

Evolution and mechanisms of facultative and obligate parthenogenesis

Sub Questions:

- Which parthenogenetic mechanisms exist and when do they occur?
- What are the costs and benefits of reproducing through obligate versus facultative parthenogenesis and which environmental conditions promote these reproductive strategies?

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Abstract

The discovery of multiple unisexual lizard populations started in the early 1900s and stirred up many scientific questions. Later, numerous usually sexually reproducing vertebrates were observed to produce successful parthenogenetic offspring in captive conditions. For many years scientists have tried to solve the long standing paradox of the maintenance of obligate sexual reproduction in the animal kingdom despite its high reproductive costs. Reptiles are a model class for this study thanks to their diverse use of reproductive strategies. This essay focuses on two main questions, 1) Which parthenogenetic mechanisms exist and when do they occur? 2) What are the costs and benefits of reproducing through facultative versus obligate parthenogenesis and hence which environmental conditions promote these reproductive strategies? There are 3 main mechanisms of parthenogenesis, i.e. apomixis (a mitotic mechanism), automixis and premitotic doubling of chromosomes (meiotic mechanisms). To this day scientists are not always able to identify which mechanism is employed by which species, especially between apomixis and premitotic doubling which both result in genetically identical female offsprings, so the associations between the mechanism and the reproductive parthenogenetic strategies have not yet all been confirmed. Many costs and benefits were identified for obligate parthenogenesis. Costs include the loss of genetic diversity, accumulation of deleterious mutations and hence the risk of a short survival time frame. On the other hand, benefits included the elimination of the two-fold cost of sex, reducing the cost of reproduction and the risk of failed reproduction in case of low mate availability. Hence, It was also found that the environmental conditions that promote obligate parthenogenesis are harsher, more unstable, thanks to their increased rate of procreation. However, facultative parthenogenesis only appeared to have benefits in most past research, its ability to combine the advantages of both obligate sexual and asexual reproduction. One would expect the most advantageous strategy to be selected for, and hence for more individuals to perform facultative parthenogenesis than what has been observed thus far. With the help of theoretical and mathematical models, I concluded that facultative female resistance against males was too costly and therefore selected towards sexual or asexual obligate strategies. Conversely, an alternative conclusion would be that facultative parthenogenesis is indeed the most beneficial reproductive strategy and is employed by many more species that research has not yet encountered. Scientific models and real life case studies suggest that facultative parthenogenetic populations require environments with low mate densities in order to prevail.

Introduction

Reproduction in the animal kingdom often consists of sexual reproduction. Although a few species were found to reproduce through parthenogenesis. The concept of parthenogenesis has been observed and studied for many years, and yet not very much is known of it, especially in vertebrates. It is of current scientific relevance for many reasons, for example the study of asexual and sexual reproductive techniques based on their geographic distribution (Tilquin & Kokko, 2016). Parthenogenesis, greek for “virgin birth” is an asexual form of reproduction (Wininger, 2004). It has been observed to occur in many species, though it is most common in invertebrates, an increasing number of vertebrate species are being discovered to perform facultative parthenogenesis as well. Though most cases of parthenogenesis in vertebrates have primarily been observed to occur in captive isolation (Lampert, 2008). There are two forms of parthenogenesis; obligate and facultative. As the terms may suggest, obligate parthenogenesis is the only reproductive technique a population employs, whereas facultative parthenogenesis is the ability of sexually reproducing species to perform asexual reproduction under certain conditions (Lampert, 2008). Facultative parthenogenesis has predominantly been observed in species such as sharks, reptiles and some birds residing in institutions and zoos (Booth et al., 2012; Feldheim et al., 2010; Ramachandran & McDaniel, 2018). These discoveries have lead to a long standing evolutionary paradox (Gibson, Delph, & Lively, 2017); many scientists struggle to understand why the majority of animals reproduce through obligate sexual reproductions, considering it comes with so many costs (Dawley, 1989; Kondrashov, 1993; Burt, 2000; Doncaster, Pound, & Cox, 2000; Butlin, 2002), especially compared to the costs of facultative strategies that appear only to combine benefits of obligate sexual and asexual reproductions (Burke & Bonduriansky, 2019).

There are 3 main mechanisms by which parthenogenesis can occur: Apomixis (a mitotic process), automixis and premitotic doubling of chromosomes (both meiotic processes). Apomixis and premitotic doubling result in offsprings genetically identical to their mother, with exception of mutations, automatically resulting in females (Lampert, 2008). These mechanisms are often used by species with obligate parthenogenesis (Arakelyan, Harutyunyan, Aghayan, & Carretero, 2019). On the other hand, automixis allows for more genetic variation (Batygina, 1988), thanks to having two product fusions; central and terminal fusion. Central fusion still produces females, while terminal fusion produces male offspring in terms of ZZ/ZW chromosomal systems (Lampert, 2008). The latter can only be found in facultatively reproducing species, as obligate parthenogenetic populations must be unisex, hence only produce females. The identification between the different mechanisms is not yet full proof. Thus far it is not clear which mechanism is used by which parthenogenetic strategies.

As mentioned previously, there are several costs to producing sexually compared to asexually. Sexual reproduction can be a disadvantageous process due to the two-fold cost of males (Kondrashov, 1993; Butlin, 2002). This is the cost of producing sons that cannot themselves produce offspring, hence halving the sexual population compared to an asexual population (Gibson, Delph, & Lively, 2017). In addition to this, the breaking up of favourable gene combinations occurs more frequently when reproducing sexually (Butlin, 2002). Finally, the cost of mate searching, which could be detrimental when no mates are available potentially due to an unstable environment (Owens & Thompson, 1994). These costs could potentially explain the evolutionary benefit of reproducing asexually, better known as parthenogenetically, whether facultatively or obligately.

Asexual reproduction is quite a rare strategy within animals and comes with many costs of its own, although they vary depending on the use of obligate or facultative parthenogenesis. obligate parthenogenesis has opposing costs and benefits to sexual reproduction, for example its costs include; a short survival time frame (Leslie and Vrijenhoek, 1978; Bell, 1982; Spinella and Vrijenhoek, 1982; Smith, 1986; Lynch and Gabriel, 1990), accumulations of deleterious mutations (Muller, 1932; Kondrashov, 1988) and consequently slower rates of adaptations (Colegrave, Kaltz, & Bell, 2002; Kaltz and Bell 2002; Allen & Lynch, 2008). On the other hand, obligate parthenogenesis eliminates the two-fold cost of sex (Kondrashov, 1993; Butlin, 2002), reduces the risk of beneficial allele combinations being broken (Butlin, 2002) and many more. Whilst most past research suggest that facultative parthenogenesis only comes with the benefit of combining both sexual and asexual reproductive benefits and lowering their costs (D'Souza & Michiels, 2010; Green & Noakes, 1995). Not many costs have yet been discovered in relation to facultative parthenogenesis. These costs and benefits must be weighed in order to truly understand and hypothesise why and when certain reproductive strategies occur.

Parthenogenesis is interesting to observe in the class reptilia, as reptiles are the only vertebrate group containing species that perform obligate parthenogenesis (Vrijenhoek, Dawley, Cole, & Bogart, 1989). Most obligate parthenogenetic populations, unlike facultative ones, however have been identified in their natural habitat thanks to their unisexual populations (Maslin, 1971). Reptiles such as *Darevskia* rock lizard have been used as model animals (Arakelyan, Harutyunyan, Aghayan, & Carretero, 2019; Barateli, Tarkhnishvili, Iankoshvili, & Kokiashvili, 2022). *Darevskia* lizards are interesting to look into as they are one of few reptilian species to have both a unisexual and bisexual population. Thanks to these opposing populations comparisons can be made and hence calculating

costs and benefits in these two reproductive strategies in natural conditions. Another example of obligate parthenogenetic species is that of Unisexual *Aspidoscelis*, these whiptail lizards are found in North American deserts, in disturbed and quickly changing environments, already hinting towards the fact that obligate parthenogenetic reptilian species are most adapted to rough environments (Schall, 1978).

On the other hand most facultative reptilian parthenogenetic cases have mostly only been observed in captive individuals, isolated in zoos and scientific institutions (Lampert, 2008; Watts et al., 2006). So far, most captive reptiles are found to be able to reproduce using facultative parthenogenesis only whilst still virgins, and hence in captive environments isolated from males (Bell, 1982; Booth & Schuett, 2016). A well known example of this is that of Komodo dragons, *Varanus komodoensis* (Watts et al., 2006). However, an exception to this rule is found in the boa constrictor, which was observed to have reproduced parthenogenetically despite having history of sexual reproduction and being housed with males (Booth, Johnson, Moore, Schal, & Vargo, 2011; Booth & Schuett, 2016). All other vertebrate classes have so far only been observed to perform facultative parthenogenesis or none at all, this may be due to their genetic predisposition, or simply the lack of research and sampling (Lampert, 2008).

Herein, this thesis compares facultative to obligate parthenogenesis in reptiles on a mechanistic as well as an evolutionary point of view. By investigating the three parthenogenetic mechanisms and which species employ them, it is possible to answer the following question; which parthenogenetic mechanisms exist and when do they occur? The second question (what are the costs and benefits of reproducing through obligate versus facultative parthenogenesis and which environmental conditions promote these reproductive strategies?) can be solved with the use of case studies focusing on multiple obligate as well as facultative parthenogenetic reptile species. In addition to this, theoretical and mathematical models will be employed in order to solve certain aspects of the question that have not yet been applied to reality.

Cases and mechanisms of obligate and facultative parthenogenesis

Parthenogenesis can be performed in 3 different ways and these different parthenogenetic modes are used by different species within the reptilia class. One mitotic mechanism; apomixis, and two meiotic mechanisms; automixis and premitotic doubling.

Apomixis and premitotic doubling are the two mechanisms that lead to offsprings genetically identical

to their mother, with exception to the mutations that may occur, meaning only females can be produced in these two cases (Lampert, 2008). In apomixis, no segregation or recombination occurs, oocytes are produced by mitosis. Whilst in premitotic doubling, the genome is doubled before meiosis. Segregation and recombination occur, but since they take place between identical homologous chromosomes, the offspring are still genetically identical to their mother (Lampert, 2008). For example, Burmese pythons, *Python molars bivittatus*, were found to have produced viable female offsprings genetically identical to the mother, only explainable by apomixis or premitotic doubling (Groot, Bruins, & Breeuwer, 2003).

The third mechanism, automixis, allows for more genetic variation thanks to segregation and recombination taking place between nonidentical homologous chromosomes (Batygina, 1988). This form of parthenogenesis produces two forms of meiotic product fusion; central and terminal fusion. In central fusion, the first polar body fuses with the oocyte. This fusion preserves most of the maternal heterozygosity, hence producing a female, and the offsprings share a high number if not all alleles with their mother. According to figures produced by Booth and Shuett, most snake species or squamates in general are found to perform automixis. Some species remain untested, though most of the automixis cases were found to produce females (Booth & Schuett, 2016), suggesting the occurrence of central fusion since most squamates and snakes have ZZ (male)/ZW (female) sex chromosome systems (Viana et al., 2020).

On the other hand in the terminal fusion mechanism the second polar body fuses with the egg nucleus. This leads to mostly homozygous offspring, producing males, sharing only about 50% of the mother's alleles (Lampert, 2008). Examples of this include monitor lizards such as Komodo dragons (Watts et al., 2006) as well as Chequered garter snake, *Thamnophis marcianus*. Captive Komodo dragons and chequered garter snakes have been found to asexually produce male offsprings when kept in isolated conditions (Watts et al., 2006; Reynolds, Booth, Schuett, Fitzpatrick, & Burghardt, 2012; Booth & Schuett, 2016), meaning they perform terminal automixis.

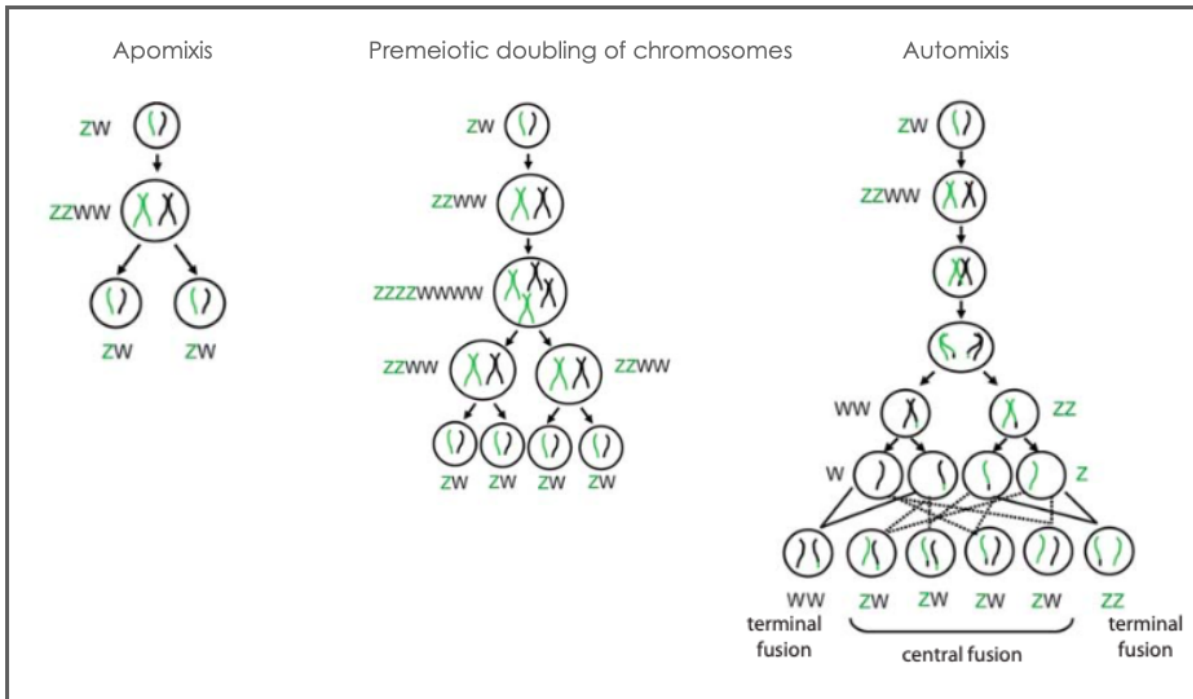


Figure 1: A simplified diagram explaining the three parthenogenetic mechanisms (Apomixis, Premiotic doubling of chromosomes, Automixis) with the use of a ZZ/ ZW sex determining system which is found in most reptiles, including all those mentioned in this paper (Lampert, 2008)

Automixis is the parthenogenetic technique that could reduce the evolutionary cost of genetic uniformity at a group level, caused by the other two mechanisms, apomixis and premitotic doubling of chromosomes. However apomixis and premitotic doubling leads to reduced homozygosity at an individual level. This supports the fact that the latter mechanisms are mostly used by obligate parthenogenetic populations, such as the unisexual *Aspidoscelis* and *Daravskia* lizards (Arakelyan, Harutyunyan, Aghayan, & Carretero, 2019). This is because a population limited to asexual reproduction would seek to minimise homozygosity which fully occurs in terminal fusion of automixis and partly occurs in central fusion due to the occurrence of meiotic crossovers. Therefore the genetic outcome of automixis would be more detrimental to a fully asexual population than that of apomixis and premitotic doubling which allows the gradual build up of mutations in heterozygous individuals, despite the costs of cloning.

Moreover, current findings state that the majority of facultative parthenogenetic squamates reproduce using automixis, mostly central (Vrijenhoek, Dawley, Cole, & Bogart, 1989) and most facultative monitor families reproduce using terminal automixis (Watts et al., 2006). Facultative reptiles, with the option to reproduce sexually have a lowered selective pressure allowing for more homozygosity to occur at an individual level.

Table 1: Summary of the species used as examples throughout the paper

| Species | type of parthenogenesis | mechanism | offspring sex | environmental conditions |
|---|--|---------------------------------|---------------|-----------------------------------|
| <i>Darevskia armeniaca</i> (Armenian rock lizards) | both obligate parthenogenesis populations and sexual populations | Apomixis or premitotic doubling | Female | Natural environment: rocky areas |
| <i>Unisexual Aspidoscelis</i> (Whiptail lizards) | obligate parthenogenesis | Apomixis or premitotic doubling | Female | Natural environment: Deserts |
| <i>Python molars bivittatus</i> (Burmese pythons) | facultative parthenogenesis | Apomixis or premitotic doubling | Female | Captivity (isolated from males) |
| <i>Boa constrictor</i> (boa constrictor) | Facultative parthenogenesis | Automixis | Female | Captive (cohabitating with males) |
| <i>Varanus komodoensis</i> (Komodo dragon) | facultative parthenogenesis | terminal automixis | Male | Captivity (isolated from males) |
| <i>Thamnophis marcianus</i> (Chequered garter snake) | Facultative parthenogenesis | terminal Automixis | Male | Captivity (isolated from males) |

Obligate versus facultative parthenogenesis

One of the most puzzling anomalies in evolution remains the long term maintenance of sexual reproduction in the animal kingdom (Gibson, Delph, & Lively, 2017) despite its many disadvantages, including its high costs (Dawley, 1989; Kondrashov, 1993; Burt, 2000; Doncaster, Pound, & Cox, 2000; Butlin, 2002) and more importantly the two-fold cost of sex or males, previously referred to in the introduction (Gibson, Delph, & Lively, 2017).

Conversely, obligate parthenogenesis comes with opposing benefits and costs to sexual reproduction. General costs of reproducing asexually include the speedy accumulation of deleterious mutations (Muller, 1932; Kondrashov, 1988), as well as the risk of a short survival time frame due to the genetic uniformity created within obligate parthenogenetic populations (Leslie and Vrijenhoek,

1978; Bell, 1982; Spinella and Vrijenhoek, 1982; Smith, 1986; Lynch and Gabriel, 1990). Finally, the higher intensity of variance that comes from sexually reproducing is lost to fully parthenogenetic population, suggesting the risk of slower rates of adaptations (Colegrave, Kaltz, & Bell, 2002; Kaltz and Bell 2002; Allen & Lynch, 2008).

Fully asexual reproduction eliminates the two-fold cost of sex, the disadvantage of halving the sexual population due to the production of sons that cannot themselves produce offsprings (Gibson, Delph, & Lively, 2017). This is thanks to the fact that only female offspring, often clonally similar to their mothers, are produced during obligate parthenogenesis (Kondrashov, 1993; Butlin, 2002). Reproducing in an obligate parthenogenetic way also reduces the risk that sexual reproduction frequently runs, that of breaking up beneficial combinations of genes (Butlin, 2002), and of course there is much lower risk of reproductive failure in the case of low mate availability (Clutton-Brock, 1994). Much research has gone into comparing unisexual communities to bisexual communities of *Darevskia* rock lizard genus. This is one of the most well known vertebrate species containing both obligate parthenogenetic communities and bisexual ones (Barateli, Tarkhnishvili, Iankoshvili, & Kokiashvili, 2022; Arakelyan, Harutyunyan, Aghayan, & Carretero, 2019). Previous research by Barateli looked into the comparison between the reproductive efforts of sexual versus asexual *Darevskia* lizard populations (Barateli, Tarkhnishvili, Iankoshvili, & Kokiashvili, 2022). They found that most of the results truly depended on the environment conditions, that parthenogenetic lizards reproduce faster than bisexual lizards, hence forming larger populations more rapidly, which means they are more adapted to survive to unstable environments (Barateli, Tarkhnishvili, Iankoshvili, & Kokiashvili, 2022). Another paper assessed evolutionary reasons for prevailing parthenogenesis through the use of Haemogregarines parasites (Arakelyan, Harutyunyan, Aghayan, & Carretero, 2019). They found that the most parasitised individuals were males, meaning the obligate parthenogenetic populations suffered least from the Haemogregarines. The observation that an all female population was less parasitised than a bisexual one could be due to the hypothesis that unisexual populations invest less energy in reproduction. This means that these obligate parthenogenetic females can dedicate more energy into their immune system function (Lehtonen, Jennions, & Kokko, 2012). Another model obligate parthenogenetic species is tested for; Unisexual *Aspidoscelis* for example, a type of lizard found in the deserts of North America, are commonly found in disturbed and quickly changing environments, hence the use of the term “weed”, plant species that grow best in difficult environments (Baker, 1974; Schall, 1978). Reproductive effort is expected to be higher and egg numbers are also found to be higher in parthenogenetic individuals (Schall, 1978), this allows the species to procreate faster and therefore survive in challenging environments.

These tests and observations all lead to the conclusion that obligate parthenogenesis is more adapted to unstable environments. Obligate parthenogenetic lizards prevail on a short term scale (Tarkhnishvili, Gavashelishvili, Avaliani, Murtskhvaladze, & Mumladze, 2010). Ergo, these findings support the general hypotheses that the faster reproductive rate of parthenogenetic species could be beneficial in more challenging environments with food scarcity, drastic seasonal changes, parasitisation (Begon, Harper, & Townsend, 1987; Glesener and Tilman, 1978; Lynch, 1984; Pongratz, Storhas, Carranza, & Michiels, 2003), as well as the lower investment in reproductive energy, when population sizes are low and male availability is scarce, obligate parthenogenetic communities have a clear advantage (Glesener and Tilman, 1978; Lynch, 1984; Pongratz, Storhas, Carranza, & Michiels, 2003).

Costs and benefits can easily be identified and hypothesised for both full parthenogenetic and sexual species. However, this is not the case when it comes to facultative parthenogenesis. Not very much previous information and research has gone into discussing the costs of facultative parthenogenesis. Many scientists actually hypothesise that facultative parthenogenesis only combines the benefits from both sexual and asexual obligate reproductions, so therefore would be most advantageous (Burke & Bonduriansky, 2019). Yet, one would expect the most advantageous strategy to be selected for and hence it to be more frequent within vertebrate populations. Scientific models attempt to solve this long-standing evolutionary paradox about the general maintenance of sexual reproduction in animals (Burke & Bonduriansky, 2019) and hence find facultative parthenogenetic costs. Burke's & Bonduriansky's theory discusses mate coercion and consequently the development of a sexual arms race: in a sexual population, a mutant allele may allow for parthenogenetic reproduction, this allele would be expected to be selected for due to the demographic advantage of producing all female offspring (Smith, 1978), and the reduction of mating costs (Williams, 1975). However, males typically have a higher mating rate than females, allowing selection to favour their suppressive strategy (Arnqvist & Rowe, 2005; Maklakov, Bilde, & Lubin, 2005; Martin & Hosken, 2003). Males could directly inhibit the spread of obligate parthenogenesis by mating with facultative mutants, since in many facultatively parthenogenetic individuals only virgin females are capable of reproducing asexually (Bell, 1982). This means that facultative parthenogenetic strategy is most favoured when male scarcity is high, as costs of resistance are reduced (Gerber & Kokko, 2016).

As previously mentioned, current scientific papers focus on the benefits that facultative parthenogenesis brings to species that have the traits. The theory suggests that facultative parthenogenesis incorporates both sexual and asexual reproduction providing all the advantages in both strategies but at lower costs (D'Souza & Michiels, 2010; Green & Noakes, 1995). Facultative

reproduction is as successful as obligate sexual reproduction at creating advantageous allele combinations (Bell, 1988; Hurst & Peck, 1996; Kondrashov, 1984), promoting adaptation (Lynch & Gabriel, 1983; Sasaki & Iwasa, 1987) and facilitating evolutionary escape (Flatt, Maire, & Doebeli, 2001; Yamauchi, 1999; Yamauchi & Kamite, 2003). Whilst simultaneously maintaining benefits from obligate parthenogenesis; it preserves advantageous allele combinations (Butlin, 2002), eliminates the two-fold cost of sex (Kondrashov, 1993; Butlin, 2002), reduces the risk of reproductive failure in case of low mate availability (Clutton-Brock, 1994) allows individuals to invest less energy in reproduction, and invest more in other functions such as immunity (Lehtonen, Jennions, & Kokko, 2012). Burke's and Bonduriansky's mathematical model concluded that all cases end in the fixation of facultative parthenogenesis (Burke & Bonduriansky, 2019). However, according to current research, a minority of reptilian species perform facultative parthenogenesis, which contradicts this model as well as the many apparent advantages most current research claim facultative parthenogenesis to have. This may however be due to a lack of understanding of all facultative parthenogenesis' costs, so they may have been unable to include all necessary factors in the model. On the other hand it may simply be due to a lack of sampling, thus a true number of reptiles with the capacity of performing parthenogenesis is unknown and may actually support the prior theory and the mathematical model's results.

The ability to perform facultative parthenogenesis assures the procreation of an individual whether or not a mate is available, while still maintaining the genetic variation that obligate parthenogenesis cannot. Many reptiles such as the komodo dragon or the Burmese pythons were only discovered to reproduce facultatively when placed in isolation in zoos and institutions (Watts et al., 2006). This may simply indicate lack of sampling and detection limitations in their natural environments. However, even in isolation, parthenogenetic reproduction does not appear to take place often and may only occur after extended time, under specific conditions and if possible developmental constraints allow this type of reproduction. This suggests that facultative parthenogenesis requires conditions with extremely low mate densities, for example populations with a skewed sex ratio, in the wild for this reproductive strategy to occur in natural conditions (Brittain, 1982; Gerritsen, 1980; Johnson, 1994; Markow, 2013; Schwander & Crespi, 2009). Theoretical models suggest that investment in facultative parthenogenesis is mainly only beneficial to females when mates are low in density, as females pay fewer costs in resistance to male coercion in these conditions (Burke & Bonduriansky 2019, Gerber & Kokko, 2016).

Conclusion and outlook

Reptiles are the only vertebrate class so far identified, capable of reproducing both obligately parthenogenetically as well as facultatively parthenogenetically (Vrijenhoek, Dawley, Cole, & Bogart, 1989), making them perfect model organisms to understand the mechanisms and contrast the benefits and costs these reproductive strategies bring to individuals as well as species groups.

There are three main ways parthenogenesis can be performed; employed by different species depending on whether they are obligately or facultatively parthenogenetic (Lampert, 2008). One mitotic mechanism; apomixis, and two meiotic mechanisms; automixis and premitotic doubling. As table 1 depicts, apomixis and premitotic doubling produce genetically identical offspring to the mother (Lampert, 2008), and is principally used for obligate parthenogenetic species. Conversely, automixis is used by most facultative parthenogenetic species with a few exceptions (Booth & Schuett, 2016), for example despite the Burmese pythons performing facultative parthenogenesis it either employs apomixis or premitotic doubling producing genetically identical female offspring (Groot, Bruins, & Breeuwer, 2003). The association between obligate parthenogenesis and apomixis or premitotic doubling of chromosomes is supported by the fact that a population limited to asexual reproduction necessitates to maintain full heterozygosity in individuals, these mechanisms allow for a gradual build up of mutations. Whereas most facultative parthenogenetic species reproduce using automixis. Thanks to their ability to reproduce asexually the selective pressure is reduced allowing for more homozygosity within individuals. It would however be interesting to look more into the comparison between the effect of reducing homozygosity at individual levels; caused by automixis, versus reducing genetic variation at a group level; a consequence of apomixis and premitotic doubling.

In relation to obligate parthenogenesis, clear costs and advantages were identified, namely the loss of genetic diversity, accumulation of deleterious mutations or even the risk of a short survival time frame. Whilst, benefits included the elimination of the two-fold cost of sex (Kondrashov, 1993; Butlin, 2002), the reduced costs of reproduction and the risk of failed reproduction in the case of low mate availability (Clutton-Brock, 1994). Real case studies observed in their natural environment combined with conclusions drawn from the costs and advantages of obligate parthenogenetic reproduction allow us to know which environment obligately asexual populations are most adapted to. Obligate parthenogenetic species were all found to be most suited to unstable, challenging environments, supported by the “weed hypothesis” (Wright and Lowe, 1968).

Most papers currently state that facultative parthenogenesis mainly combines the benefits found in

both sexual and obligate parthenogenetic reproduction (D'Souza & Michiels, 2010; Green & Noakes, 1995). However Burke's and Bonduriansky's mathematical model tries to identify the costs of reproducing facultatively (Burke & Bonduriansky 2019). They find the main cost is that of female resistance against male coercion (Smith, 1978; Williams, 1975). The lack of real case studies about facultative parthenogenetic species in their natural environments hinder a concrete conclusion on the costs and benefits of reproducing through parthenogenesis, so two opposing but yet likely hypotheses have been formed. 1) Perhaps resistance is the one cost that is slowing the total spread of facultative parthenogenesis in reptiles. It may be that cost outweighs all the costs of being sexually or asexually obligate, suggesting that either species switch to obligate parthenogenesis, and lose males, hence their coercion, or remain sexual and submissive to males. 2) An alternative theory may be that there are many more facultatively reproducing reptile species that have not yet been observed, or even those who have been identified reproduce with the use of a parthenogenetic mechanism much more frequently and liberally than is currently suggested. Arguing that facultative parthenogenesis is indeed evolutionarily advantageous, and that, on the contrary to what current statistics state, it is being selected for. As is depicted in table 1, facultatively parthenogenetic species have only been identified in captive and/or isolated conditions, so the environments they are most adapted have been so far unidentified. However, with the use of Burke's and Bonduriansky's model the following conclusion can be formed: facultatively parthenogenetic populations require environments with low mate densities in order to prevail (Brittain, 1982; Gerritsen, 1980; Johnson, 1994; Markow, 2013; Schwander & Crespi, 2009) as females then pay lower costs in resisting against male coercion (Gerber & Kokko, 2016).

Future research may touch upon phylogenetic trees and hence observe evolutionary lineages to understand the evolutionary relationships between obligate sexual reptilian populations, with facultative and obligate parthenogenetic reptiles. Associating this information with the environments each species resides in would also facilitate the correlation between environment and reproductive strategy.

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