



Clonal Reproduction in Vertebrates and Redefining Genetic Dead Ends of Evolution

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Abstract

The phenomenon of clonal reproduction in animals in general and revival of clonality in Self Incompatible (SI) animal species in particular are of immense interest to ecology, evolutionary studies and conservation genetics. Clonal reproduction in metazoan species occurs by various mechanisms, including parthenogenesis, hybridogenesis and self fertilization. The offspring generated by these mechanisms are true copies of their single parent due to lack of genetic recombination and earlier studies have observed compromised variation at population level in species that have an exclusively clonal mode of reproduction. Since the undisputed role of genetic variability acting as a raw material for natural selection and thereby for evolution is known, the successful persistence of these species and populations for such long periods of time in evolutionary history is baffling. In recent years significant levels of genetic variation have been encountered in several populations of clonally reproducing animals through more informative and highly polymorphic molecular marker data. Various strategies have been suggested to be in play in the process of maintaining variability in population and preservation of evolutionary potential of the species. It appears that populations of all clonal species uses a combination of strategies such as inter-population migrations, occasional out-crossings and hybridization with closely related species to prevent severe inbreeding and loss of viability. Interestingly, several SI species have recently been documented to resort to parthenogenetic reproduction in captivity. These observations have tremendous significance to various practical aspects of genetics such as conservation, biological containment and clinical study of numerical aberrations of chromosomes.

Keywords: Evolution, Genetic variation, Heterozygosity, Recombination, Vertebrate

Introduction

Clonal reproduction resulting in individuals who are genetically identical to the parents and/or their siblings is not a novel phenomenon in nature. In fact, several plant species and approximately 0.1% of all vertebrate species in nature resort to some form or other of clonal reproduction strategies. Many of these species and their reproductive strategies have been evolved and sustained for millions of years. This observation is interesting in that these species were able to tide over most changes in their living

environment despite an apparently compromised level of genetic variation in comparison to the bisexual mode of reproduction (Menken and Weibosch-Steeman, 1988). The major source of genetic variability in populations is genetic recombination arising during gametogenesis and subsequent fusion of these gametes. Genetic variability in populations acts as the raw material to evolution and provides populations with an upper hand in the face of a changed living environment, thus reducing the risk of extinction. This view has been supported by evidence in

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various species and populations.

Even more striking are the recent observations that genetic variability in natural populations of animal species with clonal mode of reproduction are not as genetically depleted as has been thought to be (Turner *et al.*, 1992). This information came with the availability of more informative and polymorphic molecular markers such as microsatellite and SNPs (Tatarenkov *et al.*, 2010; Maccari *et al.*, 2013; Rabeling and Kronoeur, 2013) replacing the old arsenal of AFLP and Allozyme markers (Menken and Weibosch-Steehan, 1988). This has further enabled the molecular dissection and detailed study of several species where clonal reproduction was previously unheard of (Groot *et al.*, 2003).

Mechanisms of Clonal Reproduction in Animals

Clonal reproduction in vertebrates is roughly of two types. In the first type, which is strictly asexual, the formation of zygote entails from a single gamete or parthenogenesis. Parthenogenesis or “virgin birth” in Greek, refers to a form of reproduction in which the offspring arise from the unfertilized eggs/ female gametes. Parthenogenesis has been used synonymously for natural gametogenesis by many, though the former term could also embrace androgenesis which is also a form of parthenogenesis. Parthenogenetic mode of reproduction has been reported in several insects (Hales *et al.*, 2002; Pearcy *et al.*, 2004; Fournier *et al.*, 2005), crustaceans (Scholtz *et al.* 2003; Eads *et al.*, 2007; Martin *et al.*, 2007), fishes (Hubbs and Hubbs, 1932; Vrijenhoek and Pfeiler, 1997; Chapman *et al.*, 2008; Robinson *et al.*, 2011), snakes (Groot *et al.*, 2003; Booth *et al.*, 2011), *etc.* Parthenogenesis has also been observed in some bird species such as turkey and chicken (Sarvella, 1974) though the offsprings of such reproduction are seldom viable. Androgenetic mode of reproduction has been reported in two ant species till date (Leniaud *et al.*, 2012) though the process involved a fertilization event prior to elimination of the maternal set of chromosomes. Some species reproduce mainly by means of parthenogenesis (obligate parthenogens) while some others are facultative parthenogens/ heterogons.

Parthenogenetic mode of reproduction can be broadly classified into apomictic or automictic on the basis of the underlying mechanism of generation of the gametes. Further, on the basis of the gender of the progeny developing from parthenogenesis the mechanism could also be classified into arrhenotoky, thelytoky or deuterotoky.

Parthenogenesis completely devoid of meiosis is called apomictic parthenogenesis. Here the mature egg cells produced by mitotic divisions develop into embryos and the progeny are complete replica of their mother. In automictic parthenogenesis, meiosis is involved in the generation of egg cells and various methods are resorted to restore the original ploidy level. These mechanisms include endomitosis (doubling of chromosomes before or after meiosis), fusion of first two blastomeres, fusion of meiotic products, or by restitution meiosis chromosomes do not separate in one of the two anaphases. Automixis is classified separate from haplo-diploidy (observed in honey bees).

Arrhenotoky refers to parthenogenetic development of all male offsprings, while in thelytoky parthenogenetic progeny are all female. Thelytoky typically is observed in species where females are homogametic (XX). Another mechanism is pseudo arrhenotoky where a male progeny develops from a fertilized egg by selective elimination of paternal set of chromosomes (Sato *et al.*, 2002). The time point at which this selective elimination happens as well as the mode of elimination depends on the species. In some species, somatic cells are diploid with both the parental chromosome sets active while the germline cells eliminate the paternal genome just prior to gametogenesis. The choice of thelytokous/ arrhenotokous mode of parthenogenesis is thought to rest largely on the reproductive female (Sabelis and Nagelkerke, 1988) as an aide to control the sex ratio of the progeny. However there is also evidence of some vertically transmitted endosymbionts being able to control the mode of parthenogenesis to suit its own transmission and propagation (Stouthamer *et al.*, 1990; Adachi-Hagimori *et al.*, 2008).

Clonal Reproduction Involving Two Gametes

Ironically, a form of clonal reproduction in metazoans can also involve two gametes. In one instance, hybridogenesis, a female mates with a male of closely related species to bring forth a hybrid offspring. During gametogenesis, the paternal chromosome is selectively eliminated so that the gamete carries only the maternal genome. Thus in every generation, the maternal genetic material is passed on clonally while a fresh complement of paternal chromosome is taken up. In other words, while the individuals resulting in each generation is essentially an interspecific hybrid, only the maternal genome of the parental species is transmitted to the next generation. This form of reproduction is reported in some reptiles, amphibians and fish species (Vrijenhoek and Pfeiler, 1997; Neaves and Baumann, 2011). In fact, mounting evidence now indicates that hybridogenesis is virtually the only mode of generation of asexual lineages in vertebrates (Dalziel *et al.*, 2020).

Apart from hybridization, self fertilization is also reported in several invertebrate simultaneous hermaphrodites and at least one vertebrate, *Kryptolebias marmoratus*. Self fertilization differs from parthenogenesis in that the individual generate both male and female gametes within themselves which mature at the same time and are compatible for fertilization. Thus essentially the progeny is a clone of the parent, albeit born *via* normal fusion of gametes.

Generation of Genetic Diversity in Clonal Reproduction

The role of genetic variability in a population in increasing its adaptability and evolutionary potential is well documented. Molecular data on clonal species and populations from earlier studies reported nil to negligent genetic variation in populations. However with the advent of more informative molecular markers, scientists are increasingly observing surprising levels of genetic diversity in natural populations of these species (Lu *et al.*, 2024). The mechanisms of generation of genetic variation in these species are deduced based on

various models on the observed molecular markers data.

Residual Heterozygosity in Progenitor

The level of genetic variation arising in parthenogenetic offspring is dependent on the mechanism of parthenogenesis involved. For instance, progeny from an apomictic or endomitotic parthenogenesis have virtually no variation from the parent (Adachi-Hagimori *et al.*, 2008). The conversion from heterozygosity to homozygosity in a generation depends on the mode of gametogenesis involved (Adachi-Hagimori *et al.*, 2008). In insects, the mode of parthenogenesis is known to be regulated by factors as surprising as vertically transmitted endo-symbionts (Stouthamer *et al.*, 1990; Adachi-Hagimori *et al.*, 2008) and contagious parthenogenesis (Maccari *et al.*, 2013). This could have a direct bearing on the stability of the population and might also operate as a purging mechanism to remove lineages with higher parasite susceptibility (Molloy and Gage, 2006). A lineage descending from a highly heterozygous founder would harbor more diversity than one from a more homozygous founder.

Migration and Mixing of Lineages

Short distance migrations of individuals of different lineages are also thought to explain the inter-individual variability observed within some populations. In addition to molecular biology tools and techniques, the current revolution of artificial intelligence (Dotaniya *et al.*, 2024; Saini *et al.*, 2024) will also help to shed more light on this aspect.

Mutations

Post formational mutations have been considered to be a major source of variation in populations of parthenogenetic and self fertilizing animals (Turner *et al.*, 1992; Badaeva *et al.*, 2008). The genomes of clonally reproducing species are more prone to non-synonymous mutations than the bisexual organisms (Paland and Lynch, 2006) that are subject to natural selection.

Mixed Mating Strategy

A mixed mating strategy is thought to be one of the major sources of genetic variation in self fertilizing *K. marmoratus* populations. The population consists predominantly of hermaphrodites and rare true males which mediate out-crossing events (Turner *et al.*, 1992; Turner *et al.*, 2006). ESD is reported in *K. marmoratus*, but it is however not clear whether there is a genetic factor underlying the generation of maleness as opposed to hermaphroditism. Turner *et al.* (2006) observed a persistence of higher number of males in a population with higher out-crossing upto 2 generations after being removed from their natural habitat, suggestive of a direct correlation of out-crossing rates and generation of males per generation in a population. The variability in a population due to increased outcrossing events can be clearly distinguished from that due to local migrations (Mackiewicz *et al.*, 2006; Maccari *et al.*, 2013) in terms of individual heterozygosity reaching Hardy-Weinberg equilibrium. Heterozygosity levels studied in *Mhcl* genes of the population also indicates a mixed mating strategy followed by this species (Sato *et al.*, 2002).

Leakage of Paternal Mitochondrial DNA

Inheritance of mitochondrial DNA is predominantly maternal though stray cases of paternal mitochondria leakage into zygote has been recorded in several species (Schwartz and Vissing, 2002; Bronham *et al.*, 2003; Kvist *et al.*, 2003). In human beings such instances were observed in connection to functional pathologies (Bronham *et al.*, 2003) though it is not clear if a paternal mitochondrial DNA inheritance is always bound to be deleterious. Such stray incidents might also be a source of genetic variation in cases of hybridogenesis though it has not been documented yet.

Advantages of Clonal Reproduction

Given the clear cut fitness advantages offered by the bisexual mode of reproduction, the persistence of obligate parthenogens and the other forms of clonal reproduction in nature is astounding. More interestingly populations of many of these species are found in a wide variety of habitats and in environments of severe conditions. The phylogenetic studies in these species point to their evolution to dating back times as far back as a million years. Thus it is clear that this mode of reproduction offers some significant advantage to these species and populations. Several models have been put forth for the explanation of the evolutionary advantage of clonal reproduction in species. One of the oldest and most accepted is the Baker's law (Baker, 1955) which suggests that self fertilization offers a species added advantage upon colonizing a new land. The law was put forth to explain the process of selfing in island plant species where dispersal of seeds or pollen could be a limiting factor. The law argues that in isolated ecosystems where finding a compatible mate could be limiting, self fertilization offers the immediate advantage of propagation of the species. Baker's rule has been suggested to be a satisfactory explanation in *K. marmoratus* species (Avisé and Tatarenkov, 2012) given its peculiar environment. Another explanation to the existence of self fertilization in species was put forth by Allard *et al.* (1972). Here the hypothesis is that a self fertilization strategy is aided by a strong natural selection for the preservation of co adapted alleles suited to the specific environment to which the species belongs. This natural selection operates by the restriction of recombination by linkage or by inbreeding (as in selfing). Allard's hypothesis has also been tested to hold well in the case of *K. marmoratus*, as proven by the strong gametic phase disequilibrium exhibited by marker alleles in populations (Molloy and Gage, 2006). Hedrick (1994) suggested that automictic parthenogenesis with no recombination coupled with parent- offspring mating might assist in the purging of deleterious alleles by constant elimination of recessive homozygotes in every generation. This also implies that a lineage from a female heterozygous for multiple detrimental allelic variants reproducing by such a mechanism might not take off for the low probability of viable progeny (Hedrick, 2007).

Conclusion

It would be interesting to understand the strong barrier that prevents the revival of clonal reproduction especially

in higher vertebrates. The presence of clonal reproduction strategies in the so called lower species questions the “height” of placement of the sexual species (or the so called higher species). The question seems to be one of the egg and the chicken. In the time of a catastrophe, who would fare better- a bisexual species of high genetic diversity or a selfing species with compromised diversity? In the event of a severe catastrophe who fares better- a self-sustaining clonal species or a self-incompatible species which requires a mate? So finally, who is the dead end?

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