Evolutionary Advance by Progeny Investment and Socialization

While the two branches of prokaryotic life, bacteria and archaea, emerged four billion years ago, the more organizationally sophisticated single cell eukaryotic organisms emerged two billion years later. In contrast to the prokaryotes, from their first emergence, eukaryotic species have possessed distinct male and female organisms. Each of these organisms possessed a genome consisting of a single version of each chromosome (haploid) contained within a structurally defined nucleus. These cells also possessed molecular tails (flagella) that they could use to propel themselves through ocean waters. A large proportion of modern day single cell eukaryotes preserve these basic characteristics. For the great majority of cell division events, replication of these unicellular eukaryotes occurs by clonal division into two genetically identical progeny cells in a manner that is qualitatively similar to that for the prokaryotes. However, typically in response to metabolic stress, the unicellular eukaryote occasionally undergoes a genetically encoded transformation into its male or female reproductive physiological state (Honigberg & Purnapatre, 2003). Characteristic pheromone molecules are released into the surrounding water to serve as a signal for fellow species members of the opposite sex, while specific receptor proteins are synthesized and introduced onto the cell surface to recognize the corresponding pheromone molecules produced by the opposite sex. By this process of mutual attraction, pairs of cells actively locate each other to form direct binding interactions between cell receptors that serve to verify both the species similarity and the opposite sexuality.

Upon forming an appropriate match, the cell membranes fuse and then the internal nuclear membranes fuse to form a nucleus which will then contains two parental copies of each chromosome (diploid). This combined cell undergoes the process of meiosis in which all of the chromosomes are replicated and then two rounds of cell division give rise to four progeny cells, each possessing a haploid set of chromosomes with those four resulting sets of chromosomes generally differing from the genomes of either parent. While four progeny cells could have been more straightforwardly obtained by both of the parental cells having undergone a round of asexual clonal division, these two sets of progeny cells are fundamentally different from each other. If, averaged over time, the more circuitous process of sexual reproduction had not provided an evolutionary advantage, that process would have never evolved. Given the strong correlation with the sexual reproduction cycle being induced by adverse conditions, the obvious implication is that the genetic scrambling which occurs within the sexual reproduction cycle increases the probability that a subset of the resultant progeny will have an enhanced ability to survive those adverse conditions. For those who wish to believe that the moment of life should be defined as occurring upon the fusion of the male and female sex cells, the unambiguous implication is that sexual reproduction evolved as the result of the mutual suicide of the two parental organisms as both they and their potential direct lineages unavoidably cease to exist.

From the earliest eukaryotes, there has been a sharp physiological divide between the structural and behavioral transformations that occur for the purpose of establishing procreative interactions with the opposite sex and the genetic transformations of meiosis that enable the rearrangement of the chromosomal material that will be passed along to the progeny. Among the early unicellular eukaryotes, the alignment between these two sets of complementary functions was generally achieved by clustering the corresponding genes close to each other on the same chromosome so that the pairing of the gender and sexual traits would rarely become disrupted between generations.

It would be more than a billion years before a subset of these unicellular eukaryotes began to exhibit readily observable differences between the two sexes. This process of visual differentiation only fully blossomed as multicellular organisms began to evolve which established the physiological distinction between sex cells that directly give rise to the subsequent generation and somatic (non-germ) cells that function to insure the success of that propagation. The much larger egg cell evolved by a combination of processes. The two rounds of reductive cell division during meiosis became asymmetric in the female such that virtually all of the cellular content would be partitioned into one cell (the egg) while the three much smaller cells (polar bodies) would be discarded. In parallel, the somatic cells that surround the egg cell (nurse cells) became specialized in providing additional nutrients to that egg cell to enable its further expansion. As the egg cell became positioned among its nurse cells, the utility of its flagella was eliminated and this structure disappeared. Henceforth, when the enlarged egg cell then combined with the much smaller sperm cell, the resultant zygote cell would be capable of extensive development, most notably extensive subdivision into a formation of numerous cells, before it needed to obtain additional nutrients. The rest of the cells of the organism have evolved to provide additional mechanisms for insuring the success of the sexual zygotes. Among land plants, such physiological mechanisms include the formation of seeds, flowers, and fruits. The evolutionary significance for these aspects of land plant biology is highlighted in the formal Latin name for this branch of life, *Embryophyta*.

The earliest animal species evolved a characteristic complex level of multicellularity that utilized a diploid genome for all somatic cells. The closest known sister lineage of Animalia is the unicellular choanoflagellates which possess a haploid genome. The genomes of these organisms contain a number of genes which had previously been assumed to be exclusive to multicellular animal species, including crucial genes involved in cell-cell signaling as well as numerous genes that had previously been believed to be exclusive to nerve cells. In this regard, it must be noted that the most basic functionality of nerve cells is in the regulated localized transmission of chemical neurotransmitters at the membrane synapses formed between adjacent cells. The familiar elongated axons and dendrites of nerve cells are a later day mechanism for relaying such localized information exchange over discrete long distance pathways.

While these unicellular choanoflagellates can exist as independent individuals, they commonly form organized assemblies. Electron microscopic analysis of these clonal colonies has detected specific cell membrane contacts between adjacent cells as well as formation of intercellular bridges which are not uniformly distributed across the cells of the assembly. Most surprisingly, this study also detected variations in the cell morphology and content ratios of intracellular components among the cells within the assembly, suggestive of structural differentiation among these clonal cells of identical DNA content (Laundon et al., 2019; Naumann & Burkhardt, 2019). In a related species of choanoflagellates, the individual cells associate into cup-shaped colonies in which their flagella are normally all oriented toward the interior of the cup. Upon a decrease in illumination, the geometry of this cup rapidly inverts so that the flagella point outward. In contrast to the 'relaxed' state in which the individual cells are typically actively involved in feeding upon bacteria in the surrounding ocean waters, in the inverted state of the cup geometry, the colony rapidly swims away (Brunet et al., 2019). The net effect is a systematic migration toward better illuminated waters where the density of bacteria is generally higher. While single cell organisms, the choanoflagellates exhibit a wide range of cooperative characteristics based upon intercellular interactions that would become incorporated into the earliest multicellular animals when the cellular assembly formation became integrally tied to the process of sexual reproduction and the associated conversion from a haploid to a diploid genome.

Based upon the number and diversity of different species, insects are by far the most successful branch of animal life. Among the insects, the honey bee illustrates many of the features that have led to such success. Most obvious is the beehive. The queen bee inserts an egg into each cell of the hive, while the worker bees fly off to collect nectar then convert this nectar into a jelly or honey that is fed to the developing larvae. What is truly extraordinary is the exceedingly high fraction of honey bee larvae that survive into adulthood. In striking contrast, many species of insects have females that produce comparable numbers of fertilized eggs but only a very few of these embryos ever make it to adulthood. While having only one queen honey bee serve as parent for the entire brood of the hive carries with it potentially negative implications for genetic diversity within the species, honey bees have evolved various effective approaches to generating enhanced genetic diversity. While the queen bee is physiologically highly distinct from the sterile female worker bees, they are genetically indistinguishable. This physiological distinction arises from having only a small set of larvae be exposed to the hormone royalactin being introduced into the 'royal jelly' placed within their cell. Indeed, when the queen bee dies without a young queen bee waiting in the wings, the adult sterile worker bees undergo a competition to see which one most quickly transforms into a fertile queen bee. Such socially induced differentiation into insect 'caste' behavior is even more dramatically illustrated among the highly successful leafcutter ants. The four physiologically distinct forms of leafcutter ants carry identical genomes. Their functional and physiological differentiation also develops in response to socially-derived cues.

The most striking illustration of the social interactions that occurs among honey bees is their famed 'waggle dance'. Upon returning to the hive following a particularly successful round of nectar collection, the worker bee may perform an intricate dance across the surface of the hive that tells the other worker bees the location of the flowers that she had visited. In 1973, Karl Ritter von Frisch earned the Nobel Prize in Physiology or Medicine for his successful deciphering of this dance. His key observations were that these bees moved in a characteristic direction across the hive as they engaged in a waggle-like movement of their bodies. By referencing the top of the hive as defining the sun's current angular position, the direction of the waggle dance conveys the direction of the foraging site. The length of time in which the honey bee moves in this given direction before returning back to their starting position and repeating the dance process is indicative of the distance to the site. In more recent years, it has become politically fashionable in the scientific literature to pretend that the waggle dance cannot be regarded as a 'real' language. This anthropocentric contempt is disingenuous. The waggle dance is clearly a learned behavior whose meaning is understood by the general population. Furthermore, it is clear that the rest of the worker bee population observe these dances and then decide whether to search for these described nectar sites or instead return to the flower patches that they have previously identified.

Among vertebrates, fish exhibit by far the greatest diversity in how the sexuality of individual fish is physiologically determined as well as in the plasticity of that sexual physiology. Few examples of the interplay between sociology and physiology are more dramatic than that of the bluehead wrasse. In response to only visual clues that the population balance of adult males and females has become distorted, the adult bluehead wrasse undergoes an extraordinary transformation. Within hours, its gender behavior switches to that of the opposite sex. Over the course of several days, the overall physical appearance transitions to that of the opposite sex while the transformation within the sex organs results in a fertile adult of that opposite sex. Few fish species and no higher vertebrate species exhibit this extraordinary level of sexual plasticity. Nevertheless, the overall physiological circuitry that underlies the detection of sensory cues, the cerebral processing of that data, the hypothalamic/pituitary release of hormone signaling, and the broad range of physiological re-engineering that occur in response to such hormonal signaling is shared in common among all vertebrate species.

Active brood care behavior is exhibited by the mother, by the father, or both within a large number of fish species. More exceptional are various fish species within the cichlid family that recruit largely unrelated helper fish that participate in brood care and territory defense. This comparative lack of direct relatedness stands in stark contradiction to the conventional 'kin selection' doctrine of joint evolution. The mating couples of these cichlid species dig out sand from underneath a stone to form a cavity which serves as their breeding site. These specially constructed cavities serve a second purpose as marine invertebrates such as shrimp which scavenge at night will search out such cavities to hide during daylight hours and inadvertently become food for the cichlids. These breeding couples will often recruit a small set of helper fish of both sexes to assist in expanding the size of their cavity so as to draw in a larger haul of shrimp which these helper fish then participate in consuming. While the operational distinction between the breeder couple and the helpers is generally clear, a modest but non-zero proportion of the resultant progeny are derived from the subpopulation of helper fish. Strikingly, among the *N. pulcher* species of cichlid, young fish reared by older parents or helper fish have been shown to share significantly more situation-specific behavioral responses than did control samples of fish which were not so exposed to such behaviors exhibited by other members of the species (Taborsky & Oliveira, 2012).

In anticipation of progeny investment techniques further developed among higher vertebrates, various fish species engage in internal fertilization that is then followed by retention within the mother's body until the embryos mature into tadpoles. Among the viviparous species, the developing embryo receives additional nutrition from the mother's blood supply during its period of internal incubation. In species such as the splitfin and the halfbeak, a placental-like structure develops to facilitate this nutrient transfer. Fish species such as the seahorse and the pipefish largely reverse the process of internal fertilization by having the female insert her eggs into the brood pouch of the male where they are mixed with the sperm. These fertilized eggs then remain within the brood pouch into which the male then secretes energy-rich lipids, calcium and the prolactin hormone to further nourish the developing embryos.

What evolutionary advance played the central role in enabling vertebrates to emerge from the oceans to build their existence on solid ground? The appropriately titled *PNAS*, flagship journal of the American National Academy of Sciences, has provided one such explanation (Ma, 2015):

"The mammalian penis represents such a pinnacle in mammalian evolution, which enabled internal fertilization and successful land invasion."

Among the various obvious problems with this claim is the fact that mammals did not successfully invade land. The first mammals evolved from other species of land vertebrates whose ancestors had made the transition from water onto land roughly 140 million years before. Furthermore, as noted above, internal fertilization evolved within fish species.

More relevantly, around 312 million years ago, a new class of organisms arose from the amphibian lineage which produced a fundamentally redesigned egg. In contrast to the gelatinous fish or amphibian egg that is surrounded by a single outer membrane, the egg of the newly arising amniote lineage had developed a complex set of internal membranes which enabled the development of much larger functional eggs and which, in turn, enabled the embryo to eliminate the process of metamorphosis and develop directly into a small adult form before emerging from the egg. The namesake amnionic membrane encapsulates the developing embryo. Directly connected to this is the vitellus (yolk sac) membrane that encapsulated this source of nutrients. Particularly innovative is the allantois membrane which serves to store the waste products generated by the embryo which, in simpler evolutionary forms of the egg, accumulate as toxins for the developing embryo and thus limit the practical time period of development within the egg. Lying directly underneath the newly evolved hard shell of the egg and encapsulating the other three membranes is the chorionic membrane which serves in conjunction with the porous shell to facilitate the permeation of oxygen gas from the exterior while enabling the exit of accumulating carbon dioxide which would otherwise poison the embryo. By also dramatically reducing the problem of dehydration which typically precludes the development of fish eggs or most amphibian eggs out of water, the egg shell of the amniote helped enable the entire life cycle to be carried out on dry land which greatly expanded the available habitat.

Among male evolutionary biologists there has long been an efficient selective professional advantage to portray sexuality among birds by highlighting the showy peacock which contributes nothing to progeny investment beyond an aliquot of sperm. In reality, among bird species, the peacock is largely an anomaly as the bird family has been exceptionally successful at establishing effective mechanisms for the male to efficiently contribute to direct investment in the success of their progeny. Indeed, 90% of all bird species raise their offspring by either pairwise cooperation between a male and female (80.8%) or in larger cooperative family groups (9.0%) (Cockburn, 2006).

The combination of warm-bloodedness with the advanced amniotic egg created a strikingly new evolutionary dynamic among birds. No longer could the fertilized egg simply be abandoned by the mother bird as typically occurs among reptiles. In order to properly develop, the bird embryo in its egg must be incubated at near adult body temperature until it hatches. Furthermore, as the newly hatched nestling is typically incapable of feeding itself, food must be provided until the young bird is ready to fly. This sequence of care needs generally requires the building of a nest, the incubation of the eggs within that nest, and the establishment of a ‘territory’ surrounding that nest in which that nest can be defended and food for the nestlings can be obtained. Crucially, each of these described aspects of progeny care demanded by a young bird can be satisfactorily performed by either a male or a female.

With this transformation in progeny care came a major shift in the evolutionary balance between quantity and quality in reproductive output. Among many earlier evolving species, the offspring are only allowed a quite limited opportunity to physiologically develop before being released on their own to face the world. To achieve evolutionary success, the females of such species are generally required to produce large numbers of offspring to compensate for their high mortality rate. By enabling an increased level of investment in the physiological development of the individual progeny, species can often obtain a much higher fraction of offspring that survive to reproductive maturity. On the other hand, such an increased level of individualized care can only be provided to a smaller number of offspring. Birds have been exceptional for their success in addressing the progeny investment challenge, both with respect to the active engagement of the father in this process and in the shared parental investment during the period following the birth of their progeny. Of particular significance to the process of recruiting male assistance in child care, in many bird species the female may lay her egg only two to three days after having sexual intercourse so that the male can actively engage in direct progeny care soon after the initial act of sexual intercourse. Since a nest is generally required before the egg is laid, the prospective father bird can often begin his contribution to parental care by helping build the nest ahead of time. Indeed, in a number of bird species, the males will first build a nest as a key aspect of the courting process to recruit a mate.

Mammalian evolution stands in stark contrast to bird evolution. While the bird parents can make no direct nutritional contribution to the developing embryo beyond what is originally stored in the egg, the mammalian placenta enables a highly prolonged period of embryonic and fetal development to be carried out before birth. Lactation then provides a highly specialized source of nutrition for the newborn infant. While pregnancy and lactation allow for a level of developmental sophistication to occur that is unmatched in any other branch of life, it comes at a severe cost. For this prolonged period of time, the father is largely left on the sidelines.

What is to be the counter-argument to the suggestion that the overall reproductive success of the male mammal might be better served by simply finding a new female with which to mate? Indeed, over the roughly 150 million years since the emergence of ‘true’ placental mammals, the males within a considerable majority of mammalian species have not evolved to exhibit any significant degree of progeny investment beyond their initial act of insemination. Crucial to the development of social cooperativity among mammals, not only between mating pairs but more broadly, has been the evolution of brain functionality to enable increasingly sophisticated reception and processing of communications as well as formulation of appropriately responsive behavior. Indeed, within the various branches of mammalian life, high levels of such social cooperativity have emerged in only a comparatively small subset of species.

Increasingly central to the process of evolutionary success among such mammals is the dynamic propagation of social knowledge. In general terms, it is the ability to learn and communicate such knowledge that is genetically propagated, not the specific content of that knowledge. As such, evolutionary success depends upon the continuity of that social knowledge system. One useful illustration of this process is found in the pup care among the banded mongoose. In their so-called ‘escort’ system, individual pups become attached to specific adults who train them in the challenges of leaving the den and foraging for food. Males are more likely to perform this role of escort, and despite the clear evidence that the relative quality of this escort training has a significant fitness benefit for the pup, analysis of such pup-escort pairs indicates that they are, on average, no more closely related than randomly selected pairs within the population.

Arguably one of the most dramatic illustrations of how social interactions evolutionarily shape mammalian physiology so as to enhance progeny investment is the phenomenon of menopause (Ellis et al., 2024). Humans are the only land mammals that exhibit menopause, the tendency for females to live a substantial part of their life after they cease to be fertile. Indeed, on average, women live 42.5% of their adult life after they have entered menopause as compared to female chimpanzees who spend, on average, only 2% of their adult life as post-reproductive. While the reproductive lifespan of women is closely matched to that for primates of their size, their total lifespan has been evolutionarily expanded. One common interpretation has been that grandmother humans have, on the evolutionary timescale, substantially contributed to the success of their grandchildren. More specifically, the benefit of that progeny investment must outweigh the benefit of the offspring that she might have otherwise produced during the second half of her adult life.

While evolutionary analysis of menopause has long been hindered by absence of relevant data beyond the human species, it has recently been recognized that five species of toothed whales also exhibit menopause, including killer whales, false killer whales, short-finned pilot whales, narwhals, and beluga whales. Among these species, the trait of menopause has independently evolved in at least four different occasions. With a number of evolutionarily similar whale species which do not exhibit menopause, the analysis of the evolutionary factors involved has been considerably enhanced. The ‘live longer’ rather than ‘stop earlier’ hypothesis is firmly supported by the whale data. In contrast, males in species with menopause have shorter lifespans relative to the females than do males in species without menopause. That result negates the alternative hypothesis that the longer lifespan of females in species with menopause might be the passive effect of the males in that species also living longer. These characteristics demonstrate that extending the lifetime of post-reproductive females does convey a net evolutionary benefit for these species. The presence of a grandmother whale directly enhances the survival of her grandchildren as evidenced by the fact that females with a living post-reproductive mother tend to more widely space their pregnancies than do those who live without a post-reproductive mother, indicative of a higher progeny success rate.

Social knowledge matters, and it must be communicated and learned. The more extensive is the evolutionarily crucial social knowledge, the greater premium is placed upon the efficient accumulation and propagation of that knowledge. If that knowledge takes a substantial part of one’s life to learn, then it becomes more valuable to transition into the role of trainer/nurse after one has learned what they need to share. In the case of menopausal species, it is both the children and the grandchildren who directly benefit from not only the physical assistance but the accumulated knowledge of the grandmother. There’s a long history of speculation regarding what physiological characteristic ‘really’ separates ‘the Man from the monkey’. While it seems quite unlikely that any single trait will ever be understood as the sole determining factor, any short list should almost surely include menopause.

This description of the factors that drive evolutionary success stands in sharp contrast with the doctrines of the present day neo-Darwinist orthodoxy. For any particular variation of a gene, the variant must pass through a large number of generations before it can become the dominant variant for that gene. Conventional population biology analysis assumes that each gene variant has a predetermined value of evolutionary fitness, independent of the variations that other genes in that organism possesses. While mathematically convenient, this assumption of background-independent gene fitness is manifestly absurd. A far more robust understanding of genetic propagation can be obtained from the mixability theory of Marcus Feldman and colleagues (Livnat et al., 2008; Livnat et al., 2010). Feldman argued that a far more robust predictor of success in natural selection comes from genes that exhibit a genome-wide ability to favorably interact with the various genomic combinations that are present in the breeding population so they can avoid severe counter-selection arising from unfavorable combinations. Most significantly, selection for gene variants that are most capable of performing well across different intergenic combinations will tend to jointly enrich a subset of mutational forms at each of the interacting genes on the basis of their mutual functionality. Ongoing selection for that functionality will then induce this subset of mutually compatible variants to evolve as a genetic module. Since this mechanism has no dependence upon chromosomal linkage among the various interacting genes, it enables the joint selection of clusters of variants among a set of interacting genes that are being expressed in different organisms, thus providing a genetic basis for advancing the group selection-based optimization of intra-species social interactions.

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