of enhanced juvenile survival. Sessile intertidal organisms encounter such an environment, one where the local area is literally a bit of open space. Mosquitofish, *Gambusia*, living in fluctuating Hawaiian sugar plantation reservoirs, also encounter such an environment, but in their case the local area of enhanced juvenile survival is a bit of time during which reservoir water level is high enough to submerge the bordering vegetation (Stearns 1975).
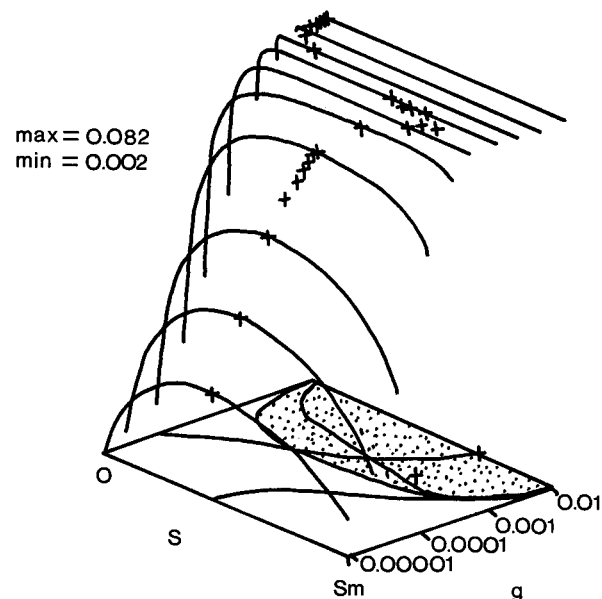
This model speaks to work proceeding in two quite different areas: the evolutionary maintenance of sex, and the co-evolution of species in communities. The rea-

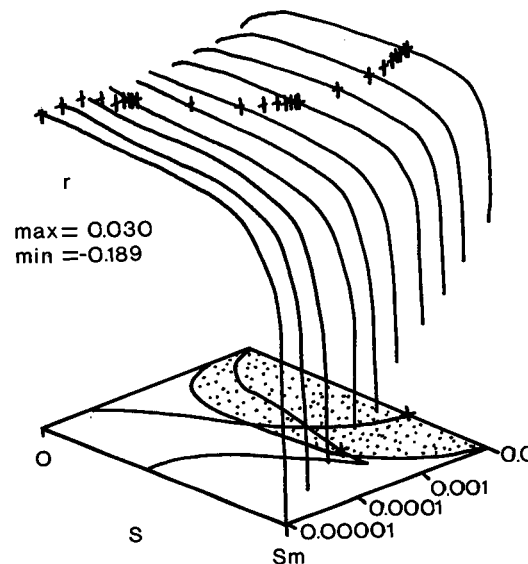→ Fig. 6. (a) As gap-frequency declines, probability of survival declines. The seed output that maximizes probability of survival first increases, then declines, but s increases monotonically over the portion of phase space in which $r>0$. (b) As gap-frequency declines, clonal growth rate, r, declines, but the seed output, s, that maximizes clonal growth rate declines monotonically with gap-frequency. This has consequences for co-evolution in communities.

Probability of Survival
$\alpha = 50.0$
$do = 0.050$
$Sm = 1000.0$

max = 0.082
min = 0.002

$\alpha = 50.0$
$do = 0.050$
$Sm = 1000.0$

max = 0.030
min = -0.189

sons usually given for the evolution of sex at the level of the individual (Williams 1975; Maynard Smith 1978b) are consistent with a gap-oriented forest-canopy colonist. Not only does the unpredictable gap distribution shape the evolution of an iteroparous tree producing a few, large, widely dispersed seeds, the nature of the gaps and the relatively high fecundity of the trees provide sufficient reason for the maintenance of sex. In the gaps, the seeds encounter an unpredictable mix of inter-specific competitors and predators, different in each gap. Where the biotic environment is complex and locally unpredictable, with each seed made encountering a different environment, and where fecundity is high, selection should favor sexuality over asexuality. One would be surprised to observe any asexual forms among forest-canopy species, and to the extent that this type of model underlies the evolution of long-lived, low reproductive-effort organisms in general, one would expect few asexual forms in that class either.

Now, consider the evolutionary transition, over a relatively long period of time (millions of years), from herbs to shrubs to trees. Competition for light is pushing the canopy up, thus delaying maturity and driving down the frequency with which gaps open. As the gap-frequency drops, the seed output that maximizes r also falls, leading to positive feedback for greater longevity when the bet-hedging definition of fitness is assumed (fig. 6a). However, under the persistence definition of fitness a decrease in the gap frequency favors, ceteris paribus, increased seed output and negative feedback on longevity (fig. 6b), followed at very low gap frequency by a switch to positive feedback (but probably in a region where r is negative and which is thus biologically uninteresting).

If plants have encountered environments in which gap-frequency has declined, while selection favored a shift downward in seed output as the result of that decline, then we would expect to see organisms pushed to the limits of longevity and low seed output. Such is the community scenario resulting from the bet-hedging definition of fitness. If, on the other hand, plants have encountered similar declines in gap-frequency, but because persistence was the definition of fitness natural selection favored increased seed output, then we would expect to see trees held at some intermediate stable point of longevity, gap-frequency, and seed output. Such is the community scenario resulting from the persistence definition of fitness.

Thus in the context of community co-

evolution, where competition for light drives increases in canopy height and delays maturity, interactions with demographic forces mediated by declines in gap-frequency result in directional selection for greater longevity if bet-hedging is the definition of fitness, and in stabilizing selection for intermediate longevity if persistence is the definition of fitness. We, of course, do not know which is in fact the case, and we are not likely to find out for a good while, but it is interesting that life-history theory can speak directly to community ecology.

ACKNOWLEDGEMENTS

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