

Virgin birth, genetic variation and inbreeding

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Watts *et al.* (2006) and Chapman *et al.* (2007) recently reported facultative parthenogenesis in Komodo dragons (*Varanus komodoensis*) and hammerhead sharks (*Sphyrna tiburo*), respectively. In both cases, the parthenogenetic events resulted in progeny homozygous for all loci, suggesting automictic parthenogenesis with terminal fusion and no recombination (Lenk *et al.* 2005). The genetic consequences of this type of parthenogenesis are analogous to intragametophytic selfing in plants (for the population genetics of this system, see Hedrick 1987*a,b*). For the hammerhead shark, Chapman *et al.* (2007) concluded that females are XX and males are XY and that both the mother and her parthenogenetic offspring were XX females. On the other hand, in Komodo dragons, females are ZW and males are ZZ (Watts *et al.* 2006) and the mothers were ZW and all their parthenogenetic progeny were ZZ males. Both reports suggest that facultative parthenogenesis could potentially be adaptive when no male mates are available but that it may also have negative consequences and lower genetic variation in populations of endangered species.

To examine this situation, assume that the frequency of allele A_i is p_i and that frequency of heterozygotes (A_1A_2) in the unmated female mother is $2p_1p_2$. Parthenogenetically produced offspring from an A_1A_2 mother are expected to be $1/2 A_1A_1$ and $1/2 A_2A_2$ (when she is homozygous, her progeny are homozygous and identical to her). Let us first examine the situation in the hammerhead shark where the progeny are all female XX. When there are n independent parthenogenetically produced female offspring from a single female, then their expected heterozygosity (because there are no actual heterozygotes, this is called diversity) is $2p_1p_2(n-1)/n$. For example, if there is only one offspring, then the diversity is 0, illustrating the combined effect of both automictic parthenogenesis and sampling. If there are two offspring, then the diversity is p_1p_2 , still $1/2$ that in the mother's population. Of course, this diversity is over multiply parthenogenetically reproduced homozygous females rather than in a population of breeding individuals. Finally, if there is one parthenogenetically produced female and she eventually mates with a random male, the expected heterozygosity in their offspring is p_1p_2 , reflecting the homozygosity in the female offspring.

Now, let us examine the situation in Komodo dragons where the parthenogenetically produced progeny are all ZZ males. Of course, these sons cannot reproduce parthenogenetically but they can potentially mate with their mother and subsequently establish a

breeding population. If the female is heterozygous and a son is A_1A_1 , then their progeny are $1/2 A_1A_1$ and $1/2 A_1A_2$, and $p_1=0.75$. As a result, the diversity is reduced from $2p_1p_2$ in the mother to $3p_1p_2/4$ in the progeny of the mating between the mother and her son, a 62.5% reduction. If she mates with multiple sons, then the diversity in their progeny is expected to approach p_1p_2 , still a 50% loss.

This type of parthenogenesis can also result in purging of detrimental genetic variation, a potentially positive outcome (Hedrick 1994). For example, assume that genotype A_2A_2 is lethal. In this case, the only viable offspring from an A_1A_2 female are A_1A_1 . Therefore, the frequency of the A_2 allele is reduced from p_2 in the population to 0 in her progeny, and the genetic load from lethals is eliminated. To examine purging in Komodo dragons, again assume A_2A_2 is lethal so an A_1A_2 female would only have A_1A_1 sons. Therefore, the frequency of the A_2 allele is reduced from $1/2$ in the mother to $1/4$ in the progeny of the mother and her sons, and the genetic load from lethals is halved.

However, when the female is heterozygous for multiple, detrimental variants, automictic parthenogenesis may result in a low probability of viable offspring and greatly reduce the likelihood of a descendant population. If there are m heterozygous lethals in the female, then the probability that each offspring is viable is only $1/2^m$. For example, with $m=3$, only 12.5% of the progeny would be expected to be viable.

The recently documented parthenogenesis in hammerhead sharks and Komodo dragons may be expected to result in both a substantial loss of genetic variation and in purging of genetic load in descendant individuals. It is not clear how common this type of parthenogenesis is, because even other reptiles vary greatly in types of parthenogenesis (Schuett *et al.* 1997; Lenk *et al.* 2005). Further, in fishes, there are a number of different sex-determination mechanisms (Mank *et al.* 2006) and it is even possible that a ZW system could produce viable, parthenogenetic female WW offspring when there is not a fully developed sex chromosome system. For the Komodo dragon, it appears that a single female and her male progeny could start a population, which would have both lowered genetic variation and genetic load. Unknown parthenogenesis in captive populations could result in unexpectedly high inbreeding, loss of genetic variation and changes in founder contribution.

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