

GENETIC FORAGING FOR VARIABILITY

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ABSTRACT: The evolution of sex still poses unanswered questions (Michod & Levin, 1988; Stevens & Bellig, 1988; Kondrashov, 1993). Current theories argue that the variations provided by sex enable organisms to: adapt to changing environments (Bell, 1982); move into new niches (Ghiselin, 1974); avoid parasites (Seger & Hamilton, 1988); disperse (Williams, 1975); out-compete asexuals in varying environments (Williams, 1975; Koella, 1988); rid organisms of genetic load (Muller, 1964); and act as a sieve which purges deleterious mutants and genes (Klekowski, 1988). Presented here is a more inclusive model which not only covers sexual and asexual reproduction but also relates the genetic variations produced by these phenomena to both variable and steady environments. The proposed model provides a method to examine and integrate selective trade-offs with genetic variations and with life-history constraints. Sexual and asexual reproduction and other genetic variations are examined via the concept of foraging for genetic variations given various life-history trade-offs. In order to maximize genetic variation while reducing its cost in nonviable reproductive attempts there are given constraints on different life-history parameters which create a complex optimal foraging problem.

Key words: evolution of sex/ genetic recombination/ life history trade-offs/individual-group selection.

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INTRODUCTION

Many theories have been presented for the evolution of sex and its maintenance (Michod & Levin, 1988; Stevens & Bellig, 1988; Kondrashov, 1993). Sexual reproduction is accompanied by an evolutionary cost of halving the genetic material (Maynard Smith, 1987). This paper will address two questions: 1), the cost and maintenance of sex given the loss of genetic material of the individual female and 2), what are the constraints in an individual's fitness to produce genetic variations relative to the various life history trade-offs. Genetic variations produced by genetic recombination can create large losses in reproductive potential via non-viable or poor genetic variations in offspring (Wiens, 1984; Wiens *et al.*, 1989). Since genetic variations are produced in both sexual and asexual genetic recombinations throughout phyla, there must be some selective advantages to balance the cost of losing one half the genetic material and the cost of non-viable genetic combinations in reproductive attempts. In addition, the amount of genetic variation needed in the offspring is tied to the life span of an individual, the efficiency in accumulating resources, mortality, and resource variability. Thus, optimizing the amount of genetic variations for one's environment, while reducing its cost, will have a selective advantage.

PART I: The Cost of Sexual versus Asexual Reproduction

Evolution of reproductive strategies has produced a century of debate. Ghiselin (1974) addressed the question of why sex evolved but not the paradox of the maintenance of sex given its costs. J. Maynard Smith (1987) argued that sex would have to increase individuals' fitness by a magnitude of two in order to be maintained. The immediate benefit of asexuality (or parthenogenesis) to the individual is a classic biological paradox, since sexual reproduction is common (Michod & Levin, 1988; Stevens & Bellig, 1988; Kondrashov, 1993). The resolution of this paradox requires looking at which individual is providing the resources to the

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offspring, as well as the genetic relatedness. The paradox has two basic assumptions: 1), the male places no resources into the offspring except his genetic material and 2), the cost of producing either sex is selected to be equal, or the cheaper sex is produced in larger numbers (Fisher, 1930). Though it is well recognized that in many species the female is a resource to the male and that the male gets half of his genetic material produced with minimal cost, the benefits to the female are not included in individual selection arguments for either the evolution or the maintenance of sex. Current research still assumes there is this two-fold advantage to asexual reproduction over sexual reproduction (e.g., Petren, *et al.*, 1993). *Sex (Amphimixis): is it a parasitic strategy of conspecifics?*

At first glance there appears no individual advantage for the female to be genetically parasitized by the male; i.e., full cost of reproduction with loss of half her genetic material. However, sexual reproduction provides the female the use of a parasitic strategy via her sons using other conspecific females' resources. A sexually reproductive female can benefit by utilizing her sons as both a means of dispersal (Williams, 1975) and a parasitic strategy of other female's resources. This is a simplification because males are known to place large amounts of energy in dispersal and other reproductive functions. Assuming that asexual and sexual reproductive strategies are both trying to maximize the individual's genetic representation in the next generation under individual selection, the amount of resources provided by which sex becomes a critical component. However, if sexually reproduced sons produce all their grandchildren with minimal costs by using other female's resources rather than their sister's or mother's resources, then the amount of resources required per amount of genetic material replicated from the original parent is largely recouped, i.e., the cost is born by the "parasitized" females. The parents' genetic material is indifferent as to whether it is all in one individual (asexual) or all in four individual grandchildren (sexual) if it is the same representation for a similar cost. Strathmann (1974) argues for the short-term advantages of large-scale dispersal of sibs when survival and reproduction varies from place to place.

Therefore the questions become: Under what environmental conditions are the parasitism and dispersal strategies selected as an Evolutionary Stable Strategy (ESS) over asexual reproduction? and, If the parasitic strategy of conspecifics were to be introduced into a population, then how should a parent allocate its genetic material, given the strategy of parasitizing others or selfing its own genetic material? Individual fitness is the overall amount of genetic relatedness through generations (Hamilton, 1964); therefore the amount of genetic representation per cost can be examined using Fisher's (1930) sex-ratio argument. This concept can be modeled by placing the parasitic strategy and selfing strategy into a sex-allocation model. An evolutionary stable strategy model which works for the sex-allocation theory (Charnov 1979) works for parasitic/dispersal and selfing strategies. The only modification of Charnov's model is that the male has been substituted to represent a parasitic/dispersal strategy and the female has been substituted to represent a selfing strategy.

"in order to find the ESS, we need a measure of fitness for a rare mutant to tell us if it is being selected for or against; this fitness measure will be shown to be of the form

$$W = \frac{\hat{p}}{p} + \frac{\hat{s}}{s} \quad \text{where}$$

\hat{p} = fitness of rare heterozygote through the parasitic function

p = fitness of common homozygote through parasitic function

\hat{s} = fitness of rare heterozygote through the selfing function

s = fitness of common homozygote through selfing function

From this simple measure follow the above result for allocation of both parasitism and selfing of genetic material. If the mutant is identical to the homozygote ($\hat{p} = p$, $\hat{s} = s$), $W = 2$; we may assign the homozygote a fitness of 2. The mutant is favored if $W > 2$ or if $(\hat{p}/p + \hat{s}/s) > 2$. If we write $p = p + \Delta p$, $s = s + \Delta s$: the rule becomes
$$\frac{\Delta p}{p} + \frac{\Delta s}{s} > 0$$

or (in words: Selection favors a mutant gene which alters various life history parameter iff the % gain in fitness through one sex (strategy) function exceeds the % loss through the other sex (strategy) function (Charnov 1979)."

For non-dioecious species the arguments for the various strategies would follow many of the arguments for sex allocation (Charnov & Bull, 1977; Charnov, 1982; Werren, 1980; Werren & Simbolotti, 1989). Therefore, the central problem is not the loss of half the genes as such, but the relative relatedness of each package of genes to the parent per unit cost, e.g., 1.0 or 0.5. Individual fitness is

more a problem of resource allocation to: energetic costs, dispersal costs, genetic-variation costs (explored later) given the mortality of gene package(s). This does not completely address individual-fitness versus group-selection arguments, but it shifts it to a resource-allocation problem and what types of reproductive strategies are best: asexual, sexual, dioecious species, selfing-annuals, hermaphrodite, etc., given environmental conditions.

Obtaining resources faster or in greater quantities of resources gives positive selection for keeping the parasitic strategy. A study which illustrates this point was done by Atsatt and Strong (1969) of the hemiparasitic plant, *Orthocarpus purpurascens*, which has genes for both heterotrophism and autotrophism and these traits were shown to vary proportionally. The heterotrophism (parasitic) phenotype has helped *Orthocarpus purpurascens* to adapt to an unpredictable host environment; thus this phenotype is maintained even with the cost of being a poorer autotroph. The benefits of parasitism of other conspecifics via sons can be a viable strategy if it provides resources quicker or in greater amounts in an unpredictable environment.

Methods for obtaining more resources will have increasing selection as resources become more scarce. Methods for resource foraging can include: parasitism of conspecifics, wider dispersal of offspring, elimination of competitors, increased longevity, and obtaining different resources through genetic variations. Sexual reproduction provides genetic variation, parasitism and dispersal. In some competitive conditions sexual reproduction also helps eliminate competitors, i.e., the elm-oyster model (Williams, 1975). It is noteworthy that species that use both sexual and asexual reproduction use sexual reproduction when the population is at its highest level and before a major environmental change (e.g., aphids and *Daphnia* use parthenogenesis in the early part of the season and the sexual cycle in the fall). In the evolutionary past this strategy of when to change into parasitism and its timing may have been determined and triggered by environmental changes. C. I. Davern (1988) suggested that the genetic load of mutations would also cause selection for parasitism such that a unit of genetic material doing poorly in resource gathering, or in a suboptimal environment, would benefit by combining its genetic material with another individual that is doing better. Parasitism of conspecifics whether for resources or for genetic viability is not necessarily exclusive. This genetic parasitism includes asexual reproduction in eukaryotes as well as prokaryotes.

For dioecious species Bell (1982) suggestion that the sexes can use different resources and that competitive exclusion can exist between the sexes similar to competitive exclusion that exists between species. Therefore the sexes would not be in direct competition for resources. A Difference in the size of home ranges between the sexes is not uncommon in some species e.g., the north American male iguana lizard's home range is at least twice that of the female's (Rose, 1982) and the male bobcat's (*Felis rufus*) home range was 1.75 times that of the female's (Wassmer, 1988). Differences exist in some species between the sexes in their mortality rates (e.g. kangaroo rats, *Dipodomys sysectabilis*) and these mortality rates can change due to changes in environment such as population density (Jones, 1988).

Discussion to Part I

The above arguments do not address the questions of the initial establishment of sex, but this has been addressed through the concept of gamete-size dimorphisms, e.g., (Parker *et al.* , 1972; Cox & Sethian, 1984). Sexual reproduction could have begun several times by incomplete splitting, parasitic genes, and doubling the genetic material and then not completing the separation. I believe, like Ghiselin (1974), that incorporating outside genetic material was a primitive mechanism with positive selection. Once the combining of outside genetic material is established in an isogamous system or in a system with size dimorphism, there is an opening for parasitism. Any mechanism (independent assortment after doubling, crossing-over, etc.) that insures that an individual is reproducing its own genetic material equally along with the foreign genetic material would have selective advantage. These mechanisms are a good defense against any foreign genetic material trying to get more of its material replicated over the individual's.

In packaging of genetic material it is important to maintain good viability, and hence allocation of genetic material into different package amounts such as 1/4, 1/5, or 1/8 may result in an increase in the mortality of offspring due to non-viability and/or difficulties in finding partners, and could have set limits on the various genetic-allocation systems that could have evolved (Hurst & Hamilton, 1992). However, many organisms do have systems where the amount of genetic material exchanged is not equal. Bacteria recombine genes (a type of sex) with viruses, plasmids, and naked DNA as well as homologous recombination, and genetic infection (or parasitism) can be by transformation, conjugation and

transduction and the genetic variability produced is critical in host-parasite interactions and coevolution (Levin 1988). Eukaryotes have a huge amount of genetic material compared to prokaryotes, and sexual reproduction in eukaryotes provides a method to keep the nucleic template (reproductive cells) safer from genetic parasites as well as safer from mutations that have accumulated during the lifespan in the somatic cells; this may have also influenced the evolution of genetic-exchange systems.

Conclusion to Part I

Though it may seem contradictory, sex is actually maintaining continuity through generations while producing variations at a fast rate with good viability. Although sex has the cost of halving the genetic material for the individual (Maynard Smith, 1974), the female can utilize other females' resources via her sons to produce her genetic material at minimal cost, i.e., genetic parasitism of conspecifics. These advantages give sexually reproductive *individuals* the edge to win out quickly over parthenogenetic individuals under many conditions. Sex can be thought of as one of the most stable and hence common Evolutionary Stable Strategies in living organisms. The maintenance of sex is the allocation of various amounts of genetic material in packages and the cost of sex (Maynard Smith, 1978) is only one constraint on an individual's fitness; the examination of all biological constraints faced by an organism gives a more comprehensive model for producing genetic variations via genetic recombinations. These constraints suggest that genetic variations should be viewed in an ecological context while still taking into account individual selection.

PART II: Foraging for Genetic Variation Given Life History Constraints

Introduction

Sexual reproduction is a major source of variation, hence many theories concerning the evolution of genetic recombination (sexual and asexual) implicitly address the issue of genetic variations; while genetic recombination produces advantageous genetic combinations it also disrupts beneficial genetic combinations. It is spurious to further debate and/or model asexual versus sexual reproductive strategies under individual selection without including the life history trade-offs. These various life history trade-offs are connected to asexual and sexual reproduction and the importance of how much genetic variation an individual parent needs to produce given the environment. This implies a model of foraging for genetic variation with each gene nested in the larger overall efficiency of the total genetic phenotype of in an individual. The individual genes may function together efficiently in the individual, but the phenotype must also match the individual's environment: e. g. an individual could have efficient genes for utilizing lactose, but if it is in a environment with only fructose, the efficiency rate of using lactose would be a mute point. There are two distinct levels which interact, the efficiency due to the phenotype of the individual and the rate of change of resources in the outside environment. This model is not exclusive but inclusive of other models for the evolution and maintenance of types of genetic recombination and it is inclusive of many life-history models/theories (e.g. Roth, 1992; Charnov, 1993). The model's novelty is the synthesis of major works and, though complex, it gives a clear picture of constraints to individual fitness and how various components have adjusted in different environments. This creates an optimal-foraging model for obtaining resources through generational time via genetic variation in relation to patchiness of the environment.

Constraints to an Individual's Fitness

The questions needed to be addressed are: How much genetic variation does an individual need to produce in its (or her) offspring and how does producing the genetic variation impact the cost of reproduction? and, How do asexual and sexual reproduction impact this system given the different constraints? To visualize the complexities of this problem imagine the ideal "fitness" for an organism. She would like an extremely efficient molecular system(s), perhaps a 95-98% efficiency rate, for turning many types of resources (if one type is scarce) from the environment to her usage, a system that did not require expensive maintenance or growth costs and that had minimal energetic operating costs. This would leave plenty of resources to put into reproduction, which ideally would be maximized for viability, variations, and genetic relatedness. Finally she would have no senescence. Thus, an ideal mammal would have a slow metabolic (usage) rate, with a well-functioning digestive system that could handle many species of food and create genetic combinations via parthenogenesis, which produces both viable and polymorphic offspring, with an extremely long reproductive life span. Other variables are also relevant, e.g. growth rate and predator avoidance. Mammals are not as ideal as they might wish to be.

To operationalize how these various biological components are constrained by each other, a single fitness equation was constructed. This model was created to more easily see these relationships and not to be mathematically rigorous. All components have been put in units of time (t), energy (E), and amount of genetic material related to an individual (G). Thus, it will hold for asexuals, sexuals, hermaphrodites, selfing annuals, and various sex ratios. This model indicates that efficiency (via molecular and other internal systems) is indeed a critical component in fitness, but this is only if other ecological factors do not first bottleneck the system. To partially model the larger verbal model we need some notation.

Let E_n be the energy allocated to other functions other than reproduction such as maintenance, growth, and foraging. Let $E(t)$ be the instantaneous rate of energy collection. Then the total amount E of energy collected over the lifespan T is

$$\int_0^T E(t) dt$$

Let $G_d + G_s$ be the total number of daughters plus the number of sons produced.

Let G_r be the degree of relatedness to the parent, i.e., 1.00 for asexual, 0.5 for sexual.

Let G_{nvs} and G_{nvd} be the number of nonviable genetic combination of sons and daughters.

Let G_{md} and G_{ms} be the number of sons and daughters lost before their reproductive age. Then the total fitness, W_i , of an individual is defined by:

$$W_i = \frac{(G_r) [(G_s - G_{ms} - G_{nvs}) + (G_d - G_{md} - G_{nvd})]}{\int_0^T E(t) dt - [E_n]}$$

This expresses fitness as benefit-to-cost ratio. The energetic costs other than reproduction are subtracted out. The energy left is then allocated into numbers of offspring with genetic variations, with given genetic relatedness, minus the losses in reproductive tries due to poor genetic combinations and the loss of offspring due to outside environmental factors before reproductive age. It might appear that this definition of fitness implies that fitness increases as the individual's capacity for extracting energy from environment decreases. But this is not so, because in that case the number of offspring would also decrease.

The individual fitness model presented here is concordant with the elm-oyster model (Williams, 1975) of competition when the rate of growth is essential in crowding out competitors -- thus diversity has an advantage. It supports trade-offs of growth versus longevity and it supports increases in energy per offspring to improve viability while decreasing numbers of offspring. Depending on what environment you place the above fitness model in, the strength and type of selection, it supports a multitude of classic biological models. Fitness models which address critical components and types of selection should have precision and flexibility. The above model does not give much information by itself, but as with the Hardy-Weinberg Law, it is changes through generations that become interesting.

These ecological tradeoffs that affect an individual's fitness have been previously described; however, few studies consider how all these components are inter-related. The costs in non-viable or less viable offspring due to producing genetic variations, or due to genetic complexity, are important (e.g., Haldane, 1975; Van Valen, 1963). "Good genetic combinations" are critical in an individual's fitness (e.g., heterozygous advantage: Zouros *et al.*, 1988; lifetime fitness in energetic allocation in rearing offspring: Burley, 1988;). However, for each "good genetic combination" produced there is a larger number of reproductive attempts it took to produce this good genetic combination; this number of attempts can vary among and within species. The number of genetically viable zygotes produced by a species depends on whether this species (or individual) produces few or many lethal genetic combinations when its genes are shuffled via sexual or asexual recombination. Wiens showed this to be the case in the shrub *Dedeckera eurekensis*, where fewer than 2.5% of seeds are viable because of high heterozygosity (Wiens *et al.*, 1987, 1989). The problem of non-viable genetic combinations in other plant species was also addressed by Wiens (1984). He measured the number of ovules that developed into seeds (S/O); in annuals this ratio is about 85% and in perennials it is approximately 50%. In addition, annuals have a

significantly higher seed set. Not all heterozygosity may negatively impact reproductive costs. If the cost of non-viable genetic combinations due to genetic diversity does have a large impact, then comparisons in fecundity should include the relative reproductive success (RRS) (Cruden, 1972). Another study, which addressed the production of genetic variation in different species, showed that chiasma frequencies in males and females in the same species show significant differences and the difference in the absolute value of the differences was significant in different taxons (Burt *et al.*, 1991). This indicates the amount of genetic variation is a critical component that has selective pressure and that there is a limit to the cost of nonviable genetic combinations that can be tolerated by an individual (and species). Each species' genetic complexity and its particular genetic mechanisms impact the overall percent of genetically viable reproductive combinations. The non-viable genetic variations can come from heterozygosity, homozygosity, mismatch genetic repair, mutations and poor genetic recombinations created by sex and other genetic mechanisms (e.g., gene silencing, cross-overs, bacterial phages). In many species this cost of producing genetic variations is small, but this is not always the case, and the cost to produce genetic variation can be significant.

The general idea of tradeoffs in the life history has been recognized (Moreau, 1944; Cole, 1954; Williams, 1966; Cody, 1966; Ricklefs, 1979; Charnov & Schaffer, 1973; Roth, 1992). There is a strong relationship between annual fecundity and adult mortality (Ricklefs, 1977). Life history tradeoffs between reproduction and natural life span have strong correlations (Rose & Charlesworth, 1981; Rose, 1984; Till-Bottraud, *et al.*, 1990). Additionally the amount of resources allocated to optimum numbers of offspring and their survival (Lack, 1947, 1954) has been shown to affect the survivability of the parents and the number of offspring they produce (Nur, 1988). There can be selection to increase longevity, if the time required to obtain sufficient resources to reproduce is increased. This is because energy use is constrained by the time it takes to obtain and process energy. For example, in the plant kingdom polyploids have been known to adapt to extreme environments and often have marked changes in their rates of growth. Besides numerous plant taxa, polyploidy has also played an important part in evolution of certain fish, snails, reptiles and amphibians (Ohno, *et al.*, 1968; Ferris & Whitt, 1980; Levin, 1983; Masterson, 1994).

The ecological component of resources in life span, i.e. rate of energy turnover, is a complex issue because the rates of energy usage vary in a linear fashion within an order; and different orders have distinct energy usage patterns (i.e., a slope which the species fall on) (Charnov & Berrigan, 1991b) and this rate does correspond to life span. Studies of orders which use similar metabolic pathways find a distinct pattern of longevity correlating to other life-history tradeoffs (Ricklefs, 1969, 1977; Charnov 1989, 1991a, 1991b; Charnov & Berrigan, 1990, 1991b; Promislow & Harvey, 1990; Finch, 1990). This total energy available is positively related to the life span, i.e., an individual living a hundred years can collect more energy than one living a year, all other things being equal. This use of energy and the rate at which energy is collected is a key factor in understanding life histories and hence reproductive strategies. For example, at the southern end of its range *Stizostedion vitreum* (walleye) lives up to four years yet in northern Canada it lives up to 20 years, but lifetime fecundity is similar throughout its range. Other species, like northern mammals, maintain a metabolism similar to their southern cousins and their life spans do not differ greatly. At present there are no complete studies to support all the tradeoffs in the fitness model presented in this manuscript. However, Charnov and Berrigan (1991b) show that dimensionless numbers in life history (DLH) parameters run throughout fish, shrimp, lizard, snakes, mammals, birds, and this would be consistent if maximization of individual's fitness were taking place given various tradeoffs.

The metabolic efficiency of an individual, given the resources available to it in its environment (patch) during its lifetime, determines the total energy available. Genetic variations produced in offspring can be thought of as genetic *optimal foraging on the molecular level* for resources. It is known that specific enzymes and/or grouping enzymes sometimes determine the type(s) of resources used and this affects the rate at which particular resources are utilized (Mitton & Grant, 1984; Zouros, *et al.*, 1988). Further, the type of resources and their utilization rates affected the longevity in *Drosophila melanogaster* (Luckinbill *et al.*, 1984, 1989).

The Environment and Resources Variations

This fitness model only addresses an individual's biological constraints and, if fitness is maximized, there is the assumption that the amount of genetic variation being produced is adjusted to the relative changes in the individual's environment. However, the total number of genetic variations required for an individual's offspring would depend on future changes in the resources. This is an analogous to an

argument from optimal foraging theories which examine the selective pressures necessary to maximize energy per given time period, given the patchiness of an environment (Mac Arthur & Pianka, 1966; Emlen, 1966; Charnov & Orians, 1973). However, if an individual is foraging for genetic variations, the amount of genetic variation required by that individual (species) is dependent on the temporal and spatial changes in the outside environment *relative to* the life span, mortality factors, and reproductive allocation (i.e., asexual, selfing, sexual, etc.) of an individual or species. The life span and the amount of genetic variation required can differ given the overall mortality of a species. For example a virus (a short-lived parasite in a variable environment) needs much more genetic variation in its short life than does a short-lived mutualistic bacterium, while a long-lived sexually reproducing plant in a variable environment may require both a long life span and high genetic diversity in order to produce enough viable seeds to track environmental changes. The relative strength of selection on any one or more of these components, given the ability of the other components to adjust, would determine the overall life history parameters.

A critical aspect of this model is that strong selection on a given component will force the other component(s) to adjust, or extinction follows. For example, the amount of genetic variation produced by an individual could be suboptimal for moving into new niches because of an existing high predation rate of their offspring. Such an individual could not sustain larger amounts of non-viable offspring combinations due to genetic variations. Natural selection would maximize the individual's fitness given all of these biological constraints, if the population survives. For example if the rate of resource foraging was limited it would limit parameters such as the rate of growth. This is seen in foraging moose (*Alces alces*), which are constrained by their sodium intake; the moose has to balance her intake of sodium-rich aquatic plants, with the intake of the energetically richer terrestrial plants (Belovsky, 1981, 1984).

Knowing that these life history tradeoff functions exist, the question now becomes How do these life history tradeoffs affect tradeoffs in the amount of genetic variation which needs to be produced in offspring given differing environments? For example, even though a selfing annual may produce less genetic variation per reproductive cycle than a long-lived woody sexually reproducing heterozygous plant, when following the entire genetic flow over a given amount of time it is possible that an annual species may produce as much or more genetic variations (through many generations) than its more genetically diverse cousin. Conversely, the amount of genetic variation an individual rodent could produce through its progeny compared to the longer-lived human given the same amount of time would likely be higher. Thus, the length of life span given probability of environmental changes is essential. Long-lived plants, such as the pines of western North America, require offspring that are polymorphic in their terpenes (Edmunds and Alstad, 1978, 1981; Sturgeon, 1979) if they are going to survive the short-lived and quickly reproducing pine scale. Humans utilize a similar strategy via Major Histocompatibility differences which exist in their offspring to help survive pathogens, in addition to humans' tremendous diversity in antibody responses.

The environmental variations of patches in time and/or geographic space will have profound effects on the genetic variations the organism requires. In optimal foraging, this would correspond both to patch renewability and to patch variability. In foraging models the predator moves from patch to patch for resources. In this model it is the individual's genetic combinations (offspring) which are moving through time from patch to patch. More precisely it is the individual's packages of genes, i.e. 1.0, 1/2, 1/4, 1/8 etc., which are moving through time. Unlike the classical optimal-foraging models, a genetic-foraging model is multidimensional. From the point of view of the gene packages, the individual is a patch, which provides a micro-environment in which the genes in concert function either poorly or well. The second patch, which also has degrees of variation, is the larger environment in which the individual is residing. Optimal times for changing patches, on both dimensions, depends on how these parameters interact. This gives a much more complex "optimal foraging" since there is a double nest of parameters which interact. The environment can differ on these various components making selective pressures difficult to perceive, unless a species has major selection on only one or two of these components. When there is intermediate selection on all/or most of these components, sophisticated modeling and sensitive measurements are required to tease apart the relative strength of the various types of selection in operation, i.e., density-dependent or density-independent, selection due to predation and parasites, rate of resource availability, etc.

Examples of Various Environments in Relationship to Genetic Variability

A desert species whose environment is variable in temperature and has high genetic variability is *Dedeckera eurekensis*, noted for its longevity (140+ years) and heterozygosity. It harbors a high

embryonic genetic load and only 2.5% or less of seeds are viable. This huge cost of nonviable seeds may be due to developmental lethal combinations (Wiens, *et al.*, 1989, 1989). Wiens' research concluded that it is not lack of resources, predation, or mortality due to environmental conditions which are the major reproductive constraints of this plant. This species may have had strong selection to maintain its high heterozygosity because of the various extremes in its environment. Heterozygosity of a particular enzyme may depend on its function as well as the ecological factors (Gillespie & Langley, 1974). The high heterozygosity would negatively effect the percentage of genetic viability in the offspring (seeds), and other components such as longevity would have adjusted to compensate. Further, there are other plants (e.g., *Mortonia utahensis*) with high heterozygosity which respond to their seed viability with long life spans (Wiens, personal communication). In opposition to high cost due to heterozygosity, sets of 100 plant species and 101 animal species had a positive correlation of fecundity with genetic variability (Hamrick *et al.*, 1979). There was strong positive correlation between fecundity and generation length and with generation length and dispersal mechanism in plants (Hamrick *et al.*, 1979). However, if there is a correspondingly higher number of non-viable reproductive attempts during the life span of these plant and animals species due to high genetic diversity, which was not examined by Hamrick *et al.*, (1979), then the positive reproductive potential is drastically reduced. If this were shown to be the case it may indicate that there is positive selection for long life spans in order to produce enough viable offspring. In this case heterozygosity and other genetic diversity may have significant costs, but be required for survival in variable environments.

Environments created by host-parasite interaction (Seger & Hamilton, 1988) can make an otherwise stable environment variable through changing resources, requiring polymorphic offspring. This concept of genetic foraging can give different perspectives to other ecological studies. For example: Ehrman (1966) showed that it did not matter which genotype was rare in *Drosophila*; what was important was the frequency (or the rarity) of males to other conspecifics which was influencing the female's choice, females were choosing novel (relatively) genetic variations.

Where resources are cyclic and vary significantly in availability in a given cycle, some organisms can avoid poor resources in a given season by waiting out a season. Organisms use diapause and dormancy to shelter themselves from seasonally harsh conditions, and germination and development times vary among cohorts. Temporal skips can be used in avoidance of parasites as well. Models for genetic variation under these conditions have been well argued as a type of bet hedging (Bull, 1987; Philippi & Seger, 1989).

Shortages of renewable resources in environments, whether because the resource is cyclic due to seasonal changes or because there are regular fluctuations of population density, impose constraints on the individual. The cost of nonviable genetic combinations could be minimized by producing fewer genetic variations if there were similar renewable resources over time. Some cyclic systems may select to keep both sexual and asexual reproduction, e.g., *aphids* and *Daphnia* use parthenogenesis in the early part of the season and the sexual cycle in the later. Where resources are both renewable and similar, sexual reproduction may be more critical as a dispersal mechanism than for creating genetic variations. In such environments reproductive systems such as selfing in sexual reproduction and asexual reproduction would be favored. Most annuals among plants are self-crossers and perennials are out-crossers (Wiens, 1984). Even though self-crossing annuals are using sexual reproduction, they are producing closer to 100% of their own genetic material, a situation analogous to cloning by bacteria. In consistently renewable resources and/or continual population cycles, cloning or selfing maximizes reproduction at a fast rate with excellent viability until the carrying capacity is filled. Selection will favor the fastest reproducer if there are consistent cyclic population fluctuations and/or cyclic resource blooms.

Where the resources have available in both a steady supply and with little variation in the types of resources, over long periods of time, there is little selection for producing and maintaining large amounts of genetic variation. The deep ocean is one habitat that produces relatively steady non-variable resources over time, and there are several species of deep-sea creatures such as *Nautilus* which are described as living fossils and the amount of genetic variability produced by these living fossils might be low. Although, changes in the deep ocean can be debated (parasites and resources), the deep ocean was the closest to an 'stable' ecosystem we could think of that has both non-variable resources and a steady supply of resources over long time periods.

DISCUSSION

Immediate-Benefit Hypotheses versus Variations-and-Selection Hypotheses

Hypotheses relying on immediate benefit or on benefit over a longer term have been reviewed by Kondrashov (1993). Further, argument for genetic parasitism has been presented by Blute (1984), although this argument was for only the parasitism based on the sex chromosomes, not the entire set of chromosomes. Even when the two sexes co-exist in the same niche the different-sexed offspring are utilizing two different resources because the females use the males for genetic phenotypes (e.g., rare phenotype advantage, Ehrman, 1966) and the males use the females as a resource. The model presented here does not dispute many of the theories concerning the evolution of sex. It argues instead that unless models of sexual versus asexual reproduction factor in all the benefits, including the parasitic strategy and cost of producing genetic variation, the immediate benefits to sexual reproduction will be difficult to perceive. Once these immediate benefits are placed in models many arguments will parallel the arguments of "when to change sex" for hermaphrodites (Charnov, 1982). The main new "concept" presented here is to view the sex gametes as "packages" of genes and then view *all* the constraints on individual fitness. In this case the question becomes. How to maximize the spread of these packages under different constraints? It is these different constraints which produce the various models and various life-histories, whether these models concern spatially structured population or one local population, or concern mutational models (e.g., Kondrashov, 1993). Arguments for optimizing the use of resources as well as the best dispersal strategies given the various niches are not new, but traditionally these arguments utilized "group selection" (e.g., Van Valen, 1971, 1973). However, when all the biologically critical components are placed into a more complete (and complex) individual-fitness model, the differences between group selection and individual selection decrease dramatically. With adjustments for the amount of competition in a population between members and the degree of relatedness between individual in a population, group fitness models could be constructed which would not violate critical assumptions for individual selection. When all costs and tradeoffs are placed into an individual fitness model then selection for the various types of life histories will become more apparent and sexual reproduction is not as costly as it first appears and becomes more of a "genetic" allocation problem utilizing various strategies. An individual's fitness has similar constraints whether the species is a virus, bacterium, mammal, plant, or human, but it is the strongest pressure from the outside environment, i.e., type and strength of selection, which produces the multitude of reproductive strategies.

Biological Systems for testing Hypothesis

With our present knowledge, there are several biological systems that by their speed and economic importance are good candidates for testing the hypothesis of genetic (optimal) foraging for variations. The extremely complex host-parasite system is a very promising system for further examination of foraging for genetic variations. Testing the genetic diversity of both host and parasite in various examples will include the dispersal of pathogens via vectors (water, sperm, vector species, etc.) that affect the travel time between individuals (resource patches) as well as the type of patches (species), and patch density (population's density). An important biological system in man is the spread of pathogens which cause AIDS, cholera, tuberculosis, malaria and small pox. Ewald (1983) has elegantly, and I believe correctly, argued that virulence of diseases (increase or decrease) is associated with the method of transmission (e.g., vector, water) and much of his work supports and parallels this model. If one thinks of a human as a "resource patch" for a pathogen, and that the human population density is a measurement of patch richness for pathogens, then the speed of transmission between patches is correlated not only to the vector but also to the patch richness (population density of host). If patches are plentiful and easy to enter (via various types of transmissions or health of the host) the quickest (virulent) parasite wins, just as in a rich medium the fastest-reproducing bacterium wins. As the resources decline (high mortality of host, or low population densities) the longer-lived pathogens (less severe) start to have an advantage over the virulent pathogens; in addition, as the resource density declines, the travel time between patches increases, and thus the mortality of the host in low population densities has severe repercussions to the parasite (Ewald 1983). Ewald's arguments parallel major arguments of this paper, if looking at humans as resource patches for the pathogen. However, the number of the different host species is critical because if there are several species a pathogen can invade (patches such as mosquitoes, cattle, and humans) then the pathogen has less selection to be mild to its host. If pathogen has several host species, it could eliminate a local

population of one of the species with minor repercussions and thus selection could favor the quick and severe pathogen.

Parasitism can exact extraordinary behaviors, e.g. photoperiod changes to avoid parasites (Feener & Brown, 1993), but one behavior that a species cannot change is eliminating reproduction. Therefore, many one-host pathogens are both long-lived and transfer via sexual reproduction or prenatally (e.g., pathogens causing AIDS, syphilis, gonorrhea). Furthermore, the transmission of some limited one-host viruses may ride via sperm and may be in transmitted in conjunction with other virus due to the various surface proteins they stick to (e.g., immunodeficiency virus, cytomegalovirus, Epstein-Barr virus, herpes simplex virus, human T-cell leukemia virus, adenoviruses, hepatitis B virus, and *Mycoplasma* spp.: Root-Bernstein and Hobbs, 1993). When the pathogen has only one host, as does HIV, patterns of spread can be predicted due to the host's migration for such reasons as economic resources (Hunt, 1989).

Another system which could be studied via a genetic-foraging model is the black pine leaf scale (Edmunds & Alstad, 1978, 1981), since there is a distinct tradeoff function between being adapted to the tree and being able to move to a new tree, and the pine tree's polymorphism in producing mixtures of toxic compounds (Sturgen, 1979). Furthermore, this system also has sex ratio changes due to the males' mortality. Another group that may be useful in genetic foraging and tradeoffs is *Drosophila*, not due to any economic or humanitarian importance, but because of our abundant knowledge, and the ease and speed at which experiments can be conducted.

Predictions

1. Holding dimensionless numbers in life histories (DLH) constant (Charnov & Berrigan, 1991b), the amount of genetic variation produced in offspring should differ between species which suffer high costs from parasitism, compared to species which have fewer parasites or species which are heavily preyed on. The reasoning is that predation increases the number of viable offspring that have to be produced, this increase acting as a stabilizing form of selection for genetic phenotypes, whereas mortality due to parasites will decrease with the production of polymorphic offspring. In contrast, examining species which differ in regard to their DLH numbers, but have similar levels of predation and parasitism, should produce similar amounts of genetic variation in their offspring.
2. Tradeoffs exist between generalists and specialized species in their ability to move quickly into new niches (patches) or adapt to changes in their old niche (patch), e.g., virulence in a virus, bacterium, or pest species should follow both patch richness (population density of hosts, e.g., trees, humans) and the travel times between these patches (genetic adaptation for black pine scale, vectors for various pathogens, etc.). Whereas specialized species have to have both renewable and consistent resources, because their ability to adapt to new patches may be slower, they can out compete the generalist by their specialized abilities (Tilman, 1982). The above arguments are not new in ecology, but being able to model across species via optimal genetic variation in offspring for environmental patchiness is. This also would include changes in sex ratio to utilize other females as a resource patch (via sons) having tradeoff curves, e.g., local mate competition.
3. Genetic variability potentially increases the rate for utilizing new resources and therefore, any species which consistently reaches its carrying capacity should maintain genetic variation, even without significant costs from parasites. Species which have strong selection for both rapid growth and genetic variation should (if possible) maintain both asexual and sexual cycles and switch strategies at critical periods; examples of organisms that switch reproductive modes are aphids, *Daphnia*, and rotifers. Other mechanisms can be substituted for sexual reproduction in cloning species to provide the needed genetic diversity, such as transformation, conjugation, and transduction in bacteria (Levin, 1988). These mechanisms should "switch on" when keyed by environmental conditions; e.g., bacteria are capable of surviving a large range of environments by having a type of genetic catastrophe insurance (Koch, 1993).

Future Modeling

In comprehensive studies with many species, orders, etc., the more complex optimization models may be preferable and reveal tradeoffs and their relationships that might otherwise be missed. Stephens & Krebs (1986) and Dixit (1990) examine various optimization models that could be adapted further. In addition, research that compares sexual species to asexual species should include the gain from using other females' resources (via sons) and any usage of different resources between the sexes. With the advent of the modern computer and structural equations many of these complexities can be statistically addressed through models with the life-history constraints in path analyses, and/or optimization using life history matrices, (e.g., Roff, 1992; Cadwell, 1989). A statistical program with

flexibility to handle a multitude of matrices is LISREL (Joreskog & Sorbom, 1985), which can be used for goodness of fit, and S+ may work for optimization programs.

Another approach for modeling is through parallel concepts in classic microeconomics models such as the tradeoffs in specialized industrial plants (e.g. a species) between time, output, and costs of specialized labor. Models used in microeconomics theory exist for maximizing outputs of industrial plants. These microeconomics models are important because they are maximizing output and minimizing costs with constraints similar to the evolutionary fitness model presented. Models for technological optimization give the maximization of output when inputs of labor and resources are limited in supply and have been modeled. Each fixed input combination has a distinct solution in optimizing the output of the industry. Imagine an organism allocating energy (capital) and time (labor) into various activities given a fixed input of energy (metabolic rates) and a fixed input of time (mortality rates). In biological terms the linear output of an individual, species, or large ecological community would fall on these various rays of energy per time. In other words, an organism can best utilize its energy and time if it allocates its resources among several independent activities. Dimensionless numbers and technological maximization models should all be suggesting similar constraints. Charnov and Berrigan (1990) showed that groups that have similar genetic groupings of genes, such as the grouping of different species of birds, several types of mammals, as well as groups of snakes and lizards, and fish have a direct correlation between the average female adult life span and the female age of maturity. These groups have their distinct slope due to their particular metabolic rates. Other work also support this argument of complex maximization, such as Ricklefs (1977) on fecundity and adult mortality (resources and time) as well as studies which examine the spacing of the of the different body sizes between many species over longer periods of evolutionary time (Van Valen, 1973). These allocations result in the most efficient use of the available resources under present technology (i.e., the genetic specialization). In economics terms, the use of the present technology has been optimized or is efficient; in biological terms, the specialization of the species has been optimized to best utilize limited resources.

CONCLUSION

These predictions and relationships differ from other models in that the scope covers organisms from viruses to whales. The novel features of the model presented in this manuscript are: 1) there can be a large cost of non-viability in producing genetic variation and this has distinct life-history tradeoffs, 2) there are immediate benefits in genetic recombination, 3) speed of obtaining resources and amount of genetic variation are usually tightly tied. This model is inclusive of other models since it connects various classic arguments for both the evolution of sex and its maintenance into a larger conceptual framework. Genetic variations in all organisms can be viewed as foraging through their reproductive efforts. Maintaining methods to create genetic variations does have a selective advantage. The various theories for genetic recombination (via sex) argue many causations and these theories are correct in the context of the particular constraint(s) under which they are presented. However, a more inclusive picture is required to perceive the strength of the selection for the amount of genetic variations required at the individual and population level. But genetic variation is just one constraint in the life history tradeoffs. The connections of these various constraints and knowing *why* they create these trade-offs are required to see how the intensity of selection changes on the different ecological components such as: availability and variability of resources, parasite density, and mortality rates, etc. Further, the lower and upper limits on these major parameters and their rates of change over time are required to understand how much genetic variation an individual needs to produce in order to hedge its bets by producing variable offspring.

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