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Parthenogenesis: Birth of a New Lineage or Reproductive Accident?

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Parthenogenesis — the ability to produce offspring from unfertilized eggs — is widespread among invertebrates and now increasingly found in normally sexual vertebrates. Are these cases reproductive errors or could they be a first step in the emergence of new parthenogenetic lineages?

The phenomenon of virgin birth has long fascinated scientists and laymen alike. The first account of parthenogenesis in the literature is the prophecy of Jesus Christ's birth in Isaiah 7:14: "Therefore the Lord himself will give you a sign: The virgin will conceive and give birth to a son, and will call him Immanuel". This reference to parthenogenesis is unusual in two ways: first, it is the only account of 'natural parthenogenesis' in a mammal. Mammals are believed to be completely unable to reproduce via parthenogenesis because of a number of developmental and genetic constraints [1]. Second, while the "Blessed Virgin Mary" might have been able to conceive a daughter via parthenogenesis, the conception of a son is highly unlikely. As male sex in humans is determined by genes on the Y chromosome, Mary, as a woman, could not have transmitted any Y chromosomes to her offspring. In contrast to humans, parthenogenetic production of sons is expected in species with other types of sex determination. For example, in birds, some reptiles and

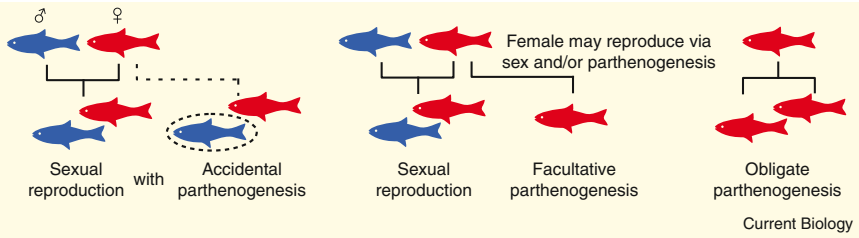

Figure 1. The efficiency of parthenogenesis varies widely.
Accidental parthenogenesis refers to the very rare hatching of unfertilized eggs in sexual populations, often due to reproductive errors, that can generate male offspring in species with female heterogamety. Given the very low hatching success, accidental parthenogenesis is often not adaptive. Under facultative parthenogenesis a female may reproduce via sex and/or parthenogenesis; hence this reproductive mode combines the advantages of sex and parthenogenesis. Under obligate parthenogenesis, females cannot reproduce sexually at all, even if mated to males of sexual lineages. Populations consisting solely of obligate parthenogens are characterized by the virtual absence of males. However, many species feature mixed reproduction, with some females reproducing sexually and others via obligate parthenogenesis. These species are characterized by sex ratios ranging from 50:50 to strongly female-biased.

butterflies, females are the heterogametic sex: they carry two differentiated sex chromosomes (Z and W) while males are homogametic (ZZ). This sex determination system can result in the virgin birth of sons if parthenogenesis is automictic [2], whereby oocytes undergo a normal meiosis that results in four haploid products (one egg cell and three polar bodies). Under sexual reproduction, the polar bodies would degenerate and the egg cell would fuse with a sperm to generate a diploid zygote. Under automictic parthenogenesis, diploidy is restored via the fusion of the egg cell and one of the polar bodies [2]. As in self-fertilization or mating with relatives, automictic parthenogenesis can cause an increase in homozygosity, including homozygosity at the sex chromosome. Hence ZW females can parthenogenetically produce ZZ sons and ZW daughters (WW individuals are generally not viable). Thus, automictic parthenogenesis is the mechanism underlying the occasional production of sons and daughters well known for many species of bagworm moths [3] and recently described in some reptile species, including Komodo dragons [4] and snakes [5].

While male-producing parthenogenesis is rare, female-producing parthenogenesis is widespread among animals and mostly obligate (Figure 1), with many documented cases in species-rich invertebrate groups such as insects, nematodes and crustaceans, and with only few examples in vertebrates [2]. A recent paper by Fields *et al.* [6] in *Current Biology* documents a new case of female-producing parthenogenesis in a critically endangered ray species, the sawfish *Pristis pectinata*. *Pristis* species — like all sawfish — are characterized by their elongated flat nose lined with teeth. *P. pectinata* occurs in coastal areas of the western Atlantic sea, mostly in bay areas around Florida. A microsatellite-based genetic screen of 190 individuals in a wild population revealed seven females that were most likely produced via parthenogenesis. Parthenogenetic ancestry was deduced because the seven females were homozygous at all or almost all screened loci [6]. Mating between relatives can also result in homozygosity, but individuals in the screened population were not related to each other. Furthermore, mating between close relatives is unlikely given the ecology of the species, leaving parthenogenesis as the most likely explanation [6].

Are these parthenogenetically produced sawfish females rare ‘accidents’, or could they be indicative of a unique case of adaptive, facultative parthenogenesis in a vertebrate? Facultative parthenogenesis, where an individual female can produce offspring either sexually or parthenogenetically (Figure 1), is exceedingly rare among animals. A much more widespread phenomenon is accidental parthenogenesis — also called spontaneous parthenogenesis, or tychoparthenogenesis [7]: the hatching of a very small proportion of unfertilized eggs in a normal, sexual species. For example, in different species of *Drosophila*, observed rates of accidental parthenogenesis in natural populations range from one egg in 100,000 to one in a million successfully developing into an adult [8]. These hatching rates are orders of magnitude lower than for facultative parthenogenesis, where the majority of unfertilized eggs hatch. However, without systematic screens for hatching success of eggs laid by virgin females, accidental and facultative parthenogenesis can be difficult to distinguish. Widely popularized examples of rare parthenogenesis in vertebrates are typically interpreted as facultative parthenogenesis [9], including reports of parthenogenesis in sharks [10,11], snakes [5] and Komodo dragons [4], producing offspring while kept solitarily in captivity. Given the current evidence, these examples are, however, most likely cases of accidental rather than facultative parthenogenesis, mimicking the high incidence of accidental parthenogenesis among invertebrates.

Distinguishing whether the sawfish females are a case of facultative, accidental, or obligate parthenogenesis would require additional studies, ideally involving breeding experiments. Although such experiments might be difficult to conduct with *P. pectinata* because of its ecological requirements, they could generate interesting insights into the evolution of parthenogenesis. For example, because of its great inefficiency, accidental parthenogenesis [7,8] is generally not adaptive (Figure 1). An exception might be situations where sexual females fail to find a mate. Stalker [12] predicted that in marginal populations or other situations where mates are limited even inefficient accidental parthenogenesis could be adaptive and thus selectively favored. This prediction is supported by evidence from natural populations of *Drosophila* vinegar flies and stick insects. In these species, accidental parthenogenesis rates are especially high in low-density populations where large fractions of adult females remain unmated [13,14]. Thus, via the accumulation of gradual changes, accidental parthenogenesis might be a stepping-stone to ‘true’ parthenogenesis and give rise to new facultative or obligate parthenogenetic lineages.

So, could accidental parthenogenesis in humans ever give rise to a new parthenogenetic lineage? Probably not, as the developmental and genetic constraints in humans and other mammals would most likely prevent the emergence of adaptive parthenogenesis in natural populations [1]. As it turns out, even the most famous speculation about parthenogenesis, Jesus Christ's birth, owes its existence not to a miracle but to a human error during the translation of Isaiah 7:14 from Hebrew to Greek: The Hebrew word *almah* can refer to a young woman of marriageable age, whether married or not [15]. The 'young woman' became a 'virgin' in the gospel according to Matthew, where *almah* was translated as the Greek *parthenos*.

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Binocular Vision: Joining Up the Eyes

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To provide a unitary view of the external world, signals from the two eyes must be combined: a new study pinpoints the location in the human brain where the requisite combination occurs.

A fundamental feature of human vision is that, despite having two eyes, we normally see only one representation of the world around us. This phenomenon, imaginatively termed cyclopean perception by the late Bela Julesz [1], requires a seamless combination of two completely separate neural signals and imposes on the brain a substantial computational burden that a cyclops would be spared. There are, however, a number of benefits to having two eyes that collectively outweigh the computational cost. Perhaps the most obvious, although not necessarily the evolutionary driver, is insurance against loss of an eye. Another is that it permits a wider field of view (only modestly wider in humans but much wider in horses, sheep and many other mammals). The most studied benefit is that having two eyes permits stereoscopic vision: the construction of accurate estimates of the distances of nearby objects based on subtle differences between the two retinal images. These benefits depend on the replacement of two representations of the world by a single, cyclopean representation. Where in the brain does this happen? It might be expected that a harmonious coalition of left and right would be constructed at the very first processing stage at which both signals are present in proximity: the thalamus; however, it has long been known that this is not the case and that the answer is "somewhere in the visual cortex". In this issue of *Current Biology*, Barendregt *et al.* [2] present evidence from functional magnetic resonance imaging (fMRI) that the transformation occurs between the primary visual cortex, known as V1, and the second visual area, V2.

Whether a given neuron is responsive to light stimulation in either eye or is driven only by one eye has been addressed in many neurophysiological studies, starting with the pioneering work of Nobel Prize winners Hubel and Wiesel, who found that the primary visual cortex of macaques contains a mixed bag of cells, some