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

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Abstract

This review focuses on three critical questions in evolutionary biology: (1) why do virtually all multicellular and many unicellular organisms reproduce sexually? (2) Why have some animals, such as peacocks and birds of paradise, evolved extravagant ornaments and complex mating rituals that appear detrimental? (3) How does natural selection maintain high-fidelity genetic replication? I present a simple "Kilimanjaro hypothesis" that attempts to answer all three questions. First, I note that the proteins that replicate DNA are themselves specified by genes that must, of course, be subject to mutation. This means that replicative fidelity must vary between individuals. Moreover, many organisms choose their mates by responding to various biochemical mechanisms, physical displays, and complex behaviors, often generated by the interaction of many gene products acting together. I propose that natural selection consistently adds unnecessary complexity to the mechanisms that transfer genetic material between individuals. Since most mutations are either harmful or neutral, mutator mutations are likely to disrupt these mechanisms - which must reduce the chance that individuals with error-prone replisomes will mate successfully. Therefore, sex, with its many diverse and intricate variations, may have evolved partly to provide an effective filter to reduce the dissemination of mutator mutations. Sex may, in particular, have allowed ancient organisms to colonize unstable environments where intense selective pressures would apply. Many puzzling biological phenomena among sexual organisms can be explained along these lines. The migration and spawning of Atlantic salmon and the complex displays of birds of paradise may, for example, be best understood as "tests" to establish that potential sexual partners 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 arctic terns and 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 publicly that she will have sex with any man, but only on the summit of Mount Everest. Moreover, the potential partners must solve a challenging Sudoku puzzle they discover 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. If practical, 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. I am unaware of any detailed scientific discussion of the circumstances in which increased fidelity is most likely to evolve.) 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 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}? This is a critical question.

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]. Similarly, 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 may support this conclusion: Lanfear et al. analyzed 32 phylogenetically independent pairs of bird families and found that rates of molecular evolution were positively correlated with net diversification [Lanfear et al., 2010]. Speciation may result from rapid environmental change or the colonization of new environments. These are events that Duffy expects to result in a higher proportion of mutations being beneficial, so Lanfear's result is compatible with her analysis.

The trend is shown schematically in figure 1. 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, 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 may be essential. Fidelity is thus valuable and may increase or decrease, but a sound long-term strategy for all life forms is to develop methods of conserving it. The hypothesis presented here is based on the premise that the more genes are involved in 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. The suggested role of many otherwise puzzling animal and plant features is, therefore, to make mutations visible, and so to help to conserve fidelity.

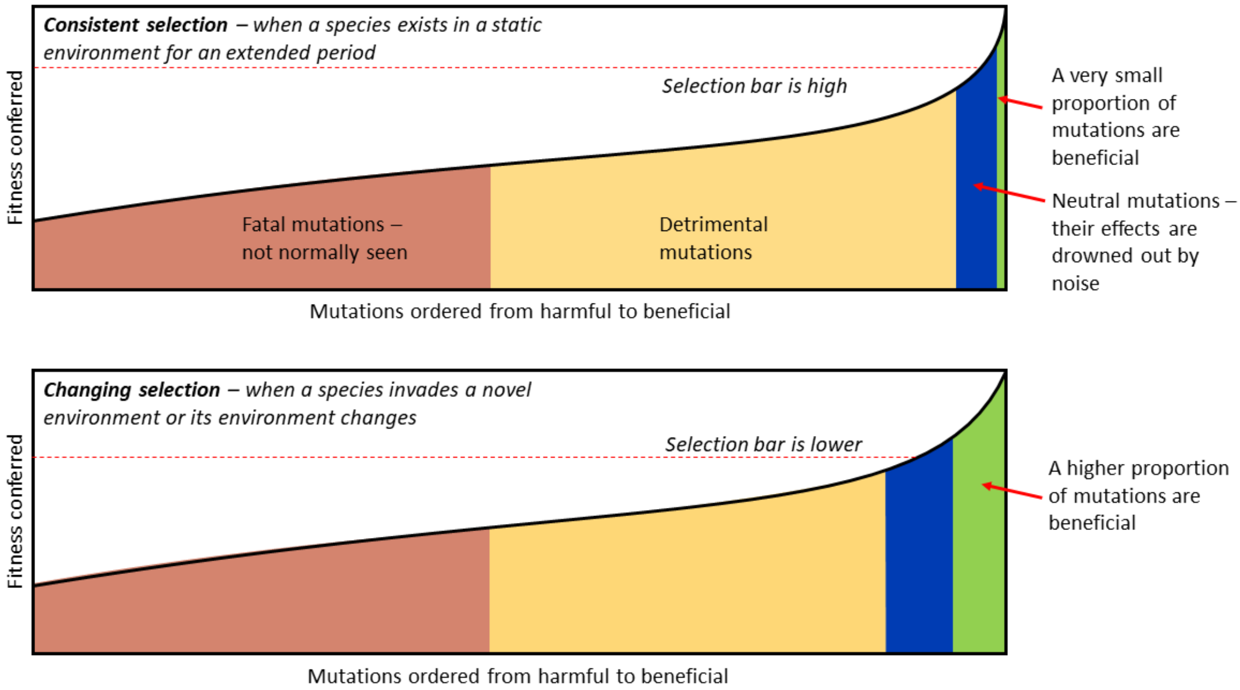

Figure 1. A schematic representation of the mutations might arise in two hypothetical populations in differing environments. Mutations are arranged from the most harmful to the most beneficial. Some mutations (brown) are likely to be fatal, and are not ordinarily visible. Others are detrimental (beige) 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 are beneficial in 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. If, however, a species' environment changes rapidly or if it invades a new ecological niche, it will be subject to strong new selective pressures. A higher proportion of mutations are now expected to be advantageous. This is because the species is less well-adapted to its new environment, and there are more opportunities for improvement. An example might be a bird or mammal when it first colonizes an island.

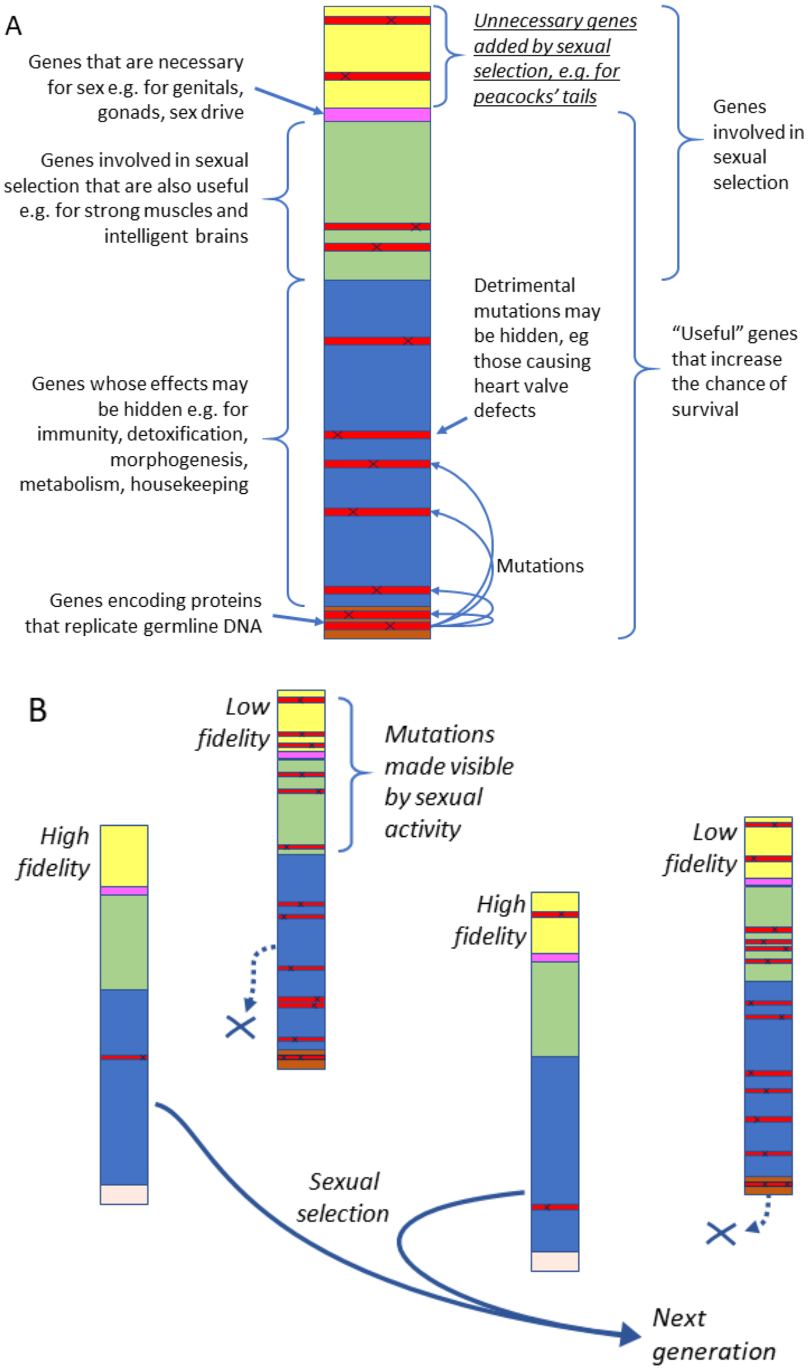

Figure 2. A schematic illustration of the Kilimanjaro hypothesis. In panel A, the column represents an individual's genome with genes sorted by category. Evolution sometimes adds extra genes that encode features that are mainly involved in sexual selection (yellow). Genes that are useful in other ways 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 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 Kilimanjaro hypothesis. Each colored column represents an individual. Sexual activity makes 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.

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. Takahashi *et al.* studied feral peafowl in Japan. They found that peahens did not prefer peacocks with more 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 high fidelity, 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. Recognizing that many species use multifactorial approaches to mate selection, I have named my conjecture the "Kilimanjaro hypothesis".

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 Kilimanjaro 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 Kilimanjaro 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 can 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. 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 at the intermediate stages.

Figure 4. Three species that are well-known for their spectacular migrations. From left to right: arctic tern, Atlantic salmon, and monarch butterfly. The Kilimanjaro 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 Kilimanjaro 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.

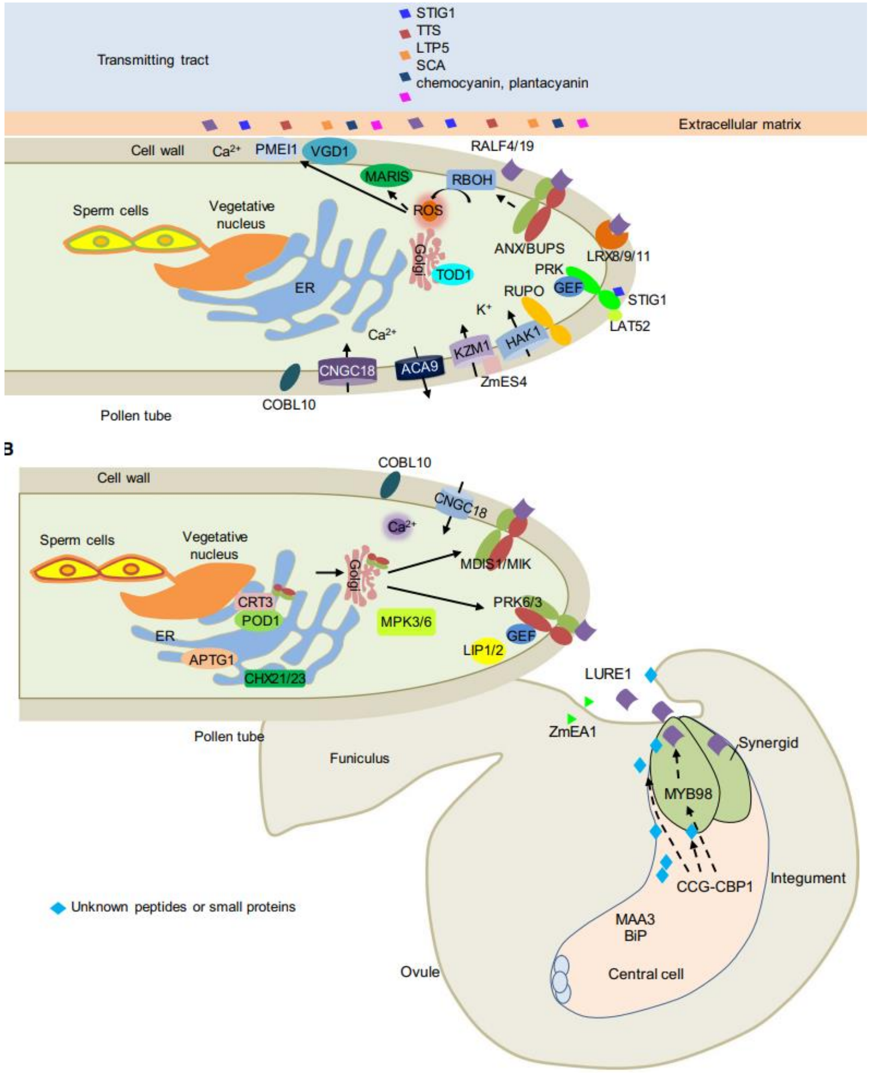

Figure 5. Fertilization in flowering plants. Pollen tube elongation in the maternal tissue and navigation to the ovule require intimate successive cell–cell interactions between the tube and female tissues [Li et al., 2018]. This procedure can create complex tests for pollen grains (which should be thought of as haploid organisms that are capable of producing sperm) using

> *multilayered biochemical signaling pathways that involve many gene products, which can weed out the more error-prone lineages.*

As noted above, the details of sexual selection may vary when selective pressures vary (figure 1). For example, Takahashi et al. studied feral peafowl in Japan (see above), where they were presumably not well-adapted [Takahashi et al., 2008]. They may therefore have been subject to strong selection for several generations, meaning that a higher proportion of mutations than usual would be beneficial (as discussed above). Peahens that put less emphasis than Indian peahens on well-formed tails might, therefore, have been selected in Japan.

Symmetry

Monitoring bilateral or other symmetry may be an effective way to detect increased mutation (figure 6). 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.

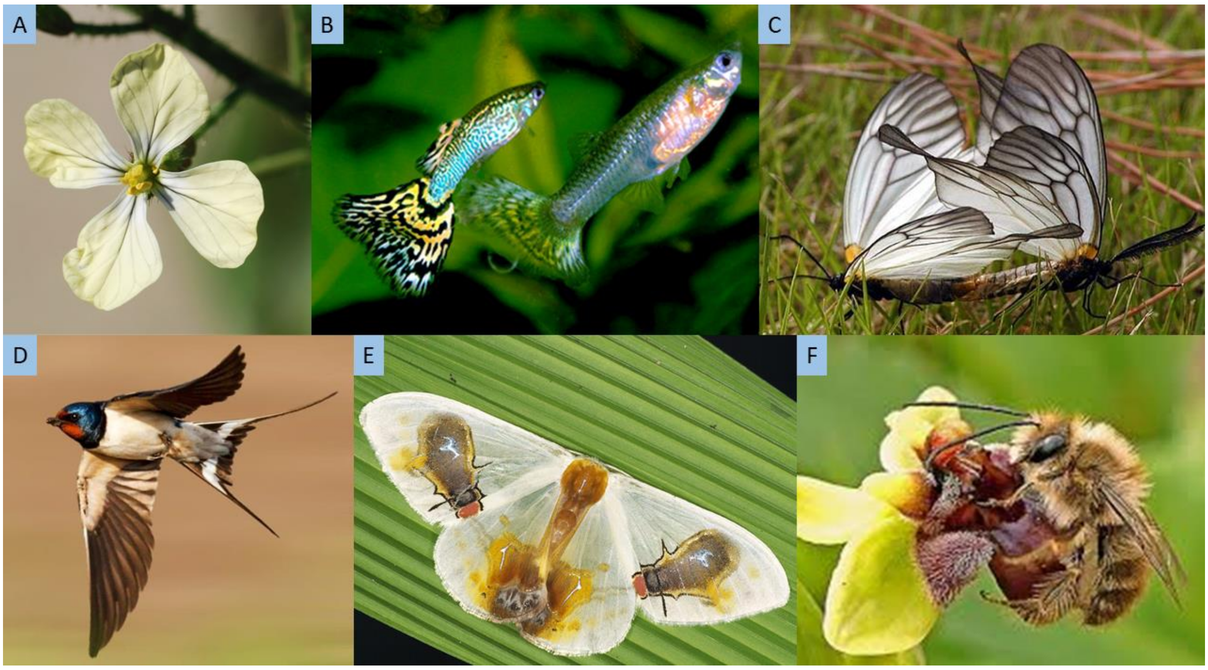

Figure 6. Several examples of sexual selection that are based on symmetry, and one based on mimicry. A: Some pollinators prefer to visit symmetrical flowers, including the flowers of arugula, Eruca vesicari *[Møller and Eriksson, 1995]. B: Female guppies often prefer symmetrical males with larger orange-colored 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. D: In the swallow* Hirundo rustica *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*

can 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 Kilimanjaro 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 how life must have functioned 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 allows beneficial mutations on different tree branches to be brought together in a single lineage.) As noted above, when a biological entity’s environment is stable, it will eventually become well-adapted to that environment, such that very few genetic changes can provide an advantage. After extended selection in a stable environment, therefore, almost all mutations are harmful and high-fidelity replication becomes particularly advantageous. Natural selection can then remove the mutator mutations that arise, presumably because they are linked to the mutations 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, 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, and populations may 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 Kilimanjaro hypothesis, are all distinct. The Kilimanjaro 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 that particular population. The Kilimanjaro hypothesis emphasizes complexity and proposes that these sought-after characters are typically the product of many genes (to show up mutations effectively), but 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]. 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 Kilimanjaro 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 mutations

Note that the mate-selection strategies proposed by the hypothesis can expose a wide range of genetic defects that would otherwise be hidden. For example, even when replisomes are of good quality, complex behaviors, displays, and biochemical mechanisms can expose hidden 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, and protein processing. The genes encoding replisomes that are active in somatic cells are also important – although they are, in principle, less critical for the long-term survival of a population than those active in the germline.

Other studies of evolution

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 greater 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 Kilimanjaro hypothesis

Various scientific approaches could test the Kilimanjaro hypothesis. Studies could be performed with any convenient sexual organisms such as yeasts, protists, insects (including Drosophila and flour beetles), flowering plants, fish, birds, and mammals (possibly in captivity, for example, in zoos.) Replisome gene sequencing is probably necessary to allow the results to be interpreted unambiguously. I suggest an experimental approach along the following lines:

(1) sequence polymerase genes in wild organisms from large, stable populations, which can be assumed to replicate with high fidelity.

(2) Take samples from inbred individuals and sequence their polymerase genes or profile their DNA. Identify inbred lineages with mutations in polymerase genes, which are expected to show increased mutation rates in most cases.

(3) Set up colonies, starting each with a single pair. Found several colonies with low-fidelity individuals and several with high-fidelity individuals. Polymerase and other genes can be sequenced (or DNA profiled) to confirm the identities of high and low-fidelity colonies.

(4) Now introduce high-fidelity individuals into low-fidelity colonies, and low-fidelity individuals into high-fidelity colonies; use sequencing to compare the rates at which the two classes of polymerase genes invade their new colonies.

The Kilimanjaro hypothesis predicts that high-fidelity genes will replicate and spread faster than low-fidelity ones. (For small organisms that are easy to breed, step 2 could be omitted, and low and high-fidelity colonies could be identified once colonies are established.)

A second experimental approach would compare the health, well-being, genetic fidelity, number of individuals, etc., over several generations in two isolated populations. In one population, individuals would be free to choose their mates, while in the comparison population, mating would be limited to preselected pairs selected at random by the experimenter. I expect the first population to outperform the second over time. Again, sequencing and DNA profiling could confirm the involvement of mutations affecting fidelity.

A third approach would test whether applying intense selective pressures encourages the emergence of low-fidelity lineages. [Studies along these lines may have been carried out already – I will investigate when I have time.] For example, colonies could be sustained on unsuitable foods or exposed to toxic compounds. Novel behaviors could be selected, for example, removing insects that are attracted to UV lamps from breeding populations. Evolutionary theory suggests low-fidelity lineages will be more prevalent after strong selection and rapid adaptation. It would be helpful to prevent or limit recombination here because, as discussed, mate selection might conserve fidelity. For example, mating could be limited to preselected pairs.

A fourth 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 rather 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. 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 Kilimanjaro hypothesis provides a more universal and straightforward explanation of most of the surprising features and behaviors that other hypotheses of sexual selection seek to explain, while also shedding light on the ubiquity of sexual reproduction and the preservation of replicative fidelity.

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