The Everest hypothesis: sexual reproduction as a conserver of replicative fidelity and an adaptation to unstable environments

Running title: The Everest hypothesis

Patrick Douglas Shaw Stewart, Newbury, UK[1]. patrick.ss.home@gmail.com

Abstract

This review examines three critical questions in evolutionary biology: (1) why do virtually all multicellular and many unicellular organisms reproduce sexually? (2) Why have some animals evolved extravagant ornaments and complex mating rituals that appear detrimental? (3) How does natural selection maintain high-fidelity genetic replication? I present a simple "Everest hypothesis" to answer these questions. First, I note that the genes that specify the proteins that replicate DNA are subject to mutation, so replicative fidelity must vary between individuals. Moreover, many organisms choose their mates by responding to various complex biochemical mechanisms, physical displays, and behaviors, generated by many gene products acting together. I propose that natural selection consistently adds unnecessary complexity to the mechanisms that transfer genetic material between individuals, and since most mutations are either harmful or neutral, mutator mutations are likely to disrupt these mechanisms. Sex may, therefore, provide a filter to reduce the dissemination of mutator mutations. Sex may also have allowed ancient organisms to colonize unstable environments where strong selective pressures would apply. This can explain many puzzling biological phenomena. For example, the migration and spawning of Atlantic salmon and the complex displays of birds of paradise may be best understood as "tests" to show that potential mates possess genes for high-fidelity genetic replication. Animals that have developed ornaments that appear harmful, such as peacocks, and animals that undertake remarkable migrations, such as monarch butterflies, may provide conspicuous examples of such tests. I also make suggestions for experiments to test the hypothesis.

Introduction

Imagine a woman who announces she will have sex with any man she meets on the summit of Mount Everest. In case she finds more than one man there, she devises a tie-breaker: the potential partners must solve a challenging Sudoku puzzle they receive on the way up, and (so that she can choose quickly) they must write – *display* – their solutions in large numerals on a banner they bring along. This would be a reasonable mating strategy for both sexes: both mother and father would likely have better-than-average genes. In this review, I suggest that many plants and animals adopt similar strategies, setting up practical "obstacle courses" for potential mates. They may also demand complicated physical displays, all of which can only be generated by the interaction of many genes. For example, Atlantic salmon follow a strategy similar to climbing Mount Everest when they migrate from saltwater to freshwater and then swim up rivers to reach their spawning grounds. Peahens prefer to mate with peacocks with large and symmetrical displays comprising the cocks' considerably elongated upper tail feathers. The hypothesis presented here, however, also tackles two more fundamental problems in evolutionary biology: why sex is so ubiquitous and how replicative fidelity is maintained. (This review will not focus on how high-fidelity replication might have originally evolved. Briefly, it seems likely that special conditions might be required for fidelity to increase. Very stable conditions might be necessary, possibly combined with serial colonization of

successive sites. As discussed below, previous studies of the evolution of mutation rates seem not to have carefully considered the short-term response of fidelity to fluctuating environments.) Mutations must occasionally arise in all genes, including those that specify the proteins that replicate the genetic material – the nucleic acid polymerases and their associated proteins. Some of these mutations must increase the error rate without actually being fatal. Lineages that replicate with reduced fidelity must, therefore, exist in all biological kingdoms, although we do not know how common they are. (Harris [2015] showed that human mutation rates vary, with specific transitions being more common in African, European, and Asian populations.)

Moreover, we have to consider small changes in fidelity. For example, the human mutation rate has been estimated to be around 2.5×10^{-8} mutations per nucleotide site per generation [Nachman and Crowell, 2000]. Could a human (or another animal) identify and reject as a potential mate an individual with a mutation rate of, say, 10^{-7}? If not, we might expect fidelity to fall slowly.

There is another important issue: Sung et al. pointed out that as natural selection pushes a trait toward perfection, further improvements are expected to have diminished fitness advantages [Sung et al., 2012]. At the other extreme, as Siobain Duffy pointed out, if a biological entity is "suddenly thrust into an environment that it's not well adapted to . . . there is a larger fraction of potentially beneficial mutations available and having a nonzero mutation rate would be preferable to all descendants always staying exactly the same" [Duffy, 2018]. An observational study supports this conclusion: Lanfear et al. analyzed 32 phylogenetically independent pairs of bird families and showed that rates of molecular evolution were positively correlated with net diversification [Lanfear et al., 2010]. Rapid environmental change or the colonization of new environments may give rise to speciation. These are events that Duffy expects to result in a higher proportion of mutations being beneficial, so Lanfear's observation is compatible with her analysis. The trend is shown schematically in figure 1.

Since a greater proportion of mutations are beneficial during periods of rapid change and strong selection, slightly lower-fidelity replisomes may be preferable and may be selected. (Replisomes are the complex molecular machines that replicate DNA. They comprise many proteins, including DNA polymerases, exonucleases, ligases, helicases, gyrases etc. In this analysis, we are mainly concerned with the replisomes that are active in the germlines of organisms rather than those active in somatic cells.) At later times, however, reduced fidelity becomes a problem: firstly, once the population becomes well-adapted to its new environment, a greater proportion of the mutations that arise will be undesirable, and a high mutation rate will become a disadvantage; and, secondly, mutator mutations may arise in the replisome genes themselves, which could set up a feedback loop of increasing mutation. Fortunately, some individuals in a large population are likely to retain high fidelity, so appropriate mate selection can, in principle, restore fidelity, but some means of identifying high-fidelity individuals is necessary. Fidelity is thus valuable and may increase or decrease, but a sound long-term strategy for all life forms is to find ways to conserve it. The hypothesis presented here is based on the premise that the greater the number of (preferably highly-optimized) genes that are involved in both mate selection and the physical or biochemical mechanisms of mating – including genes that usually do something else – the lower the chance that low-quality replisome genes in females or males will be chosen or transferred during mating. Figure 2 illustrates the hypothesis schematically. Figure 2A shows how evolution may add extra genes to the genomes of sexual species and repurpose other genes to advertise high replicative fidelity. Figure 2B illustrates that individuals with error-prone replisomes are likely to have more mutations in the genes that advertise fidelity and are thus less likely to mate. Therefore, the suggested role of

many otherwise puzzling animal and plant features is to make mutations visible and help conserve fidelity.
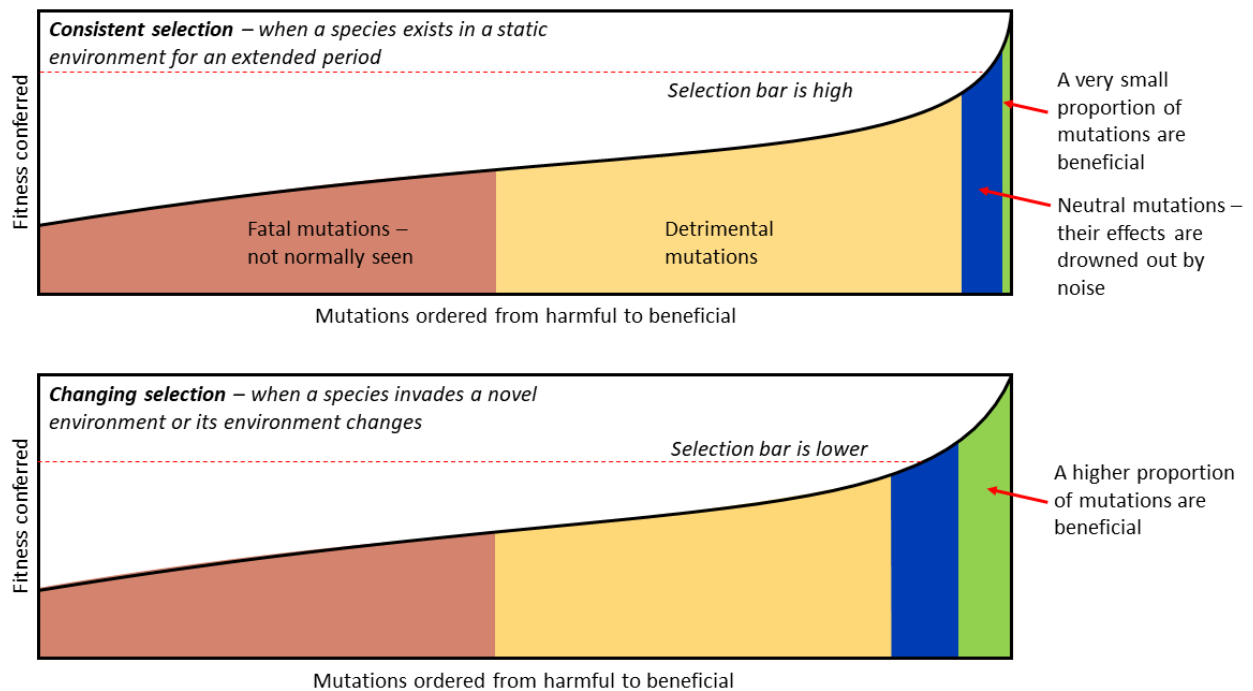

Figure 1. A schematic representation of the mutations that might arise in two hypothetical populations in differing environments. Mutations are arranged from the most harmful to the most beneficial. Some mutations (brown) are likely to be fatal and are not ordinarily visible. Others are detrimental (beige) and must be removed by "purifying" selection. Some mutations (blue) may be mildly harmful or beneficial, but their effects are so minor that they are effectively neutral and are likely to be conserved or lost randomly. Finally, a proportion of mutations are beneficial (green) and tend to be conserved by natural selection. Only a small proportion of mutations benefit species that experience consistent selection over extended periods in stable environments (top). This is because many advantageous mutations have already been selected, and there are few opportunities for further improvements. Clams that live in a stable marine mud bank might be an example. However, if a species' environment changes rapidly, or it invades a new ecological niche, it will be subject to strong new selective pressures. As a result, a higher proportion of mutations are expected to be advantageous. This is because the species is less well-adapted to its new environment, and there are more opportunities for improvement. Birds and mammals when they first colonize islands are examples.
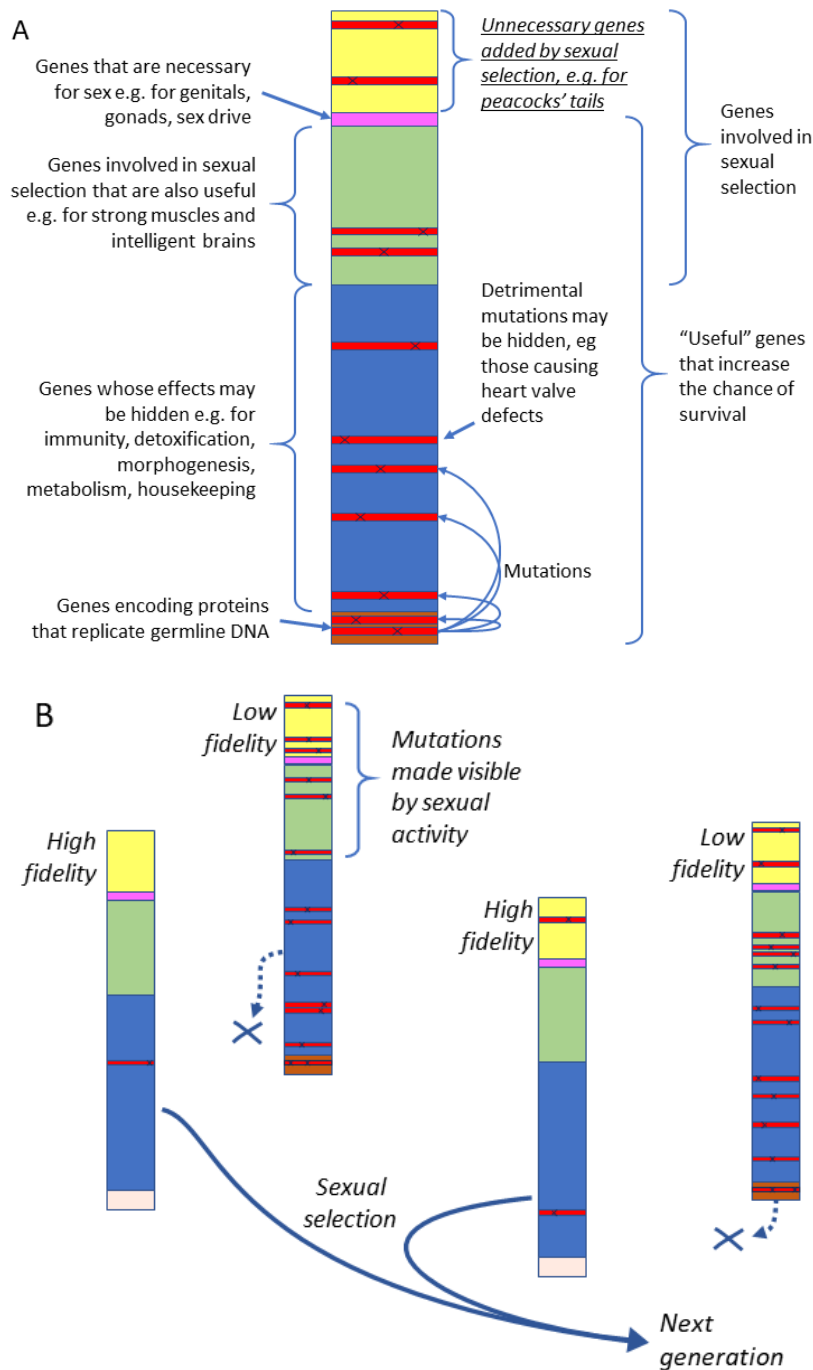
Figure 2. A schematic illustration of the Everest hypothesis. In panel A, the column represents an individual's genome with genes sorted by category. Evolution sometimes adds extra genes that encode features that are mainly involved in sexual selection (yellow). Genes that are useful in other ways also frequently play roles in sexual selection (green). Suppose that one or more mutations that increase the error rate occur in the replisome genes (brown). More mutations (crosses on red bars) are likely to arise throughout the genome, including the genes involved in sexual selection (yellow and green). Panel B illustrates sexual selection according to the Everest hypothesis. Each colored column represents an individual. Sexual activity can make mutations in the yellow and green categories visible. Individuals capable of high-fidelity replication tend to have fewer mutations in these areas and are, therefore, more likely to be selected as mates and to reproduce.

Other important mutations

Note that the mate-selection strategies proposed by the hypothesis can expose a range of genetic defects that would otherwise be hidden. For example, even when replisomes are of good quality, complex behaviors, displays, and biochemical mechanisms might expose rare mutations in "housekeeping" genes that are active in all cell types. Such housekeeping genes include ribosomal and cell-cycle proteins, histones, mitochondrial proteins, and factors for transcription, RNA splicing, translation, protein processing etc. The genes encoding replisomes that are active in somatic cells are also important – although germline replisomes are, in principle, more critical for the long-term survival of a population.

Replicative fidelity, fitness, "good condition"

Note that replicative fidelity is not the same thing as fitness. Indeed, one may increase while the other decreases. As an example, consider a typical cycle of change and adaptation when a population's environment suddenly changes or it invades a new territory (such as an island). Its fitness declines, *instantly,* because it is no longer well-adapted to its environment. Its mutation rate, however, is unchanged at first. As it adapts to its changed environment, the population's fitness is subsequently expected to increase over several generations. I would, however, expect its mutation rate to increase in parallel. There are two ways to look at this: (1) since a smaller proportion of mutations are harmful (that is, more are either neutral or beneficial) any linked low-fidelity replisome genes are less strongly selected *against*; (2) certain beneficial mutations are likely to sweep through a population, and such mutations are more likely to arise in low-fidelity individuals. Moreover, they are at first genetically linked to the replisome genes that gave rise to them. Therefore, reduced-fidelity replisome genes may be temporarily advantageous and may be selected. At later times, sexual selection and recombination may allow well-adapted lineages with high fidelity to evolve.

Note also that fitness and related concepts such as "good condition" are terms that are difficult to define or measure. By contrast, the replicative fidelity of an organism or population (measured as the error rate of genetic replication) has a precise meaning that can be measured, in principle accurately, by scientists.

Multifactorial mate selection

The peacock's tail (figure 3) can make increased mutation visible because many genes are required to make it, and defects in any of these genes are likely to disrupt its appearance. However, there are complications. Takahashi *et al.* studied feral peafowl in Japan. They found that peahens did not prefer peacocks with symmetrical tails or tails with more ocelli or greater length [Takahashi et al., 2008]. However, the authors noted that tails showed a small variance among males across populations. One interpretation is, therefore, that peahens do favor males with well-formed tails, but the population that the authors studied already had a low mutation rate (possibly because tail-selection provides a very effective filter), leaving females to focus on other attributes. Therefore, a reasonably well-formed tail may act as a peacock "entrance exam", but peahens do not seek perfection in tails. (Much of the remaining variation in tails may, in any case, be the result of random life events that are unimportant.) A better human analogy may therefore be a woman who looks for a partner on the summit of a mountain such as Kilimanjaro, which many men can climb. Getting to the summit might be her entrance exam – after that, she uses other criteria to make her final choice.

Figure 3. The extraordinary symmetry of a peacock's tail, with the positions and lengths of feathers carefully controlled to produce regular spacing of the "eyes". In 1975, Amotz Zahavi proposed the "handicap principle" to explain the evolution of features such as these [Zahavi. 1975]. The principle suggests that by squandering scarce resources by growing and maintaining such ornaments, peacocks and other animals show potential mates that they are of "good quality" and are selected. However, the handicap would be almost identical without the elaborate markings and exact symmetry, suggesting that these features have some other benefit. The Everest hypothesis notes that a well-formed tail shows that the peacock has an intact set of genes for making tails, suggesting a low mutation rate. Similarly, a female that recognizes a well-formed tail has an intact set of genes for tail-recognition.

Natural phenomena that the Everest hypothesis can explain

The hypothesis can explain many puzzling features and behaviors among complex organisms. For example, many species complete long migrations each year or, in some cases, once in a lifetime (figure 4). You might expect natural selection to favor lineages that avoid the risk and energy expenditure of such long journeys. Migratory populations persist, however, in many species. Arctic terns complete the longest migrations known in the animal kingdom, with birds nesting in Iceland and Greenland completing annual round-trip migrations of over 70,000 km. The species is thriving, with an estimated two million individuals. They are also unusually long-lived birds, some reaching 30 years of age, possibly because migration is an effective filter of low fidelity. In many migratory species, "breakaway" populations that either do not migrate or migrate less far exist, but they do not generally outcompete the populations completing longer migrations. Atlantic salmon often migrate from freshwater to the ocean and then return. Both sexes undertake dangerous journeys, including adapting to changing salinity, leaping up waterfalls, avoiding predators, and swimming in shallow water, usually returning to mate in the streams where they hatched. "Landlocked" lineages that spend their entire lives in freshwater exist, but populations that migrate from the ocean to freshwater to breed are more numerous [Hutchings et al., 2019]. Some invertebrates are migratory. Some populations of monarch butterflies do not migrate, but many North American populations east of the Rocky Mountains complete a dangerous multi-generational migration between overwintering sites (the largest being in Michoacán in Mexico, where around 150 million monarchs overwinter) and their northern breeding grounds, mainly near the Great Lakes. It seems that selective or genetic advantages compensate for the dangers of migration. Note that this cycle requires four generations

to complete, so many genetically encoded behaviors and physiological changes required for the complete migratory cycle cannot be conserved by selection en route.

Figure 4. Three species that are well-known for their spectacular migrations. From left to right: arctic tern, Atlantic salmon, and monarch butterfly. The Everest hypothesis suggests that such migrations tend to limit reproduction to high-fidelity lineages because error-prone lineages may fail to survive or navigate to their breeding grounds.

Other animal features and behaviors that require the interaction of many gene products could provide similar benefits. Birdsong is an example of a behavior that can only be produced by individuals with many functional genes specifying the proteins and peptides that generate the physical structures of the syrinx, appropriate instinctive behavior, and the ability to learn by imitation. Any deviation from the norm in a particular individual is broadcast to its neighbors. Humans are attracted to partners with athleticism and pretty faces (which are close to, but not identical to, average faces [Perrett et al., 1994]), as well as intelligence and a sense of humor, both of which are products of an extraordinarily complex organ – the human brain. Invertebrates may adopt similar strategies for mate selection. For example, fireflies receive and transmit flashed encoded messages to attract mates, while medflies and some spiders perform complex dances. Male fiddler crabs wave their enlarged claws in a species-specific pattern to attract females. Females decide whether to approach males based on male traits, including the wave rate and claw size, but characteristics of the male's burrow, including depth and temperature, then determine whether mating occurs in a multifactorial selection process [Backwell and Passmore, 1996]. Corrals may provide another example since they synchronize their spawning by monitoring water temperature, light, and the moon's cycles (or tides). Some flowering plants may have evolved novel pollination mechanisms not because they are particularly effective at transferring pollen but because many functional gene products are required for successful pollination, and such mechanisms can effectively screen out low-fidelity lineages. For example, some orchids mimic the sex pheromones and the appearance of female wasps and bees to attract males, which pollinate their flowers (see below). In many species, including many plants and fungi, complex biochemical mechanisms are in operation that could prevent the dissemination of low-fidelity replisome genes. For example, the fertilization of flowering plants involves multilayered signaling pathways, involving many gene products expressed in both pollen and the female tissues (figure 5). The Everest hypothesis suggests that much of this complexity is unnecessary but that such biochemical "lock-and-key" mechanisms can reduce the chance that low-fidelity lineages will successfully reproduce.
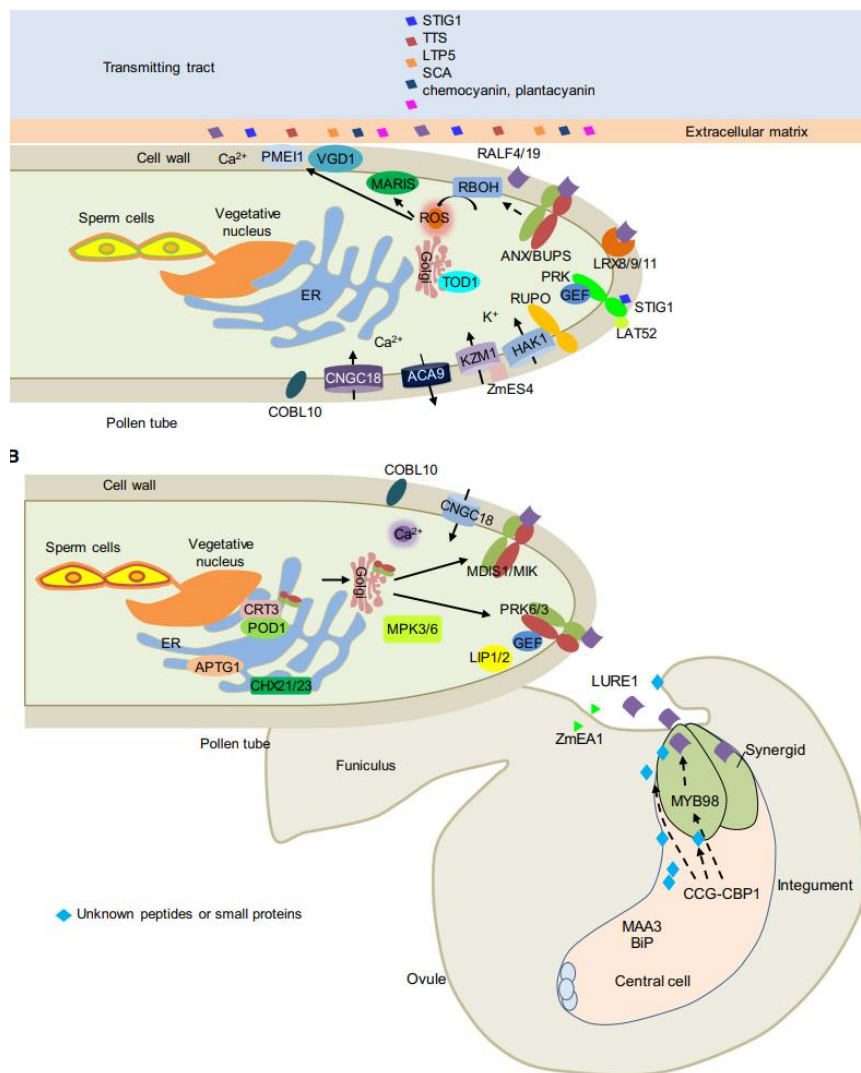
Figure 5. Fertilization in flowering plants. Pollen tube elongation in the maternal tissue and navigation to the ovule require intimate successive cell–cell interactions between the tube and female tissues [Li et al., 2018]. This procedure can create complex tests for pollen grains (which should be thought of as haploid organisms that are capable of providing sperm) using multilayered biochemical signaling pathways that involve many gene products, which can weed out the more error-prone lineages.

Symmetry

Biological development is complex, involving regional specification, cell differentiation, morphogenesis, and tissue growth. Moreover, inducing factors, hormones, chemokines, cytokines, survival factors, and their receptors, are subject to mutation, and mutant proteins that are less active may give intermediate levels of metabolites, resulting in incomplete switching with less consistent outcomes and decreased symmetry. Moreover, defective immune systems in animals may increase infections, disrupting symmetry. Monitoring bilateral or radial symmetry may be an effective way to detect increased mutation (figure 6. A-E).
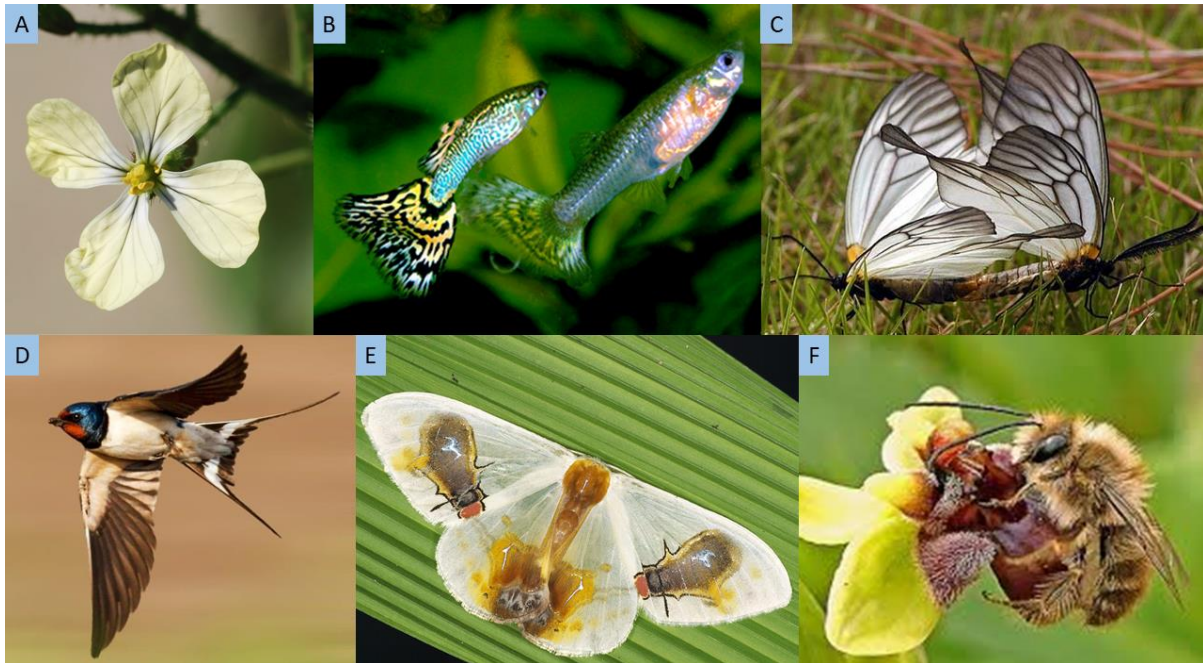
Figure 6. Several examples of sexual selection based on symmetry, and one based on mimicry. A: Some pollinators prefer to visit symmetrical flowers, including the flowers of arugula, Eruca vesicari *[Møller and Eriksson, 1995]. B: Female guppies often prefer symmetrical males with larger orange-colored ornaments [Stephenson et al., 2020]. C: Females of the white-tailed zygaenid moth* Elcysma westwoodii *prefer males with longer and more symmetrical hind wings and antennae [Koshio, 2007]. D: In the barn swallow, female preference for long and symmetric male tails has been inferred from both observational and experimental studies [Bańbura, 2005]. E: The moth* Macrocilix maia *has patterns on its wings that closely resemble two flies approaching a bird dropping. Merilaita and Lind showed that birds such as great tits could identify symmetric artificial prey significantly faster than asymmetric [Merilaita and Lind, 2005]. Nevertheless,* M. maia *has retained almost perfect bilateral symmetry, suggesting that symmetry may be strongly sexually selected in that species. F: Sexual selection based on mimicry: bee orchids mimic the sex pheromones and appearance of female bees to attract males, which pollinate the flowers. The Everest hypothesis suggests that, whether or not this is the most efficient way to ensure pollination, it acts as an effective filter of low-fidelity orchid lineages.*

The evolution of sexual reproduction

It is interesting to consider the nature of life before sexual reproduction evolved. Ancient asexual lineages must have existed as quasispecies, similar to modern asexual biological entities such as viruses. Such entities exist as diverging phylogenetic trees that form "clouds" of rapidly-mutating related genotypes. (Presumably, simple mechanisms that allowed recombination between lineages soon evolved, like those of viruses, because recombination gives the huge benefit of allowing advantageous mutations on different tree branches to be brought together in a single lineage [Muller, 1932].) As noted above, when a biological entity's environment is stable, it will slowly become well-adapted to that environment, such that a decreasing proportion of genetic changes are advantageous. After extended selection in a stable environment, therefore, a greater proportion of mutations will be harmful and high-fidelity replication becomes more advantageous. Natural selection is then more likely to remove the mutator mutations that arise because the mutations are linked to the mutations that they generate [Kimura, 1967]. Since life exists today (and since asexual

self-replicating entities such as viruses also exist), we can deduce that such systems can be stable and were so in the remote past. Early life might have persisted in a limited number of stable environments, but lineages that spread to more changeable environments would be predicted to lose fidelity (because selection for high fidelity would be reduced), become unstable, and have limited longevity. By introducing sexual reproduction with complex structural or biochemical lock-and-key mechanisms together with mate selection, ancient life forms may have gained the ability to colonize unstable environments. Moreover, error-prone lineages that acquired beneficial mutations could more frequently recombine sexually with high-fidelity lineages to create new, well-adapted but stable lineages. Sexual reproduction can, therefore, plausibly be seen as an adaptation to unstable environments. A similar argument can explain why sex is so popular among complex modern-day organisms. Many are subject to transient strong selection, meaning that populations sometimes need to recover replicative fidelity when it is lost in otherwise well-adapted lineages.

Fisher's runaway selection and Zahavi's handicap principle

Scientists have developed other hypotheses to explain the exaggerated features produced by sexual selection in some animals. In the early 20th century, Ronald Fisher suggested that any slight preference in females for a male character, such as slightly longer tails in birds, might create a positive feedback cycle [Fisher, 1930]. The preferred trait and the female preference for it would increase together, he suggested. In this model, females would continue to prefer males with long tails even if they were so long that the individuals possessing them were not the best survivors. In 1975, Amotz Zahavi made an alternative proposal. He suggested that animal traits that confer handicaps may evolve by sexual selection because they "test the quality" of the individuals that possess them [Zahavi, 1975]. These two hypotheses, and the Everest hypothesis, are distinct from each other. The Everest hypothesis and Zahavi's handicap principle both suggest that sought-after characters can advertise the quality of genes whose effects would otherwise be hidden. Fisher's "runaway" sexual selection, on the other hand, says the selected characters are attractive in themselves simply because they are "fashionable" in a particular population. Unlike previous hypotheses, the Everest hypothesis emphasizes complexity and proposes that these sought-after characters are typically the product of many genes (to show up mutations effectively). Moreover, they can be either beneficial (such as strong muscles and intelligent brains) or harmful (such as the massive tail of a peacock). By contrast, Zahavi suggests that the sought-after characters must "lower the fitness of the selected sex in relation to the main ecological problems of the species" and must squander scarce resources [Zahavi, 1975]. In this context, "fitness" is changeable and ill-defined, whereas a mutation rate has an exact meaning and can be measured by scientists. According to both runaway selection and the handicap principle, species and populations with more significant handicaps (such as peafowl and migratory species such as arctic terns and Atlantic salmon) are expected to be at a selective disadvantage compared to comparable groups with more modest handicaps. However, the Everest hypothesis says that such species and populations may be at a long-term selective advantage compared to comparable groups, and they may thrive if the handicaps successfully reduce the dissemination of error-prone replisome genes.

Other theories of the evolution of sexual reproduction

Muller pointed out in 1932 that sex can simultaneously combine two or more advantageous mutations in one individual through recombination, speeding up evolutionary progress [Muller, 1932]. Later, Kimura proposed that mutator alleles are indirectly selected against through linkage with the detrimental alleles that they generate elsewhere in the genome [Kimura, 1967]. Lynch et al. presented the hypothesis that natural selection primarily operates to improve replicative fidelity,

pushing mutation rates down to a lower limit set by the power of random genetic drift. They noted that the closer a trait comes to perfection, the smaller the fitness advantages of beneficial mutations become [Lynch et al., 2016]. Roberts and Petrie used simulation and analytical modeling to show that female choice for males with beneficial mutations may have a much more significant impact on "genetic quality" than the choice for males with low mutational load. They suggested that selection for beneficial mutations might be a more powerful explanation for the prevalence of sexual reproduction than the alternative [Roberts and Petrie, 2022]. However, these studies did not consider in detail how selection for fidelity might fluctuate in changing environments or how evolution might create sexual activities and processes specifically to conserve fidelity.

Suggestions for experimental and observational testing of the Everest hypothesis

Various scientific investigations could test the Everest hypothesis. Studies could be performed with any convenient sexual organisms such as protists, plants, insects (including Drosophila, flour beetles and seed beetles), fish, birds, and mammals (possibly in captivity, for example, in zoos.) Sequencing of replisome or polymerase genes may be necessary to interpret the results clearly. The suggestion for experiments shown in Figure 7 seeks to investigate the effect on fidelity of strong selection (series S1), while also determining the power of recombination with a wild strain to restore fidelity (series S2 and S3).
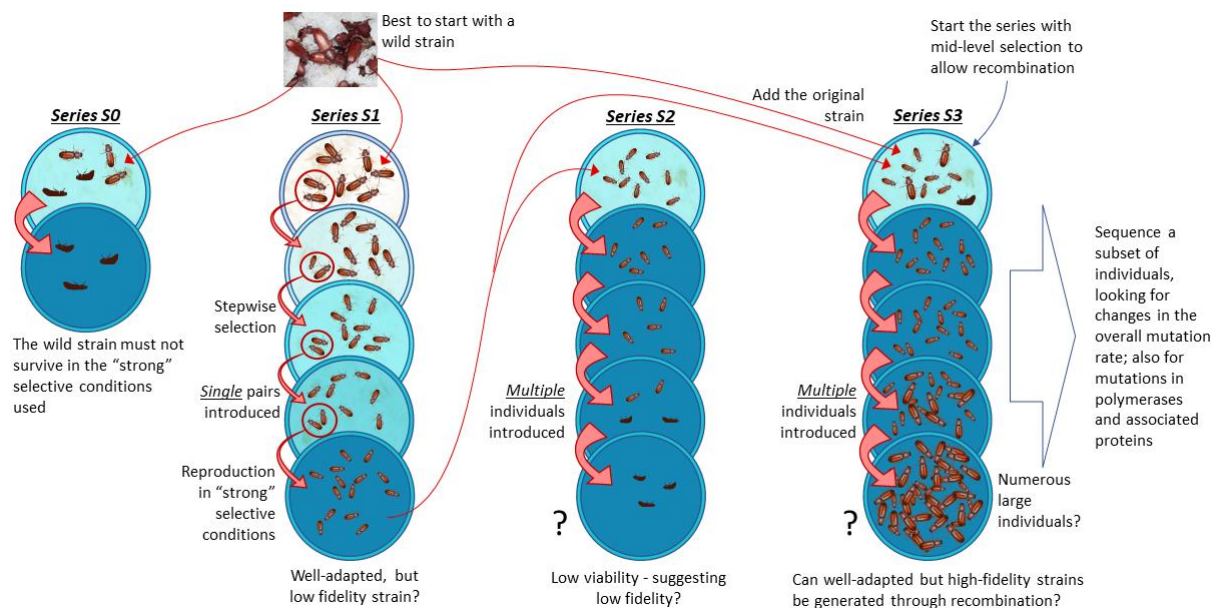

Figure 7: An experiment to investigate the maintenance of replicative fidelity in sexual species. Beetles are shown, but any suitable sexual animal, plant, fungus, or protist could be used. Selection might involve disadvantageous physical or chemical environments or the modification of behavior (for example, by eliminating insects that are attracted to UV light). Darker blue circles indicate more severe selection. A wild strain could provide a high-fidelity lineage to use in the experiment. Selective conditions should be chosen such that the starting strain can replicate slowly in mid-level conditions but not in conditions with the highest selection (dark blue) as shown in series S0. In series S1, wild-type individuals are exposed to selective conditions that increase in severity stepwise. Only one male and one female (chosen randomly) should be transferred at

each step in S1 to prevent recombination. Sequencing of individuals from S1 can identify mutations in polymerases and related proteins, and measure the mutation rate at intermediate positions. The hypothesis predicts that individuals that replicate in the most severe selective conditions of S1 (at the end) will be well-adapted but have high mutation rates. This high mutation rate can be confirmed by running S2, where it is predicted that mutations will accumulate until the lineage dies out. S2 can be compared to S3, where a few wild-type individuals are introduced to give the opportunity for mating with well-adapted individuals. The hypothesis suggests this can result in a well-adapted lineage with a low mutation rate (S3). Again, sequencing can allow the clear interpretation of results.

A second suggestion is observational. Since the hypothesis suggests that long migrations reduce the prevalence of mutator mutations, it predicts that migratory lineages will tend to infiltrate non-migratory populations more rapidly than the reverse. This prediction could be investigated in migratory and related non-migratory populations by constructing phylogenetic trees based on DNA sequences. Careful selection of populations would be required to allow a clear interpretation of data: for example, Pierce et al. found evidence in monarch butterflies of serial founder effects across the Pacific, suggesting stepwise dispersal from a North American origin [Pierce et al., 2022]. North American populations are mostly migratory, but they are also the largest, and large populations are, of course, more likely to spread than small ones. For clear interpretation, comparisons of infiltration rates by migratory populations that are roughly equal to or smaller than neighboring populations would be necessary.

Another approach investigates the suggestion that since the mutation rates of species that complete long migrations may be lower, such species may also be more long-lived. To examine whether a significant trend exists, the life spans of migratory species or populations could be compared to those of their closely-related non-migratory relatives.

A final approach would measure the mutation rates of migratory species or populations and compare them to those of their non-migratory relatives.

Conclusions

Zahavi pointed out that more than one hypothesis can explain the evolution of sought-after characters [Zahavi, 1975]. Likewise, I am not claiming that the handicap principle (or any other theory of evolution) is wrong. In the example given above in the introduction, if a man carried a bunch of flowers to the summit of a mountain to impress a woman, he would be applying the handicap principle (because he would be deliberately wasting scarce resources). It might work. Similarly, a trait that initially evolved as a test of fidelity might become "fashionable" in particular populations and so become exaggerated to a maladaptive degree; such selection could be considered "runaway".   I suggest, however, that the Everest hypothesis provides a more universal and straightforward explanation of most of the surprising features and behaviors that other sexual selection hypotheses struggle to explain while shedding light on the ubiquity of sexual reproduction and the preservation of replicative fidelity.

References

Andersson, Malte, and Leigh W. Simmons. "Sexual selection and mate choice." *Trends in ecology & evolution* 21.6 (2006): 296-302. https://doi.org/10.1016/j.tree.2006.03.015

Backwell, Patricia RY, and Neville I. Passmore. "Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, Uca annulipes." Behavioral Ecology and Sociobiology 38 (1996): 407-416. https://doi.org/10.1007/s002650050258

Bańbura, Jerzy. "Sexual selection in the Swallow Hirundo rustica-A review." (2005). http://hdl.handle.net/11089/12107

Baur J, Berger D. Experimental evidence for effects of sexual selection on condition-dependent mutation rates. *Nature Ecology & Evolution*. 2020 May;4(5):737-44. https://doi.org/10.1038/s41559-020-1140-7

Duffy, Siobain. "Why are RNA virus mutation rates so damn high?" *PLoS biology* 16.8 (2018): e3000003. https://doi.org/10.1371/journal.pbio.3000003

Fisher RA. The genetical theory of natural selection: a complete variorum edition. Oxford University Press; 1999 Oct 21. https://www.google.de/books/edition/The_Genetical_Theory_of_Natural_Selectio/sT4lIDk5no4C?hl=en&gbpv=0

Harris, Kelley. "Evidence for recent, population-specific evolution of the human mutation rate." *Proceedings of the National Academy of Sciences* 112.11 (2015): 3439-3444. https://doi.org/10.1073/pnas.1418652112

Hutchings, J.A., Ardren, W.R., Barlaup, B.T., Bergman, E., Clarke, K.D., Greenberg, L.A., Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L.E. and Fraser, D.J., 2019. Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(10), pp.1697-1708. https://doi.org/10.1139/cjfas-2018-0413

Kimura, Motoo. "On the evolutionary adjustment of spontaneous mutation rates." Genetics Research 9.1 (1967): 23-34. https://doi.org/10.1017/S0016672300010284

Koshio C, Muraji M, Tatsuta H, Kudo SI. Sexual selection in a moth: effect of symmetry on male mating success in the wild. Behavioral Ecology. 2007 May 1;18(3):571-8. https://doi.org/10.1093/beheco/arm017

Li, Hong-Ju, Jiang-Guo Meng, and Wei-Cai Yang. "Multilayered signaling pathways for pollen tube growth and guidance." *Plant reproduction* 31 (2018): 31-41. https://doi.org/10.1007/s00497-018-0324-7

Lynch M, Ackerman MS, Gout JF, Long H, Sung W, Thomas WK, Foster PL. "Genetic drift, selection and the evolution of the mutation rate." *Nature Reviews Genetics.* 2016 Nov;17(11):704-14. https://doi.org/10.1038/nrg.2016.104

Merilaita S, Lind J. Great tits (Parus major) searching for artificial prey: implications for cryptic coloration and symmetry. Behavioral Ecology. 2006 Jan 1;17(1):84-7. https://doi.org/10.1093/beheco/arj007

Møller AP, Eriksson M. Pollinator preference for symmetrical flowers and sexual selection in plants. Oikos. 1995 May 1:15-22. https://doi.org/10.2307/3545720

Muller, Hermann Joseph. "Some genetic aspects of sex." *The American Naturalist* 66.703 (1932): 118-138. https://doi.org/10.1086/280418

Nachman, Michael W., and Susan L. Crowell. "Estimate of the mutation rate per nucleotide in humans." *Genetics* 156.1 (2000): 297-304. https://doi.org/10.1093/genetics/156.1.297

Pierce AA, Zalucki MP, Bangura M, Udawatta M, Kronforst MR, Altizer S, Haeger JF, de Roode JC. "Serial founder effects and genetic differentiation during worldwide range expansion of monarch butterflies." *Proceedings of the Royal Society B: Biological Sciences.* 2014 Dec 22;281(1797):20142230. https://doi.org/10.1098/rspb.2014.2230

Perrett, David I., Karen A. May, and Sin Yoshikawa. "Facial shape and judgements of female attractiveness." *Nature* 368.6468 (1994): 239-242. https://doi.org/10.1038/368239a0

Roberts G, Petrie M. "Sexual selection for males with beneficial mutations." *Scientific Reports*. 2022 Jul 23;12(1):12613. https://doi.org/10.1038/s41598-022-16002-y

Stephenson JF, Stevens M, Troscianko J, Jokela J. The size, symmetry, and color saturation of a male guppy's ornaments forecast his resistance to parasites. The American Naturalist. 2020 Nov 1;196(5):597-608. https://doi.org/10.1086/711033

Sung W, Ackerman MS, Miller SF, Doak TG, Lynch M. Drift-barrier hypothesis and mutation-rate evolution. *Proceedings of the National Academy of Sciences*. 2012 Nov 6;109(45):18488-92. https://doi.org/10.1073/pnas.1216223109

Swillen I, De Block M, Stoks R. Morphological and physiological sexual selection targets in a territorial damselfly. Ecological Entomology. 2009 Dec;34(6):677-83. https://doi.org/10.1111/j.1365-2311.2009.01114.x

Takahashi M, Arita H, Hiraiwa-Hasegawa M, Hasegawa T. Peahens do not prefer peacocks with more elaborate trains. Animal Behaviour. 2008 Apr 1;75(4):1209-19. https://doi.org/10.1016/j.anbehav.2007.10.004

Zahavi A. Mate selection—a selection for a handicap. *Journal of Theoretical Biology.* 1975 Sep 1;53(1):205-14. https://doi.org/10.1016/0022-5193(75)90111-3