The Evolution of Selection

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Summary

A paradigm of evolution is proposed in which the attribute of redundancy in the genetic architecture, known as diploidy, not only facilitates sexual reproduction but establishes the context in which Mate-Selection emerges as a dominant form of selection. It is proposed that Mate-Selection drives the selection for traits in mates that favor the Trans-Generational Fitness of progeny at the expense of the fitness of adults and as a result drives the evolution of sexually dimorphic traits and non-dimorphic traits such as senescence.

Mate-Selection is identified as an example of a fundamental type of selection labeled here as "Algorithmic Selection" which is the selection of genetic algorithms by genetic algorithms. By its nature "Algorithmic Selection" represents a highly unconstrained self-boot-strapping information based process that enables and drives the "evolution of selection". It is proposed that the evolution of selection is the ratchet that has driven and defined complexity in eukaryotes.

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Introduction

Charles Darwin proposed that organisms evolved primarily within the context of natural selection and to a lesser extend by Sexual-Selection. These two types of selection have essentially been seen as static or bounded processes with the exception of arms races which have also generally been seen as bounded or constrained to escalating iterative interactions. This paper proposes that sex and sexual selection or more precisely Mate-Selection has a primary role in the evolution of all complex multicellular life, and that a primary role of sex is to establish a context in which selection itself evolves. It is proposed that "the evolution of selection" has driven the evolution of increasing complexity in eukaryotes.

Richard Dawkins and others have argued pervasively for the paradigm that the genes constitute the "replicator" and the organism or animal is the "Survival Machine" that does the bidding of the replicators. In this paper I will argue against the primacy of the
replicator in favor of a return to the intuitive perspective of the primacy of the individual organism. I propose that there is a more insightful paradigm from which to view the eukaryotic organism, not just as a survival machine which carries the genes to the future, but more importantly as a "Selection Machine". This paper proposes that the role of Selection Machine is a primary function in the evolution persistence of complex life forms.

"The Evolution of Selection" (EOS) proposes a new information based paradigm for selection founded on the perspective that the primary effect of sex is to facilitate mate-selection and its evolution. The EOS paradigm emphasizes the perspective that mate-selection plays a far larger and critical role in the evolution of complex traits in eukaryotes than had been previously thought. Sex drives mate-selection, not just in the conventional sense of the production of ornaments, but in its most fundamental and general form, as selection by algorithm or selection by mechanisms defined by algorithms.

This paper proposes, not new data, but a different perspective on the concept of selection. EOS proposed that the dominant form of selection that drives the evolution of complex life forms is not "raw" natural selection but algorithmic selection and that a primary function of sex is to establish an environment in which multiple levels of complex information systems such as genes, individuals, sexes, species and ecosystems, etc are locked into multi-level, multifaceted arms races. Stated succinctly, sex drove the invention of algorithmic selection and also established the arms races that drives the continued evolution of algorithmic selection.

EOS proposes that it is the attribute of diploid redundancy in the genetic architecture of eukaryotes that makes possible the bifurcation of inherited traits into separate gametes derived from separate individuals. This constitutes the perspective that can bring clarity to the evolution of complexity. It is the externalization of genetic material into separate gametes derived from separate individuals that allows the selection of genetic algorithms by genetic algorithms. Diploidy enables the bifurcation of goals, the bifurcation of cost, the bifurcation of reward, the bifurcation of intentions and the bifurcation of desires. Fundamentally diploidy established the redundancy and symmetry that makes possible the bifurcation that enables and drives algorithmic selection and its more narrow casting referred to here as Mate-Selection. It is the multiplicity of bifurcations, facilitated by diploidy, that enables the multiplicity of arms races which drive the evolution of Algorithmic Selection (AS) to favor traits beyond ornamentation and sexual dimorphisms.

Viewed mechanistically, Algorithmic Selection (AS) is selection of genes by the actions of genes. Stated more generally, AS is the selection of genetic programs by genetic programs or information selecting information. Natural Selection (NS) when defined non-inclusive of AS is constrained by the laws of physics, chemistry and probability, where algorithms, by their nature, existing simply as information, exhibit vast degrees of freedom as they are primarily constrained by combinatorial considerations. As a result, selection based on algorithms is far less constrained. The greater degrees of freedom
afforded by algorithmic selection and the arms races it affords drives the evolution and diversity of complex life forms. Algorithmic selection, viewed in respect to species constitutes a recursive process that applies its selective actions, deliberately, in real time, without dependence on the happenstance of selective events that characterize the extrinsic processes of natural selection. Evolutionary literature has proposed that many aspects of life can and are sequestered from direct action by processes of NS. However AS does not suffer from such constraints and can apply selective processes more discriminately, more consistently and more strongly. AS increases the speed in which selection is applied to a gene pool and it also applies selective forces more predictably to larger portions of the gene pool. In aggregate these effects greatly increases the rate at which a sexual species can evolve relative to an asexual species.

As a process of information processing, selection by algorithm or selection of genes by genes, also acts recursively to select for genes that improve the efficiency of gene selection. This selection process is "self bootstrapping" and drives the evolution of selection toward novel selection mechanisms and it accelerates the repeated bifurcation of selection processes to perform selection on continually more traits. Algorithmic Selection is not just a form of selection it is selection on selection and selection of selection, it is "meta-selection". In aggregate, these effects accelerate the evolution of complex traits and as a result drives the persistence of sex as a reproductive method.

Intuitively it would seem that the selection of genetic programs by genetic programs would occur essentially without constraint. However the natural world demonstrates that the mutually selecting binary systems we call sexually reproducing species limit the magnitude of sexual dimorphism’s and exhibit shared patterns of constraint across species. This paper proposes that genomic redundancy as expressed as diploidy is the critical trait of eukaryotes that both directs and constrains the degrees of freedom inherently contained in Algorithmic Selection and as a result defines the arrow of evolution of complex life.

Scope

The origin of eukaryotic life and with it the origin of sexual reproduction remains undetermined and lies beyond the scope of this paper. However the function and persistence of sex has also resisted adequate explanation and is the subject of this paper.

Neo-Darwinism has long struggled to account for the "two fold cost of sex" as described by Maynard Smith and others. How can sexual reproduction persist when asexual reproduction is a far more efficient way to pass genes to the next generation? In recent years mathematical models has demonstrated that the prevalence of sex can be accounted for in part by the effects of masking of deleterious alleles, and genetic recombination, on fitness of the individual relative to clonal reproduction in eukaryotes. These and other proposed effects do not seem to constitute the complete
explanation for the evolution and persistence of sex nor for the examples in which clonal reproduction has been employed exclusively for as much as 60 million year as in the case of deloid rotifers. This paper proposes that eukaryotic sex persists because it increases the efficiency of evolutionary adaptation relative to clonal reproduction by facilitating a positive selective process (algorithmic selection) that coexists with and amplifies standard processes of natural selection.

Algorithmic Selection

Algorithmic Selection as used in this paper is defined as any process of selection that is driven by processes that are themselves driven directly or indirectly by genes. Some examples of algorithmic selection is pollination of flowering plants, sexual ornaments, vaginal plugs produced by male rats, the relative height of trees, mimicry, camouflage, bird song, intelligence, etc. In this context it can be said that "Natural Selection" encompasses algorithmic selection since algorithmic selection is "natural", however for clarity I segregate out algorithmic selection leaving natural selection to mean selection due to physical attributes of the environment such as drought, fire, heat, cold, radiation, flood, avalanche, rock slide, toxic materials of a non-biological origin, etc. The sensibility of this distinction will be made clear later in this paper.

The Foundation of Algorithmic Selection

It is proposed that diploid redundancy is the primary feature of eukaryotes that facilitates algorithmic selection and as a result drove the emergence of complexity that constitutes the foundational element that defines the arrow of evolution toward increasing complexity. The evolution of intelligence and the evolution of aging are examples of complex traits that are driven in large part by algorithmic selection. Here forward I will generally use the term algorithmic selection since sexual selection has come to constitute the label for a more narrowly defined type of selection that results in the evolution of traits described as sexual ornaments and other sexual dimorphism's.

Definition of Key Terms

For the purposes of this paper the following terms have been defined to prevent confusion with more common meanings of the terms.

"Algorithmic Selection" is defined as: Any process, trait or condition, directly or indirectly produced by life processes, that favor or dis-favor the fitness of the individual.

Algorithmic Selection can be thought of as the selection of a trait
or phenotype by the same or another trait or phenotype. I have chosen "Algorithmic Selection" as the label for life based selection processes because traits, or phenotypes, are defined by genes. Genes represent a form of program code or "algorithms" that determine the behavior of the cellular machinery. Algorithmic Selection is the appropriate descriptor of the selection processes when the primary driver of selection for genetically defined traits are other genetically defined traits.

Algorithmic Selection can occur between genes within single cells, between organelles between cells in a tissue, between tissues during embriogenesis, it can exist between individuals as when constituting Mate-Selection drivers and processes, and it can occur between the collective effects of the entire gene-set of individuals of different species as occurs in symbiosis. Finally, Algorithmic Selection can occur between the collection of genes active in an ecological nich with the complete gene-set active in the individuals within the niche. Algorithmic Selection can occur across species and across great spans of time as when centuries of bat droppings define the ecology and the resulting selective forces acting on organisms found on the floors of caves.

"Trans-Generational Selection" is defined as: "Processes that favor the fitness of present and future generations of offspring that results from dis-favoring the fitness of adult individuals".

"Trans-Generational Fitness" is defined as: The fitness through time of present and future generations of non-adult offspring.

"Mate-Selection" is defined as: Any process implemented by an individual or group of individuals of a species that influences the success or failure of the same or another individual in combining a haploid complement of its genes with a haploid complemet of another individuals genes in the production of a diploid offspring.

The term "Mate-Selection" is introduced to define a concept that is broader in scope than the conventional meaning subscribed to the terms Sexual Selection, Kin Selection, or Mate Choice. Mate-Selection, as used here, does not require an overt act as it can be represented as selection on the individual or the gametes of the individual, as for example, when a vaginal environment is hostile to the vitality of sperm that express a specific phenotype.

Inclusive Fitness VS Trans-Generational Fitness

As a point of clarification the term "Inclusive Fitness" is a term that occurs in the evolutionary biology literature that conveys a conception of the fitness which includes multiple generations of offspring and Kin. To differentiate this
term from Trans-Generational Fitness it can be said that Inclusive Fitness is focused on the "value" to the individual of itself exhibiting altruistic traits or behaviors that benefits the fitness of Kin. Trans-Generational Fitness is focused on the "value" to the individual of its mates and offspring exhibiting altruistic traits that benefits the fitness of it's present and future offspring. This distinction will be made clearer later in the paper.

Even though the individual does not bare the cost of selecting mates with altruistic traits that favor trans-generational fitness it is not free to select mates with exaggerated examples of altruistic traits. Selecting for extremely altruistic traits in it's mates expose the individual to a high probability of negatively effecting the fitness of its offspring that inherit and express such traits.

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The Taxonomy of Natural Selection

To reach new insights into the evolution and persistence of sex and complex life it is necessary to differentiate and categorize the variety of selection forces in order to establish a taxonomy of drivers constituting the whole of Natural Selection. Through this structuring, inferences can be drawn that illuminate the processes of eukaryotic evolution. Surely other orderings of selection forces are possible, I have selected this taxonomy because I feel that it is the most instructive structuring I have found and it reflects fundamental divisions of causality.

At the top of this taxonomy, as shown in the Table 1. below, Natural Selection can be seen as bifurcated into two, essentially opposing, "Arrows" of selection, Individual selection which acts on the individual to favor the survival of the Individual and Trans-Generational Selection which also acts on the individual but favors the survival of progeny at the expense of the adult.

Within the context of these opposing arrows of selective pressure, Natural Selection can be further bifurcated into two main classes of selection. One class being "Physical Selection" which is selection by non-life processes such as mineral resource availability, fire, heat, cold, accidents, floods, etc. The other class of selection I call "Algorithmic Selection" is selection that results from life processes such as, predation, sexual selection, immunity, intelligence, strength, speed, etc.

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Table 1. below titled, Trans-Generational Selection VS. Individual Selection constitutes a sample of traits and conditions that drive Trans-Generational Selection and the traits and conditions that drive Individual Selection. Individuals are subject to many of the selection drivers, listed in the table, at the same time. I
propose that it is the aggregate effect of the ensamble of the synergistic and opposing
selection drivers, that ultimately determine the balance between trans-generational
selection and individual selection. It is the life histories of the species, as defined by
the unique combination of these same traits/drivers, that determines a unique balance
between these opposing arrows of Trans-Generational and Individual Selection and as
a result defines the reproductive phenotype and the evolution of complex life.

The first part of the table lists some of the attributes of the physical world that can
produce differential selective pressure on individuals. These selection drivers have
been classified by the type of selection they favor more, Trans-Generational Selection
or Individual Selection.

Below the second break in the table the remaining drivers are classified as "Algorithmic
Selection Drivers" which consist of traits, phenotypes and consequences of the actions
of organisms themselves. These drivers are listed as either neutral, (appear in both
columns), or they are shown in either the Trans-Generational Selection or Individual
Selection columns, depending on which type of selection they favor more strongly.

Table 1.

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<thead>
<tr>
<th>The Taxonomy of Natural Selection</th>
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<td>( Trans-Generational Selection VS. Individual Selection )</td>
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<td>Trans-Generational Selection</td>
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<td>(Favors Offspring)</td>
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<td><strong>Physical Selection Drivers</strong></td>
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<td>(Non-Life Processes Favoring Offspring)</td>
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<tr>
<td>- Dis-Economies of Scale -</td>
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<tr>
<td>- Temperature Extremes &gt;</td>
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| - Constancy of Resources - | - |}

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<tr>
<th>Algorithmic Selection Drivers</th>
<th>Algorithmic Selection Drivers</th>
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<td>(Life Processes Favoring Progeny)</td>
<td>(Life Processes Favoring the Individual)</td>
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<td>Reproductive Selection Drivers</td>
<td>Reproductive Selection Drivers</td>
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<td>- Sexual Reproduction +</td>
<td>+ Asexual Reproduction &gt;</td>
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<td>- Gestation +</td>
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<tr>
<td>- Breast Feeding +</td>
<td>+ Filial Cannibalism &gt;</td>
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<tr>
<td>(Selfish) Mate-Selection Drivers</td>
<td>(Selfish) Mate-Selection Drivers</td>
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<td>- Preferring Healthy Mates +</td>
<td>+ Preferring Healthy Mates &gt;</td>
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<tr>
<td>Preferring Delayed Reproduction In Mate +</td>
<td>+ Preferring Delayed Reproduction in Mate</td>
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<tr>
<td>(Altruistic) Mate-Selected Selection Drivers</td>
<td>(Selfish) Mate-Selected Selection Drivers</td>
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<td><strong>&lt; Preferring Growth-Terminated Mates +</strong></td>
<td><strong>+ Preferring Growth-Terminated Mates &gt;</strong></td>
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<td><strong>&lt; Preferring Mates that Protect Offspring +</strong></td>
<td><strong>+ Preferring Mates that Protect Offspring &gt;</strong></td>
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<td><strong>&lt; Preferring better Ornamented Mates +</strong></td>
<td><strong>+ Preferring better Ornamented mates &gt;</strong></td>
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<td><strong>&lt; Preferring Graying Patterns in Mates +</strong></td>
<td><strong>+ Preferring Graying Patterns in mates &gt;</strong></td>
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<td><strong>&lt; Preferring Senescence in Mates +</strong></td>
<td><strong>+ Preferring Senescence in Mates &gt;</strong></td>
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<td><strong>&lt; Preferring More Intelligent Mates +</strong></td>
<td><strong>+ Preferring More Intelligent Mates &gt;</strong></td>
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<td><strong>&lt; Preferring Mates that Compete for Mates +</strong></td>
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<td><strong>&lt; Preferring Stronger Mates +</strong></td>
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<td><strong>&lt; Preferring Semelparous Mates +</strong></td>
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<td><strong>&lt; Preferring Iteroparous Mates +</strong></td>
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<td><strong>&lt; Preferring High Sex Drive in Mates +</strong></td>
<td><strong>+ Preferring High Sex Drive in Mates &gt;</strong></td>
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<td><strong>&lt; Semelparity +</strong></td>
<td><strong>+ Iteroparity &gt;</strong></td>
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<td><strong>&lt; Monogamy +</strong></td>
<td><strong>+ Polygamy &gt;</strong></td>
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<td><strong>&lt; Delayed Reproduction +</strong></td>
<td><strong>&lt; Protecting Offspring +</strong></td>
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<td><strong>&lt; High Sex Drive +</strong></td>
<td><strong>&lt; Male Competition +</strong></td>
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<td><strong>&lt; Sexual Ornamentation +</strong></td>
<td><strong>&lt; Growth-Terminating +</strong></td>
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<td><strong>&lt; Growth Non-Terminating &gt;</strong></td>
<td><strong>&lt; Graying Patterns in Hair and Fur +</strong></td>
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<td><strong>&lt; Senescence +</strong></td>
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<td>Survival Selection Drivers</td>
<td>Survival Selection Drivers</td>
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<td>&lt; Health +</td>
<td>+ Health &gt;</td>
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<td>- Infant Starvation &gt;</td>
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<td>&lt; Adult Starvation -</td>
<td>+ Symbiosis &gt;</td>
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<td>&lt; Parasitism -</td>
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<td>&lt; Predation -</td>
<td>+ Carnivorousness &gt;</td>
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<td></td>
<td>+ Greater Strength &gt;</td>
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<td></td>
<td>+ Higher Intelligence &gt;</td>
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<td>&lt; Interspecies Competition -</td>
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<td></td>
<td>+ Flight &gt;</td>
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<td>+ Greater Speed &gt;</td>
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<td></td>
<td>+ Adaptive Immunity &gt;</td>
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<td>&lt; Meiotic Drivers -</td>
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<td>&lt; antagonistic pleiotropy -</td>
<td>+ Mimicry &gt;</td>
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<td></td>
<td>+ Toxic to Eat &gt;</td>
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<td></td>
<td>+ Venomous &gt;</td>
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<td>&lt; Tissue Fibrosis -</td>
<td>- High Infant Mortality Rate &gt;</td>
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<td>&lt; High Adult Mortality Rate -</td>
<td>+ High Maximum Lifespan &gt;</td>
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<td></td>
<td>+ Negligible Senescence &gt;</td>
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In the Table above the minus sign near the center line of the table indicates that the selection driver functions as culling or negative selection pressure. The plus sign indicates that the diver operates as positive selection pressure, selecting winners in a population not losers as the negative selection drivers do. It should be noted that positive selection drivers produce greater selective pressure that negative selection
Physical Selection: is selection by non-living processes. Physical Selection is primarily a negative selective process as it results in death or loss of fitness to individuals. Physical Selection is a relatively non-discriminatory process because it can act multi-generationally on all individuals in a large sub-populations over a large geographic area.

Note: It could be argued that the presents of oxygen, hydrogen sulfide and other effects are the result of biological processes and biological algorithms. However these processes occur over vast multi-generational time constraining there effect to discrimination at the level of the individual, for these reasons they have been placed under Physical Selection part of the taxonomy.

Algorithmic Selection: represent all life-based selective processes and comprises the remaining balance of selective process to which organisms are subjected. These selection processes derive from the direct or indirect and recent action of algorithms executed by organisms or to recent environmental effects of the actions of organisms algorithms. Algorithmic Selection is inherently evolvable.

Survival Selection: is the form of Algorithmic selection that acts by reducing or increasing the fitness of the individual of the individual. Inter-species competition for resources also exemplifies this group.

Reproductive Selection: is the the form of Algorithmic Selection that is a direct result of sexual reproduction. This is an inherently positive process that acts by selectively amplifying the fitness of some individuals at the expense of other individuals.

Artifical Selection: Generally "Natural Selection" refers to all process of selection with the exception "Artificial Selection" which is selection processes directly or indirectly influenced by man. Within the context of the definitions in this paper, Artificial Selection represents just a specific class of algorithmic selection that does not warrant special distinction.

The Power of Algorithmic Selection

As described above, the power of algorithmic selection relative to natural selection also derives from the degrees of freedom that it can manifest. Stated another way it can be said that the selective power of algorithms is derived from its ability to generate high degrees of complexity, even from very simple algorithms possessing simple rule sets demonstrate this capability. An example of this is Steven Wolfram’s rule 30. The output of Rule 30 cellular automata, which constitutes it "behavior" can be
seen to be highly complex. Steven Wolfram has gone on to demonstrate that the computational universe contains many simple algorithms that possess highly complex behaviours. Additionally he has demonstrated that and the behaviour of more complex algorithms exhibit an increased probability of exhibiting complex behaviors.

The Arrow of Evolution

The Algorithmic Selection paradigm also maps well with the in site that evolutionary processes do not always conform to an arrow that drives the evolution of species from simple forms to more complex forms over time. Evolutionary end points span a continuum from the traditional conception that organisms evolve from simple forms to more complex forms over time, while other species essentially do not evolve in any substantial way over long periods of geologic time, and a third group of species evolve from complex forms to simpler forms.

Algorithmic Selection is fully compatible with the observation that evolution need not exhibit an "arrow" toward increasing complexity. The spectrum of optional outcomes for algorithmic systems has been succinly demonstrated by Steven Wolfram in his chapter titled "The World of Simple Programs" page 55 in his book "A New Kind of Science". Here he demonstrates that by varing the starting conditions (the Rule) of a set of similar, simple, programs or algorithms provides multiple examples of systems evolving to greater complexity, while others evolve to a specific level of complexity and then plateau, and others evolve to a medium level of complexity and then drop back to a lesser complexity before becoming stable, while another form evolve to a level of complexity before regressing in complexity to the point that they become "extinct".

Computational Irreducibility

Steven Wolfram has also demonstrated that a great number natural systems or the outputs of possible "natural algorithms" in the computational universe are computationally irreducible. This means that no system or program can predict the behavior of another system that have attained a threshold level of complexity without simply carrying out the same steps and starting with the same inputs.

The law of Computational Irreducibility expresses a fundamental attribute of complex systems which greatly precludes the ability to apply mathematical formula (algorithms), to predict the behavior of even simple systems, with accuracy. The "idealization" or simplification of the attributes of natural systems for the purposes of making them amenable to "compression" via mathmatical formulation (algorithms) has, since R. L. Fischer, constrained progress.

Natural Selection As A Tool

The primacy of algorithmic selection often goes unrecognised because algorithmic selection frequently uses natural selection as a tool with which to implement its actions. As a result a significant percentage of algorithmic selection is disguised as natural
selection. For example, when females drove the selection of ornamentation in the peacock to the point that the tail became a physiological burden that raises the risk of predation, increases metabolic demand, and increases the demands on the agility of perspective mates, the female by simply selecting for vigorous males with large ornaments will in effect be selecting for many traits beyond ornamentation at the same time. Females are in effect deliberately and consistently subjecting males to the forces of natural selection in a "focused way".

Another example when species of frogs select males on the basis of loudness of call, duration of call, or complexity of call, the female is selecting on traits such as size, ability to resist predators, stamina, intelligence, along with the specific ornamental trait. The longer a population of females drive the exaggeration of a specific sexual ornament the more the trait will also function as a stressor that subjects males unavoidably and persistently to natural selection processes on traits that are fundamental to survival and fitness.

An extreme example of females using natural selection as a tool exists in species of ants, bees and wasps in which the males develop from haploid eggs. In these cases males are stripped of their ability to mask non-adaptive genes from natural selection, the female is presented with an essentially "unmasked" male against which the female can apply mate selection criteria with a higher probability of success, she can directly observer the unambiguous effects of the genes she is selecting.

**Running The Algorithmic Selection Gauntlet**

Algorithmic Selection is not totally dependent on mate-selection as it's mechanism. Algorithmic selection can also occur at the level of chromosomes and competition between alleles at the same or different loci. Indirect forms of mate selection that utilize natural selection processes to de-select less fit mates or less fit offspring for example are also constructed by making the vaginal environment harsh to sperm, or making the implantation of the fertilized egg into the uterine wall a difficult process. Any behavior that adversely effects, gestation, or the nurturing of the young, or prospective mates can be a direct result of the action of algorithmic selection. This type of mechanism is feasible for any species that has evolved the capacity to conceive more offspring than can be sustained to reproductive age.

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**Diploidy Favors Algorithmic Selection**

**Redundant Genomes Favor Traits That Favor Future Generations**

The role of redundancy in the genome has been examined by John Maynard Smith and others in a paper titled: *Evolution of Genetic Redundancy* where they examined redundancy that existed in the genome across loci, however they were not focused on the redundancy of diploidy which drives algorithmic selection.
A pivotal role of diploidy rests on the logic that a potentially adaptive mutational event to a given allele must be expressed if it is to be exposed to selective pressure and as a result have an opportunity to exploit its own adaptive value to increase its frequency in the gene pool. In nature, diploidy prevents the average individual from attaining a high probability of having a unique adaptive trait expressed strongly in the next generation once it is paired with its sister allele when diploidy is reconstituted at conception and allelic dominance is reestablished. This logic applies to all alleles in an individuals genome. This limit on the probability and strength of expression of any given allele provides the selective pressure that favors traits that favor "the fitness of multiple successive generations of offspring" (Trans-Generational Fitness). "Trans-Generational Selection" is the term used here to describe the selective pressure that favors traits that favor Trans-Generational Fitness. Trans-Generational Selection is implemented via mechanisms of algorithmic selection of which conventionally described mate-selection is a subset.

Note: For a discussion of the implications of Trans-Generational Selection and mate-selection to the evolution of complex life, see the section titled "The Evolution of Algorithmic Selection".

**Selection for Traits that Dis-favor the Individual**

The inability of the individual to deliver more than half of its genes to any given offspring and the arms races by alleles for expression drives the individual to select for traits in prospective mates that dis-favor the interest of the prospective mate. In response to these selective pressures individuals evolve strategies that attempt to circumvent or fool the selection strategy of the selecting mates. This then leads to selection of additional strategies on the part of the selecting individual to further refine its selection strategy to defeat the negating strategy of its prospective mates. This process can continue as an arms race that can persist throughout the evolution of the species. These effects lock the sexes into arms races fought by genetic algorithms of selection and algorithms that are selected to defeat selection algorithms.

**The Evolution of Dominance In Redundant Genomes** (needed?)

Some attention has been paid to the evolution of dominance, currently without the emergence of consensus, however it is a proposal of this paper that the concept of recessive and dominant alleles is a reflection of an arms race that occurs between alleles for expression in the phenotype. Allelic competition occurs because it is a genes relative rate of expression that determines the probability that it will sustain or increase it frequency in the gene pool either by exposing itself to selection forces, or by masking itself from selective forces when its expression is deleterious relative to the effects of the allele with which it is paired in the individual.

Complete repression of alleles are known. For example, Goto Y, Gomez M, Brockdorff N, Feil R, demonstrate that all genes on a given X chromosome can be repressed in the case of female offspring.
The **differential allele-specific methylation of histone proteins** and the vast array of promoter and repressor gene switches found in the genome could constitute the battleground upon which genes not only are regulated to support metabolism but also wage their arms race for dominance and sometimes non-dominance. It seems feasible that **RNA interference** could also be a mechanism by which alleles compete for dominance.

The concept of "wild type alleles" which has been used to express the idea of highly dominant alleles that have won the arms race for dominance can represent the process by which once the majority of allele arms races across loci have been resolved a species can become evolutionarily static, examples of this can be seen across taxa.

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**Favoring Trans-Generational Fitness**

The following sections describe some of the ways redundant genomes increases Trans-Generational Fitness by favoring "Trans-Generational Selection". Specifically how Trans-Generational Fitness is increased via mechanisms that implement resource conservation is described. It is the level of activity of these resource conservation mechanisms that directly cause senescence and define it rate of accumulation across animal species.

The role of the dynamics of gene pool size and rates of reproduction will first be described, at it provides the context in which diploid redundancy drives mate-selection to favor the selection of traits that increase Trans-Generational Fitness.

**Increasing Gene Frequency In Shrinking Gene Pools**

Over the short term the population of a species can fluctuate significantly, however on average, in mature ecosystems animals produce approximately two offspring that grow to maturity and reproduce themselves. Whether a species has a relatively static population or a fluctuating population the gene pool will experience natural selection within the context of a relatively static or falling population half of the time. As a result the majority of individuals in a gene pool attempt to reproduce in the context of static or falling reproduction rates across the population. For this reason **natural selection** favors the emergence of mechanisms that can increase the frequency of an individual genes in a static or decreasing population. This does not preclude the evolution of other mechanisms that rely on a rare emergence of a large reproductive advantage to increase the frequency of an individuals genes in a gene pool. However, for a typical individual to succeed in maintaining or increasing the frequency of its genes in the gene pool it achieves its highest probability of success by utilizing mechanisms that increase the chances of exposing its genes to natural selection forces over successive generations of offspring by implementing a "trans-generational strategy". This process allows the individual to succeed in increasing the number of copies of its genes without relying on the occurrence of a highly improbable mutational or combinatorial event capable of dramatically increase the individuals reproduction rate.
For example, when a mutational event or particular combination of genes produce a phenotype that significantly increases the reproduction rate in an individual, this gene or combination of genes will rapidly increase and come to dominate the gene pool. As this new phenotype approaches dominance in the gene pool most adults will exhibit the phenotype and the reproductive advantage will end. The stress on the ecosystem of the increased population will quickly drive down the rate of reproduction back to the level of two offspring or lower. During these periods of time, natural selection will again be working within the logic of acting trans-generationally to fix traits in a gene pool, likely favoring Trans-Generational Fitness mechanisms more strongly than it did before the increased rate of reproduction had occurred. Negative population growth, that results from the effects of overpopulation on the ecosystem favors mechanisms that increase Trans-Generational Fitness even more strongly that it is favored during periods of static population size.

Again, the mechanisms favoring Trans-Generational Fitness do not preclude the emergence of a trait that upregulate the reproduction rate of an individual harboring such a trait, nor does it prevent the traits spread through the population. However, because the increased population effect is inherently transitory, these episodic events cannot prevent the evolution of mechanisms that favor Trans-Generational Fitness and its persistence in the gene pool.

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**Diploidy Drives And Directs Mate-Selection** 77777 review from MSSA paper

Because sperm and eggs contain only half of the chromosomes required to produce a fully functioning reproductive adult, animals must select mates in order to collect the genes necessary to reconstitute diploidy in their offspring. This obligatory contribution of genes by mates constitutes a fundamental asymmetry of interest between the selecting individual and the selected individual. Even when there are equal numbers of both sexes and both sexes are selecting equally, the individual selecting has a choice of more than one prospective mate, this is the fundamental asymmetry of Mate-Selection.

Many processes of choosing a mate affords the individual the opportunity to evaluate or discriminate the quality of genes as they are expressed in mates through the processes of Mate-Selection. Mate selecting individuals are both free and driven to select for altruistic traits in their mates because these traits favor the fitness of current and future progeny. The fundamental asymmetry of selection exacts little to no cost from the selecting individual as nearly the entire cost of the altruistic traits are born by the selected mate and their shared progeny.

The selection of mates with genes that produce an altruistic offspring-favoring phenotype is the only tool that the individual has that can project traits and behaviors beyond its life span into the future which, in turn, are capable of driving future generations of offspring to autonomously act in ways that benefits its ancestors.
reproductive agendas. To support the reproductive agenda of the selecting individual the genes must survive and be expressed over many generation of offspring. For this reason, these genes must be part of an evolutionarily stable strategy (ESS). These constraints combine to conform the Mate-Selection process in such a way as to define an arrow or directionality to Mate-Selection that is expressed as discrimination by the selecting individual for traits in their mates that favor Trans-Generational Fitness.

Examples of Traits that favor the fitness of Progeny

Other than senescence, traits that favor the fitness of progeny include traits such as, gestation, nurturing the young, terminated-growth, menopause, and death mechanisms. This class of trait I have designated as "Progeny Enhancing Traits" (PET) as they contribute directly or indirectly to the fitness of offspring.

There also exists what can be called second order PET's designated Progeny Enhancing Trait Indicators (PETI), these traits act as indicators that can be used by Mate-Selection processes to help the selecting individual to discriminate the strength of PET's in their mates. Examples of these traits are: sex-drive, patterned graying hair or fur, loss of beauty.

Traits That Favor Trans-Generational Selection

A final, perhaps most important, class of traits that favor the fitness of progeny are the Mate-Selection traits exhibited by the selecting individuals in a mating pair. These traits I call Progeny Favoring Mate-Selection Traits (PFMST). These traits drive individuals to select for mates that exhibit PET's or PETI's. PFMST's consists of any trait that drive the individual to select of mates which exhibit traits that favor fitness of progeny that comes at the expense of their own fitness. For example a female perfering to mate with a male that is visibly aged over a male that shows no sign of aging constitutes selection for a senescing mate and is an example of such a PFMST. PFMSTs are not altruistic but instead are standard Darwinian traits of self-interest that drive the selection of altruistic traits in their mates.

END MSSA paper

Diploidy Favors Trans-Generational Fitness

Diploidy favors Trans-Generational Fitness and dis-favors individual fitness in individuals that are reproducing at or below the two offspring replacement rate, in a variety of ways. here are a few examples.

Recessive Alleles Favor Trans-Generational Fitness
Recessive alleles require the production of multiple successive generations of offspring in order to raise the probability that a given allele will be paired with another allele with which it can be dominantly expressed in a phenotype. When an allele is highly recessive it will have to wait multiple generations for expression, it may have to wait until it is by happenstance paired with another copy of itself, in an individual that is homozygous for the trait.

**Multi-Gene Traits Favors Trans-Generational Fitness**

Many traits result from the expression of more than one gene, any given allele can be adaptive or non-adaptive when co-expressed with any other given gene in the species genome. Many successive generations are required for the individual to have its set of alleles combined with a large number of alternative alleles from the gene pool and be tested as distinct phenotypes by selective processes.

**Diploidy Favors Sexual Choice**

It almost goes without saying that sex and therefore sexual choice or mate-selection is meaningless without the production of offspring that posses redundant genomes. However, diploidy not only facilitates sex and mate-selection but favors the evolution of mate-selection because it is highly improbable that the haploid gene set contributed to offspring by the individual will dominate the gene set across all phenotypic traits. Mate-selection allows the individual to "attempt to insure" that if any give allele it contributes to an offspring is recessive to the allele from its mate, the mates allele will be adaptive and enhance the propagation of its own masked allele in the next generation.

**The Enforcement of Diploid Redundancy**

As has been discussed diploid redundancy is instrumental to the functioning of Mate-Selection, so the question should be asked how is this redundancy preserved? Why do organisms fail to economize on DNA by having alleles diverge to the point that they become totally different in their function such as they do in sex chromosomes? And perhaps others may have proposed that policing the redundancy of diploidy is one of the primary roles of recombination. Because a crossover event occurs randomly at any location along the DNA strand with no regard to where genes begin or end, if a crossover event occurs within the genes of highly diverged alleles this would result in a high probability of producing two disfunctional versions of both genes.

**Haploid Gametes Enforce Diploid Redundancy**

Haploidy is an additional mechanism that enforces the genetic redundancy of diploidy. Because haploid eggs persist as autonomous or nearly autonomous cells for extended periods of time the haploid complement of their genes also define a
phenotype, meaning that basic cell physiology of a haploid cell must remain capable of producing all of the cells required components necessary to maintain basic metabolism.

The metabolic autonomy of haploid cells constrain the genes that define basic cell physiology but does not constrain the genes for traits the define the multicellular organism, such as eye color, coat patterns, etc. Based on this reasoning it is clear why the genes that define basic cell physiology are highly conserved while other genes that define developmental biology, or coloration, for example, have undergone much more change over evolutionary time.

**Sexual Dimorphism Favors Trans-Generational Fitness**

Any given gene derived from a particular parent may have selective advantage when expressed as part of one gender and be neutral or provide disadvantage when expressed in the alternative gender. Because on average animals produce only approximately two reproductive offspring in the next generation there is a fifty present chance that both of an individuals offspring will be of the same sex. Multiple generations are required to provide a high probability that all of the parents gene defined sexual dimorphism's are exposed to natural selection forces by being expressed within the context of both genders. For example in sexually dimorphic species such as peafowl, if a peacock has more eye spots in its tail feathers than the standard male in the population and this male is represented by only female offspring in the next generation, Mate-Selection will not be able to act on this sexually selected trait during this generation of offspring. The parents will needs at least one more generation to provide the opportunity to transmit this trait to a male offspring which can again exposed as an adaptive trait and increase its prevalence in the gene pool.

Sexually selected traits are particularly powerful in spreading genes in a gene pool because it has a double effect of increasing the offspring of one individual at the direct expense of all other individual not selected for mating. In contrast, increased reproductive success as measured by litter size does not reduce the absolute success of rival individuals.

When a female selects a male based on an arbitrary trait that has no effect on fitness from a natural selection perspective, the male and the female both benefit because Mate-Selection forms a strong self-reinforcing trait pair. For example, the male and the female is passing the selected trait on to both their male and female offspring and the male and female are passing on to their male and female offspring the trait in the females that selects for the mate selected trait in the males.

**Inter-Species Arms Races Favor Trans-Generational Fitness**

Animal species that are subject to inter-species arms races need to evolve rapidly to meet the challenges of the arms race for continual adaption. By combining its alleles with others in the gene pool, individuals increase their chances that positive mutations
in alleles from other individuals will rescue their alleles from elimination caused by predation for example. The more deeply blended an individuals alleles are in the gene pool the lower the probability that their alleles will be eliminated and the higher the probability that their alleles will be paired with the most highly adaptive alleles in the population.

**How Trans-Generational Fitness Prevails Over The Fitness Of The Individual**

One of the most significant conceptual obstacles to proposing mechanisms of senescence founded on the concept of Trans-Generational Fitness lies in explaining how natural selection can favor the long term Trans-Generational fitness of progeny of it's offspring over the fitness of the individual alone.

In general it is accepted that the short term interests of the individual will outweigh long term trans-generational interests of the individual and this is well supported. However, natural selection can favor the evolution of traits that influence the mate-selection process to favor the selection of mates that exhibit traits that increase Trans-Generational Fitness over traits that promote individual fitness. This strategy can be favored whenever the traits being selected are in the interest of the individual doing the selecting.

This process can and does occur even when the trans-generational traits being selected for are not in the interest of the prospective mate. As long as the trans-generational trait being selected-for in the mate-selection process is neutral or is in the interest of the selecting mate this process will continue. This is true even when the trait being favored by a prospective mate dis-favors the fitness of the individual being selected as a mate. Another element that favors this mate-selection strategy is that it is often is in the interest of the individual to pass a phenotype on to its offspring that exhibits behaviours that favor Trans-Generational Fitness as well.

Note: For further discussion of the role of Trans-Generational Fitness in group selection and altruism see Appendix F. "The Evolution Of Altruism".

**Examples of Trans-Generational Traits**

The mating habits of the Australian red back spider is an extreme example of a traits of both the male and female that favors the Trans-Generational Fitness of offspring. Once mating has been successfully initiated the male spider flips itself over into the jaws of the female and is eaten. This behavior, since it does not favor the individual fitness of the male must be selected for through **mate-selection processes of the female Redback Spider**, an interesting question remains however as to how the female knows before the sacrificial act that the male is likely to exhibit the trait. Perhaps other male mating behaviors are linked to this trait and operate as a "tell" of this behavior to the female. Again, this behavior does not server the short term interests at the level of the individual male, which could theoretically go on to mate again with another female, but it does server the short term interests of the female. The behaviours of both the
male and female that result in the consumption and death of the male favors the Trans-Generational Fitness of their shared male and female offspring. As a result both the male and the female are benefited by passing on these paired traits to all of their offspring.

Because sexual reproduction often involves mate-selection, individuals of most species will possess a mix of traits that balance the interests of the individual against the trans-generational interests of its mates. The resulting set of traits frequently prevents the implementation of the individuals short term interest to the exclusion of the interests of future generations of its offspring.

This mechanism helps to explain the infrequency of sexual dimorphism for senescence. It should generally be in the interest of senescent females to select males with correspondingly similar life spans so as to mitigate tendencies on the part of males toward cannibalism or inferior traits for nurturing offspring. Finite life spans that match or are somewhat shorter than the females lifespan more fully invests the males in the Trans-Generational Fitness of offspring.

**Resource Conservation Increases Trans-Generational Fitness**

The previous sections described how the redundant architecture of the Eukariotic genome provides significant selective pressure that favors Trans-Generational Fitness, but how is this accomplished, what does it mean to favor the fitness of future generations of offspring? Do general purpose universal mechanisms that favor the fitness of multiple generations of offspring exist across species? The sister paper, titled "Mate-Selection Scale And Aging" (MSSA), proposes that mechanisms that increase Trans-Generational Fitness are implemented through processes that conserve resources by partitioning off resources preventing there consumption by adults. MSSA proposes that this occurs as an optimized process that extracts a real cost to the vitality of the individual through senescence.

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**The Evolution of Algorithmic Selection**

The diploid redundant nature of the eukaryotic genetic architecture and self interest of the individual as expressed through the practice a type of algorithmic selection known as mate-selection is the mechanism that underlies traits that favor altruistic Trans-Generational Fitness.

**Kin Selection**

Diploidy strongly favors "Kin Selection" when a population is static or falling in size, in these circumstances a given individual will likely be producing two or fewer reproductive offspring, as a result such individuals will have only a fifty percent chance of passing on the full complement of its alleles. In these circumstances the individual must rely on kin to propagate to the next generation those alleles that it shares and has failed to pass on
to subsequent generations.

**Group Selection - Species Selection**

The redundant architecture of the genome is strong enough to drive higher order group selection and sufficient to favor species fitness as long as these traits do not disfavor trans-generational traits, but how does this work?

Though the redundant diploid genome drives natural selection to favor Trans-Generational Fitness at the expense of the fitness of the individual, in most circumstances the effects of diploidy is not a sufficiently strong effect to drive natural selection to favor Trans-Generational Fitness over individual fitness, directly. It has been observed for a long time that Mate-Selection is capable of producing traits in the opposite sex that are, by nearly any definitions, not in the interest of the individual possessing them, this demonstrates the power of sexual or mate-selection. When Mate-Selection goes beyond selection for selections sake and involves traits that are directly in the short or long term interest of the selecting individual this effects can be amplified.

The redundant diploid genome is more than sufficient to drive selection to favor traits in individuals that favor traits in their mates that favor the Trans-Generational Fitness of offspring as this has no fundamental cost to the individual doing the selecting.

**From Trans-Generational Fitness to Ecosystem Fitness**

Based on the same logic already provided, It is in the interest of the individual to not just favor traits in their mates that increase Trans-Generational Fitness but it is also in their interest that their mates possesses traits that increase species fitness (deep altruistic traits) as long as these traits do not reduce Trans-Generational Fitness.

For Example: As described earlier, populations are contracting nearly 50 percent of the time. Therefore it is very likely that an individuals offspring in the future will fail to produce any offspring, in these cases the best that can be achieved by the individual is that kin will harbor many of its genes and that some of these kin will succeed in reproducing. If the individuals offspring help kin succeed in reproducing it will be in the interest of the individual to also select a mate on this criteria as well.

The conclusion to be drawn is that because mate-selection exacts so little cost on the selecting individual, mate-selection is capable of negating the fitness priorities of the selected individual in favor of a focus on second, third and forth order fitness priorities that have the breath of extending to encompass complete ecosystems and the depth to reach multiple generations into the future. The only chasm this mechanism cannot span is the ability to violate the fitness hierarchy that is defined by genetic distance, the fitness of first generation offspring is prioritized above the fitness of the second generation offspring, which is above species fitness which is subsequently above
ecosystem fitness. Stated another way, natural selection will select against individuals that select for traits in their mates that favor species fitness over, Trans-Generational Fitness, etc. It is abundantly clear that mate-selection can select for traits in mates that are not in direct interest of the individual being selected, however this capability essentially stops at this point since the next generation constitutes the offspring of both the selected and the selecting mate. From this point forward natural selection and mate-selection will both follow a hierarchy defined by genetic distance from both parents.

Notes: Synopsis of Evolutionary Mechanisms

The Logic of Selection for Trans-Generational Fitness

- The redundant architecture of the eukaryotic genome makes possible a continuum of possible relative contributions each allele can make to the implementation of a phenotype.
- Natural selection does not act on the alleles directly, genes must be expressed in the phenotype for natural selection to act.
- The requirement for gene expression drives alleles of the same locus to compete for expression in the phenotype.
- Competition between alleles results in winners and losers, over expression in the phenotype of the current generation. Losing alleles can be expressed marginally or not at all.
- Losers in allelic competition in one generation can win the competition for expression in future generations.
- Traits in adults that can improve the future fitness of its offspring raising the probability that the offspring will reproduce and pass its alleles to subsequent generations of offspring allowing its alleles to compete again for expression improving the long term reproductive success of the individual.
- Traits that favor the fitness of future generations typically involve conservation of resources in the present preserving them for use by offspring in the future.
- Traits the conserve resources preserving them for use by future generations often exact a cost to the individual.
- Natural Selection is a negative selection process a filtering process that acts on the individual in real time, natural selection is not efficient at directly selecting for altruistic traits, such as future oriented trans-generational traits that reduce short term fitness of the individual.
- Algorithmic Selection known as mate-selection enables the individual to select for traits in mates that favor the Trans-Generational Fitness of the individual offspring without incurring a short term cost to its own fitness, this cost to fitness is shifted to its mates.
- There is essentially no limit to the types of selection that can be applied to organisms. Natural selection represents a collection of death mechanisms that operate as the cause of death on multiple generations that is applied before the end of the species reproductive period.
Algorithmic Selection is a fundamentally different kind of selection, it has a positive "selective" element that "selects for" a given trait or set of traits, it is not just a culling mechanism. Positive selection can increase the speed at which evolution of a species can take place.

Algorithmic Selection is selection by genetic programs, these programs behaviors can be as simple as chemical signaling or as complex as cultural preference.

Algorithmic selection can be arbitrarily complex.

Algorithmic Selection in complex animals includes selection by mind, it is self directed evolution.

In sexually dyomorphic species female choice will select for male ornamentation but will also select for males with traits that will be valuable to future male and female offspring.

In species where only females choose, the females ability to drive sexual dimorphism is limited to ornamentation since their selection algorithms must also select for female phenotypes as well. Radically different male forms would defeat the ability of the female to detect and select for adaptive female phenotypes.

Algorithmic selection enables the individual to select for traits in mates that favor the Trans-Generational Fitness of the individual offspring without incurring a short term cost to its own fitness, this cost to fitness is shifted to its mates.

Individuals utilize algorithmic selection as expressed as mate-selection to select mates that conserve resource making them available for use by future generations of offspring.

The resource conservation mechanisms selected for through algorithmic selection sacrifice body repair in their mates to produce the conservation of resources.

Redundant genomes mask alleles from expression over multiple generations of offspring requiring

Differential rates of allelic expression favors mate-selection.

Practical limits of the carrying capacity of ecosystems limits the average individual to producing 2 or fewer reproductive offspring.

Leaving only two offspring that will go on to be reproductive makes it very improbable that all of an individuals genome will be expressed vigorously enough to define the phenotype.

- Genes must be strongly expressed and often be expressed in combination with alleles from other loci so that they can be optimally exposed to selection forces and increase the probability that they will increase there frequency in the gene pool.
- The practical constraints on reproduction of the average individual makes them rely on the reproduction of multiple successive generations of offspring and kin to increase the likelihood that all of its genes will be exposed to selective pressure.
- The need to rely on the reproductive success of multiple successive generations of offspring and kin drives the individual to favor the reproductive success of successive generations of offspring and kin at their own reproductive expense and at the reproductive expense of their mates.
○ Favoring the reproductive success of successive generations of offspring and kin at the expense of the individual is accomplished through conserving resources for future generations precluding there use for tissue and intracellular repair by adults.
○ Resource conservation traits are traits that favor the fitness of multiple generations of offspring and kin traits that favor Trans-Generational Fitness.

A Synopsis of Logic of Trans-Generational Fitness

- Redundancy in the genomic architecture, known as diploidy, drives natural selection to favor a mechanism that is capable of favoring the fitness of present and future progeny, "Trans-Generational Fitness" and dis-favoring the individual, that mechanism is mate-selection.
- Individuals utilize mate-selection to select mates that conserve resources making them available for use by future generations of offspring.
- The resource conservation mechanisms selected-for through mate-selection sacrifice body repair in their mates to produce the preservation of resources.
- Practical limits on the number of reproductive offspring produced by the average individual drives mate-selection to favor traits in mates that favor the Trans-Generational Fitness of offspring often at the expense of the individual.
- Trans-Generational Fitness is implemented primarily through mechanisms that conserve resources precluding there use by mechanisms the perform tissue and intracellular repair.