

Inbreeding depression and its effects on captive *Uroplatus* populations



F1 captive-bred *Uroplatus henkeli* nesting (top) and depositing eggs (inset).

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Introduction

Over the last two decades the number of rare and endangered Gecko species being kept in captivity has risen sharply. Associated with this rise has been a similar increase in the level of understanding of basic husbandry issues and the environmental factors affecting the survival of these species. Testament to this achievement by

'hobbyist' keepers is the switch in organization of captive breeding programs from being exclusively the realm of zoos and research institutes, to a more diverse group. There is now a move towards organized captive breeding programs between non-professional organizations, with private keepers uniting to further the understanding of, and the survival of rare species in captivity. This development is not without its potential pitfalls however, a lesson which countless captive breeding programs from history have learned the hard way. With a new breed of private keepers working together, it is more important than ever to create breeding programs which will be not only scientifically sound, but will also stand the test of time.

Perhaps one of the most affected genera in the Gekkonidae is *Uroplatus*, a genus of species endemic to Madagascar. This genus represents a monophyletic group, the taxonomy of which is the subject of frequent changes, with new species identifications occurring with relative frequency over the last 200 years. Unfortunately, the cryptic nature of these species makes morphological identifications difficult, especially as the amount of variation between species is often confused with intra-species variation.



Uroplatus henkeli.

DNA analysis is going some way to identifying new species, but the sheer extent of population level variation and current subspecies classifications makes for confusing reading. It is perhaps unsurprising that the main threat to *Uroplatus* sp. in the wild is deforestation to make way for coffee plantations. This is having a profound effect on population numbers, with species such as *Uroplatus henkeli* now surviving at very low densities. The plight of *U. henkeli*, and other species within the genus has been recognized by both CITES and IUCN with protected species status being granted. With this in mind, it becomes more important than ever that scientifically sound captive breeding programs are initiated for this, and other species within this genus.

Inbreeding theory

The long-term detrimental effects of prolonged inbreeding have been well documented in both captive and wild populations for many years (Darwin, 1868; Wright, 1977). Early work on Mendelian genetics developed our understanding further, with inbreeding leading to increased homozygosity and a resultant decrease in fitness being termed “inbreeding depression” (Lerner, 1954). The effects of inbreeding and selection have been studied intensively for many decades (Haldane, 1937; Reeve, 1955; Charlesworth & Charlesworth, 1987) and yet the consequences of

the joint application of these two evolutionary processes are still relatively poorly understood. Undoubtedly the reason for this is the array of complex interactions, which are apparent when combining the two processes in different situations. Further to this, the effects of inbreeding and selection are poorly understood when populations become extinct as a result of these processes. It is exactly this complex situation that small captive populations of endangered species face, with inbreeding being a ‘necessary evil’ the ultimate goal of which is avoiding extinction.

The genetic goals of these captive breeding programs are to avoid inbreeding depression, and to maintain genetic diversity (Hedrick & Miller, 1992). Franklin (1980) attempted to provide a base-level population size estimate that would avoid the detrimental effects of inbreeding for captive populations. His theory suggested that breeders would need to accept inbreeding coefficients (the proportion of loci at which an individual is homozygous) of around a one per cent increase per generation. By this logic the effective population size (N_e) would need to be 50. This logic behind this theory would suggest that a relatively slow rate of inbreeding would allow selection to remove any deleterious alleles without affecting the fitness of the population.



Uroplatus henkeli.

Somewhat converse to this idea, Templeton & Reid (1984) suggested that a rapid and effective reduction in inbreeding depression could be achieved through an appropriate breeding program. There have been various interpretations of this theory, with the most parsimonious being that deliberate inbreeding can be used to purge a population of the deleterious alleles responsible for inbreeding depression. This is due to the creation of selective conditions, which can favor individuals with certain genes or gene combinations that do well under conditions of inbreeding. However, for this to work there are several requirements.

- 1: Sufficient inbreeding must occur to create the proper selective conditions (but not so intense as to kill off most individuals), and
- 2: Sufficient genetic variation is carried over into the founder population, so that the animals can genetically respond to the selective conditions induced by inbreeding.

Furthermore, it has been suggested that natural populations can become effectively adapted to inbreeding because of the selective elimination of detrimental alleles (Lacy, 1992). This theory would then predict that after a period of either very small population size or substantial inbreed-

ing, there will be a reduction in detrimental alleles remaining in the population, with any further inbreeding not resulting in a decrease in population fitness. If these theories are true, then purging captive populations of animals with reduced fitness becomes extremely important to the success of any breeding program.

Concerns for captive breeding programs

Avoiding inbreeding depression in captive *Uroplatus henkeli* populations (among others) by either method

would not be without its pitfalls. There are several potentially negative consequences of purging within captive populations that will undoubtedly be of major concern for those who work with both *U. henkeli* and other endangered species. As the wild population is very limited, the main concern is preventing this population from reaching extinction. This makes the rate of purging, and the increased risk of extinction this leads to, of the utmost importance.

During the process of purging in the captive environment, increased homozygosity may reduce the fitness of the population, adding to the potential risk of extinction. Furthermore, detrimental alleles may become fixed in the population, which would effectively permanently alter the fitness of the population, again increasing the long-term prospects of extinction. There is circumstantial evidence of this happening in some captive lines.

Purging of individuals with reduced fitness may also effectively reduce variation at other loci, which again will have the result of reducing the effective population size, and could prevent future adaptation potential. This means that there are clear advantages in eliminating a large part of the genetic load (a measure of the cost of alleles lost due to selection) of a species in a short period. This benefit may be outweighed by a long-



term risk of extinction or reduction in adaptation potential.

Inbreeding depression presents a real concern for captive breeding programs, and the creation of a viable breeding program that will not lead to the long-term reduction in fitness of the species with which it is concerned is clearly of the utmost importance. For this reason, basing your breeding program on the correct type of data becomes essential. Many captive breeding programs sponsored by zoos rely heavily on pedigree analysis; however, estimating relatedness of individuals with no prior knowledge of their genealogy can be difficult. This is the problem faced by many species without a long history of captivity in a controlled environment. In incidences like this, molecular markers (polymorphic loci which allow determination of relatedness) can make a very valuable contribution to the creation of a breeding regime.

In the simplest of terms, genetic data can resolve issues such as unknown parentage. This can be

Captive-bred *Uroplatus henkeli*.

very useful if an incomplete pedigree is available. In situations where no pedigree is available for a species, molecular markers can be used to estimate the pair-wise relatedness between an individual and the rest of the population.

While most captive breeding programs assume that the founder individuals are unrelated, being wrong about this could have profound effects on the program's ability to maintain genetic diversity over a long time period. A marked increase in inbreeding in early generations, above what is factored into the program, due to full sibling mating can effectively reduce genetic diversity and fitness in very few generations (Rudnick & Lacy, 2008). For this reason, early use of molecular methods may overcome this potential obstacle, by allowing the avoidance of breeding closely related animals, and effectively reducing the amount of inbreeding that would be accumulated relative to wrongly assuming that the founder individuals were unrelated.

For captive breeding programs with no pedigree available, the use of microsatellite markers (rapidly evolving polymorphic loci within the genome) could lead to an improvement in captive management in the following ways: 1) resolve unknown parentage among contemporary breeders; 2) allow molecular estimates of kinship to inform future breeding recommendations; 3) give a clear understanding of the effective population size; and 4) allow the creation of an accurate stud book.

Merging molecular markers and an effective breeding schedule

The use of modern molecular techniques for captive breeding programs is seen by many as essential for the further development and propagation of a host of Gekkonidae species currently in captivity, not least those species contained within the genus *Uroplatus*. Clear guidance delimiting relatedness of individuals will allow for the founda-

tions of a breeding schedule to be created. However, this technique should never be considered a stand-alone. Careful scheduling of breeding individuals is as important as ever, especially when effective population size is small. Determination of effective population size becomes very important in these circumstances, and this will directly affect decisions for propagation, and with this the criteria for purging, which will be needed for small populations. The increase in the accuracy and application of modeling techniques should allow a mathematical approach to a breeding schedule based on genetic data. This will allow an insight into multiple generations of offspring, and the theoretical deleterious genetic load, even before two individuals have been introduced. These technological advances really do take much of the uncertainty out of captive breeding programs, and should allow more statistically sound decision making regarding pairings, effective population size, deleterious allele burden, and purging.

Discussion

There is continued debate over the most effective method to eliminate inbreeding depression, or reducing inbreeding burden to a manageable level. Templeton & Read (1984) suggested that inbreeding depression could be rapidly reduced by the use of a suitable breeding program, and that inbreeding depression does not have to be a barrier in species where inbreeding cannot be avoided. Conversely however, Barrett & Charlesworth (1991) concluded that a program, which aimed to purge inbreeding depression, could effectively decrease population fitness, with little recovery under inbreeding. The apparent discrepancy here however could be due to the rate and extent of inbreeding in the populations themselves. This again highlights the necessity for an accurate understanding of the effective population size for each species.

One thing that becomes clear is that no single breeding program should be applied to every



Captive *Uroplatus henkeli* mating.

species in captivity. There are a great number of species currently involved in breeding programs around the world that potentially face serious negative consequences if we, as herpetologists, fail to use the most appropriate methods to ensure not only species survival, but also healthy captive individuals.

Uroplatus henkeli has been bred in captivity for over 15 years, but resultant generations have experienced a drastic reduction in fitness characterized by a dramatic SVL reduction. It really is imperative that we, as a community, do everything possible to address this situation, and aim to halt the fitness reduction in captive populations. This is not something that will happen overnight, but it is certainly something that everyone should consider before we simply breed two individuals together. The future of the species really is under pressure.

It is also important to note at this point that although *Uroplatus* sp. are CITES II listed, and many appear as “vulnerable” on the IUCN Red List, their popularity in captivity is driving the illegal trade in wild-caught animals. I cannot stress enough how this trade must be stopped. If we reduced the wild population below its current levels it may become non-viable, which will undoubtedly lead to the loss of many beautiful species forever.

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