ARTICLES

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Observations on Parthenogenesis in Monitor Lizards

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Abstract - In this article I report observations on multiple parthenogenetic events in the Argus monitor (*Varanus panoptes*) in captivity. Two individually-housed females produced a total of 14 clutches of eggs in the absence of a male over a period of seven years. To date, 23 out of 69 eggs received from eight clutches have been incubated; all others eggs were noticeably infertile and discarded. Embryos developed in at least ten eggs; nine of which died shortly before hatching. Only one offspring successfully hatched and survived. Two non-surviving embryos showed cranial deformities. Also discussed are the different forms of parthenogenesis known to birds and reptiles, specifically highlighting the details of facultative parthenogenesis in the genus of *Varanus*.

Introduction

Parthenogenesis is not commonly reported in reptiles. Vrijenhoek *et al*. (1989) recorded parthenogenetic reproduction in the following lizard families: Gekkonidae, Teiidae, Uromastycidae (Agamidae), Chamaeleonitidae, and Xanthusiidae. Böhme (1975) and Frey & Madden (1995) reported parthenogenesis in two additional lizard families: Corytophanidae and Iguanidae. Parthenogenesis has also been documented in several snake groups (Magnusson, 1979; Vrijenhoek *et al*., 1989; Dubach *et al*., 1997; Schuett *et al*., 1997; Scalka & Vozenilek, 1986; Groot *et al*., 2003; Kuhn & Schmidt, 2004).

In recent years, several reports of parthenogenesis in captive monitor lizards have been published. Lenk *et al*. (2005) documented a successful parthenogenetic breeding of *Varanus panoptes horni*, Watts *et al*. (2006) described a case for *V. komodoensis*, and Hennessy (2010) reported a case for *V. ornatus*. Incidents of parthenogenesis in captive monitor lizards could potentially be noticed more frequently if individuals were housed separately and not in pairs, although this is only speculation. Typically, if a clutch of eggs is produced while a sexual pair is housed together, it is automatically assumed to be the result of normal sexual reproduction. The following is a report of my observations on the husbandry and parthenogenetic reproduction of *V. panoptes* in captivity.

The animals

A single *V. panoptes* was purchased from a pet shop as a sub-adult on 15 September 2003 (Figs. 1 & 2). This animal was captive-bred in Germany, and had hatched in January 2003. It was offered for sale together with seven other siblings from the same clutch. This lizard and its siblings were assumed to be hybrids of *V. p. panoptes* and *V. p. horni* because of their coloration and pattern. Some of the siblings showed coloration and markings typical of *V. p. panoptes*, whereas others resembled *V. p. horni*. This assumption was later confirmed in an interview with the breeder. On 12 October 2003, the snout to vent length (SVL) of this animal measured 20 cm; total length (TL) was 52 cm.

Keepers of *V. panoptes* have reported that males of this species tend to grow much larger, but are easier to handle than females. Keeping this in mind, I sought to

Figs. 1 & 2. The first female (*Varanus panoptes panoptes* x *V. panoptes horni*), photographed in June 2006.

purchase a single animal, preferably a male. At the pet store, the largest individual from the group was chosen; it displayed the coloration and pattern of *V. p. panoptes.* Unfortunately, this animal turned out to be female, and in December 2004 produced its first clutch of eggs. Since this animal was a sub-adult when purchased in September 2003 and did not have contact with another monitor lizard since it was acquired, it was presumed that the clutch might have been produced through parthenogenesis.

Upon the discovery that this initial specimen was female, I set out to purchase a suitable male of the same subspecies. This, however, was not possible, as only *V. p. horni* offspring were available. Therefore, the largest animal from a clutch of *V. p. horni* hatchlings which had hatched just a few days earlier was purchased directly from a private breeder on 9 September 2006 (Figs. 3, 4 & 5). Unfortunately, this animal also proved to be female when it laid a clutch of eggs in 2009.

Husbandry

Past experiences from other private keepers suggested that housing two or more individuals of this species together in the same enclosure could lead to problems of aggression. Even housing two females together can be hazardous and often does not work out. Knowing there was a possibility of aggression, it was decided that both animals should be housed separately. The enclosure for the first individual offered 2.8 m^2 of floor space; the enclosure for the second individual offered 5 m^2 of floor space.

The diet offered to both animals was identical. Nearly every day, the monitors were fed insects

Fig. 3. The second female (*V. panoptes horni*), photographed in October 2006, just a few days after hatching.

Figs. 4 & 5. The second female (*V. panoptes horni*) in an outdoor terrarium, April 2008.

(cockroaches, crickets, and *Zophobas* larvae). Once a week chicken hearts were offered, but before feeding the hearts, the fat was removed and the hearts were dusted with a vitamin and calcium supplement. Once a month the chicken hearts were substituted for a freshly killed sub-adult rat as a way of offering some variety to the diet. All insects were offered to the lizards outside their enclosures, which gave the animals 10-30 min to roam around the reptile room, which measured about 8 m^2. Only one lizard at a time was given free run outside its enclosure. The strategy here was to tame the animals during this time to make handling easier.

A 300 W Osram® Vitalux was installed in each enclosure to provide a source of UV. The lamps were switched on two or three times a week for ca. 30 - 45 minutes at a time. The temperature in the reptile room ranged from 25-30 °C between April and September, and 20-28 °C between October and March. Both enclosures were partially located under a window, which allowed natural sunlight into the enclosures (Fig. 6.). Each enclosure also featured a 100 x 50 cm area of floor space which was heated with a heating cable. A 75 W halogen spotlight and the Osram® Vitalux were positioned over this area to provide additional light, heat, and UV. A wooden box measuring 60 x 45 x 25 cm, half-filled with fine, dust-free and slightly dampened sand was also provided in the enclosures for refuge or egg laying.

Fig. 6. The second female in its terrarium.

Table 1. Clutch data for the initial female *V. panoptes*.

Date of oviposition	Clutch size	No. eggs incubated	Incubation period [d]	Remarks
21-22 Dec 2004	7	3	154 - 187	Two dead embryos with cranial malformations (no eyes, upper jaw shortened)
1 Apr 2005	5	2	-	Laid 101 days after previous clutch
15 Jun 2005	7	4	-	Laid 75 days after previous clutch
6-10 Sept 2005	6	-	-	Produced after female had sustained a spinal injury

Egg deposition by the first animal

The first female was approximately 23 months of age when it produced its first clutch. One month prior to laying, it measured 37 cm SVL and 86 cm TL, and weighed 1.18 kg. Data for clutches produced in 2004 and 2005 are listed in Table 1. One of the eggs laid between 21-22 December 2004 ruptured after 154 days of incubation, most likely due to an excessively wet incubation medium, and contained a partially developed embryo. The remaining egg from this clutch incubated for 187 days before beginning to deteriorate. Upon dissection, a deceased, but near fully-developed embryo was discovered. Both embryos showed similar cranial deformities (Fig. 7).

On 16 June 2005, this animal was found lying in the enclosure with what appeared to be a fractured spine. The location of the injury was just in front of the pelvic girdle, and veterinary examination confirmed a fractured spine. Over the next four weeks, daily injections with a nerve-stimulating drug (Thiamin) were administered into the base of the tail. After about six months, the monitor began to walk again in a reasonably coordinated manner. The cause of the injury remains unknown; however, the fact that this young female produced three clutches of eggs within a span of 200 days may have contributed to metabolic bone disease.

In 2006 and 2007, four more clutches of four to six eggs (two clutches per year) were produced. This female produced another clutch of four eggs in early August 2008, but then died unexpectedly one week later. Eggs from the clutches produced between 2006 and 2008 lacked any signs of viability.

Egg deposition by the second animal

The second female produced its first clutch at 32 months of age. One month prior to laying, it measured 44 cm SVL and ca. 100 cm TL, and had a body mass of 2.95 kg. This animal was clearly older and larger than

Fig. 7. This fully developed embryo came from the clutch of my first animal from December 22, 2004. Clearly visible are the absence of eyes and the shortened upper jaw.

Table 2. Clutch data for the second female *V. panoptes*.

Date of oviposition	Clutch size	No. eggs incubated	Incubation period (d)	Remarks
17 May 2009	11	4	174	One fully developed dead embryo with no visible malformations; egg yolk was not completely absorbed
27 Jul 2009	11	2	-	Laid 71 days after previous clutch; egg mass was 534 g
23 Aug 2009	9	2	196	Laid 27 days after previous clutch; egg mass was 484 g; 1 fully developed dead embryo with no visible malformations; egg yolk was not completely absorbed
3 Jul 2010	11	3	196 - 225	All eggs contained fully developed dead embryos with no visible malformations; egg yolks were not completely absorbed
8 Sep 2010	8	3	212*, 95 - 218	One live offspring hatched

* *incubation period for live hatchling*

the previous lizard at the time of its first clutch. Data for clutches produced in 2009 and 2010 are listed in Table 2.

Following the third clutch of 2009, which was laid only 27 days after the second, the husbandry of the female was modified. The amount of food offered was reduced from about 30 cockroaches a day to 5 to 15 crickets, cockroaches or giant mealworms per day. The female was also encouraged to chase these food items, which were offered from long forceps (Fig. 8). The animal had to chase the food until nearly reaching exhaustion. As soon as the monitor's effort in chasing the food decreased, the feeding was stopped. This was done in a manner to exercise the animal and enhance its physical fitness on daily basis. For subsequent clutches, only small rations of food were offered following egg laying. It was believed that this reduction in dietary intake following egg laying could increase the amount of time between subsequent clutches.

On 3 July 2010, a clutch of 10 eggs with a total mass of 543 g was laid (Fig. 11 & 12). Three of the eggs were white in color, turgid, and appeared fertile, weighing 67, 68, and 73 g, respectively. These eggs were transferred to an incubator, whereas the remaining seven did not appear to be viable and were discarded. An additional egg was found with the feces of the female on 9 July. All three eggs incubated for 196-225 days before they began to deteriorate. Upon dissection, it was discovered that each egg contained developed embryos which had died shortly before hatching.

On 8 September 2010, a second clutch of eight eggs was produced, weighing a total of 414 g. Shortly after producing this clutch, the female measured 50 cm SVL and 110 cm TL, and weighed 2.3 kg. Three eggs from this clutch (65, 64, and 63 g) appeared fertile and were transferred to the incubator. They initially developed well, but one egg began to deteriorate after 95 days. Upon opening this egg, a small embryo was visible. Egg number two began to sweat and was opened after 218 days. It contained a dead, fully developed embryo which still had a fairly large yolk sac remaining. After 212 days of incubation, the remaining egg hatched on 8 April 2011 (Fig. 13). The hatchling had a SVL of 12.0 cm, a TL of 27.5 cm, and a body mass of 29 g. A large yolk sac was still attached (Fig. 14). After 94 days, the juvenile had grown to 15.5 cm SVL and 37.5 cm TL, with a body mass of 88 g.

Incubation

Eggs were incubated in a commercially available BRUJA 3000/REP® incubator, where temperatures ranged from 28-29 °C. Vermiculite (medium grade), mixed equally with water by weight, was used as an incubation medium. Eggs were placed in individual 600 ml plastic containers and partially buried to approximately half their diameters. Six water channels within the incubator were kept filled during incubation

Fig. 8. To promote exercise, the second female *V. panoptes horni* was encouraged to chase food items offered from forceps.

Figs. 9 & 10. A dead, fully-developed embryo produced by the second female. No external abnormalities are visible.

Fig. 11. The second female shortly after egg deposition on 3 July 2010.

Fig. 12. Nine egg clutch produced by the second female on 3 July 2010. Three embryos developed, but died prior to hatching.

Fig. 13. Successfully hatched parthenogenetic *V. p. horni* on 8 April 2011.

Fig. 14. A large amount of residual yolk remained inside the egg following the hatchling's emergence.

Fig. 15. The parthenogenetic offspring seven days after hatching.

Fig. 16. The parthenogenetic offspring at the age of 50 days.

Fig. 17. The parthenogenetic offspring at 261 days old.

to help maintain a high level of humidity. Allowing the incubation medium to become too wet may have contributed to one egg bursting. Eggs that did not hatch became moldy, displayed flecks of discoloration, or collapsed.

There was clearly an increase in egg viability with both clutches produced in 2010. This may be the result of modifying the female's husbandry (reduced feeding and increasing physical exercise). Both embryos produced by the first female showed similar cranial deformities, whereas the seven fully-developed embryos from the second female had large residual yolk sacs.

Sex determination of four embryos

Three embryos from the 3 July 2010 clutch, and the fully developed embryo from the clutch laid on 8 September 2010 were stored in alcohol and subsequently dissected to verify their genders. These investigations, however, were inconclusive. Neither testicles nor ovaries could be positively identified within the abdomen, and none of the embryos displayed fully-everted hemipenes. Furthermore, the size and form of the hemipenal pouches at this stage of development were similar to those of hemiclitoral pouches, making sex determination not possible.

Parthenogenesis in the genus *Varanus*

Both female *V. panoptes* in this study did not have any contact with males after they were purchased, although the first animal was acquired as a subadult (ca. 8 months in age). According to Paden (2008), copulation has been observed in *V. panoptes horni* as young as 186 to 202 days old, with oviposition taking place just 23 days later. The female described in Paden (2008) had a SVL of 29.8 cm. The first female in the present study was purchased at an age of 245 days, but was only 20

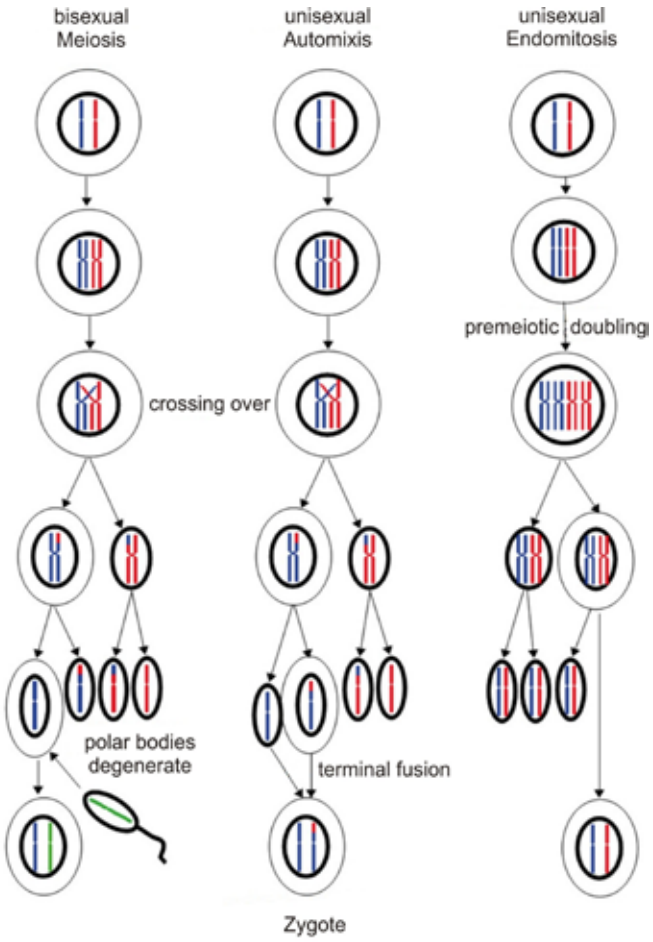

Fig. 18. Chromosomal development during sexual and asexual reproduction (after Lenk *et al*., 2005).

cm SVL. Given this smaller size and the fact that its first clutch was laid 463 days after purchase (on December 21, 2004), it is unlikely that copulation and sperm storage (amphigonia retardata) had occurred while at the pet shop. Therefore, it is likely that parthenogenesis was responsible for the development of both embryos produced by this female. Since the second female was only a few days old when purchased, parthenogenesis is also the most likely explanation for the development of embryos in eight of its eggs.

In recent years, reports of parthenogenesis in *V. panoptes horni* (Lenk *et al*., 2005), *V. komodoensis* (Watts *et al*., 2006), and *V. ornatus* (Hennessy, 2010) have been published. Several parthenogenetic *V. komodoensis* eggs were viable and actually hatched. A single offspring was reported for *V. panoptes horni*, whereas all *V. ornatus* embryos died within their eggs. Surviving offspring from Lenk *et al*. (2005) and Watts *et al*. (2006) were genetically examined, and the resulting data determined that the DNA from these hatchlings was not identical to that of their mothers. They were, however, very similar to the mother genetically, and all offspring were male. Genetic examinations have not been performed on the two parthenogenetic *V. ornatus* embryos described by Hennessey (2010) nor the ten potentially parthenogenetic *V. panoptes* specimens described in this article. All known cases of parthenogenesis in monitor lizards have occurred in captive situations where a male was not present. In only two reported cases have the same parthenogenic females also successfully reproduced sexually at a later date (Lenk *et al*., 2005; Watts *et al*., 2006).

Genetically examined parthenogenetic monitors have been found to be automictic with terminal fusion (Lenk *et al*., 2005; Watts *et al*., 2006). The most prevalent form of parthenogenesis in reptiles, however, is endomitosis (see Fig. 18). In endomitosis, the resulting offspring are all female and very similar to their mothers genetically. This form can be found in some populations of Gekkonidae, Teiidae and Lacertidae (e.g., *Darevskia "armeniaca"*), and is the most common form of propagation in these taxa (Lenk *et al*., 2005; Kearney *et al*., 2009). The observable breakdown of meiosis during endomitosis may be caused by the hybridization of closely related species (Kearney *et al*., 2009).

During automictic parthenogenesis, meiosis proceeds in a normal manner, which results in a haploid ovum capable of fertilization (Fig. 18). A diploid zygote forms through fusion with a polar body, which is generated during meiosis. Automixis is therefore a kind of self-fertilization, and it is possible that the absence of a male might induce this phenomenon (Lenk *et al*., 2005).

The male gender of the examined offspring might be explained by the type of sex chromosomes present in monitor lizards. King & King (1975) indicated that gender is genetically fixed in several species of *Varanus* and that this condition is very likely identical in all monitors. Many reptile and bird species lack the X- and Y-sex chromosomes seen in humans, and instead have a system of W- and Z-sex chromosomes in which females have WZ chromosomes and males have ZZ chromosomes. During automictic parthenogenesis with terminal fusion, both sex chromosomes originate from the female's chromosome set, and therefore only two variations are possible (WW or ZZ). Although zygotes with two W-chromosomes are not viable, zygotes with two Z-chromosomes can develop, producing males.

In 1952, two American agricultural researchers discovered that some level of development (*e.g*.,

membranes, blood, embryos) occurred in about 17% of unfertilized turkey eggs, although larger embryos developed in only about 0.2% of eggs from the 1952 breeding season (Olsen & Marsden, 1953). Given this discovery, a breeding program was initiated to increase the occurrence of parthenogenesis in turkey eggs. By 1962, over 40% of incubated eggs showed some form of development, and well-developed embryos were seen in 13% of the eggs (Olsen, 1965). However, only 94 chicks hatched out of the 8,519 eggs incubated, and only 25% of these hatchlings survived. All chicks raised were males, because gender in turkeys is fixed by a WZ- sex chromosome system. Some of these offspring were even able to produce viable sperm. This example of parthenogenesis in turkeys can be applied to monitor lizards since the reproductive biology, fixation of gender, and relating matters are similar between birds and monitors as well as many other reptiles.

The costs of parthenogenesis

The main advantage of sexual reproduction is that it produces offspring with largely heterogenetic information which can better enable populations and species to adapt to changing environmental conditions. But sexual reproduction also has significant disadvantages. For instance, males, which in most cases are only sperm donors, are competitors with their own siblings, females, and offspring in the fight for resources (*e.g*., territory, food). Offspring resulting from endomitosis, the most common form of parthenogenesis in reptiles, obtain their genetic information from their mother. Because the heterogeneity from one generation to the next will not decrease, this form of parthenogenesis can easily replace sexual propagation, and can be the predominant mode of reproduction for more than 100 generations (Kearney *et al*., 2009). Nevertheless, endomitosis is rarely found in nature. Since the genetic information will not change from one generation to the next, existing DNA-defects probably cannot be repaired (Archetti, 2004). Adaptation to abrupt environmental changes is also highly unlikely, because individuals from such a population have nearly identical gene pools.

Automixis is very rare among vertebrates, and this phenomenon has only been observed in some lizards, birds, and sharks under artificial conditions, where male animals were absent (Schuett *et al*., 1997; Olsen, 1965; Feldheim *et al*., 2010). Offspring resulting from this form of parthenogenesis only acquire genes from their mothers; therefore, the majority of these genes are homozygous. Harmful recessive mutations, which could be masked in the heterozygous condition, could become homozygous and operative. The decrease in fitness observed in turkeys (fertility, infection resistance, life expectancy, etc.), for example, also occurs with the inbreeding of mice after four to twelve generations (Bowman & Falconer, 1960). In the case of automixis, this decrease happens in just one step (Watts *et al*., 2006). Offspring mortality could be very high, as demonstrated in the above mentioned turkeys. It can be assumed that viable offspring resulting from automictic parthenogenesis may coincidentally have a reduced amount of harmful recessive mutations. This reduction of recessive and harmful mutations can be beneficial since it constitutes a purging of the genetic load (Crnokrak & Barrett, 2002). However, the negative impact of recessive mutations in large and heterogeneous populations is negligible.

Offspring resulting from a mating between a mother and one or more of her parthenogenetic sons can decrease the genetic diversity by 50–60% (Hedrick, 2007). This result could have a negative impact on the ability of small populations (*e.g*., Komodo dragons) to adapt to changing environmental conditions.

Discussion

With automictic parthenogenesis documented in three different species of monitor lizard, it is possible that all female monitors possess this ability. Over the past several decades, this form of facultative parthenogenesis has been discovered in several different vertebrate groups (*i.e*., monitor lizards, rattlesnakes, garter snakes, turkeys, sharks), and it is possible that many other reptile genera possess this ability. Aside from long-term sperm storage, parthenogenesis could also explain the production of viable eggs or offspring when mating has not taken place in months, or even years.

The viability of automictic offspring appears to be significantly limited. The most important potential benefit of automictic parthenogenesis may be the ability to colonize new insular habitats, reached by unfertilized females. In the case of monitor lizards, such a female could produce a male companion for itself, or for other females arriving at the same location in the future, through parthenogenesis. Following this, normal sexual reproduction could increase the population size. The inevitable loss of genetic diversity could be compensated with more individuals migrating to this isolated population in the future. The ability to reproduce through automixis may be increased by target-oriented breeding programs. In contrast to *V. panoptes* or *V.*

ornatus, parthenogenetic offspring from *V. komodoensis* may have a higher viability. *Varanus komodoensis* may have used this form of reproduction in the past while populating other islands in its current distribution.

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