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Breeding amphibians in captivity

[Plates 6–8]

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THE PARADOX

Amphibian breeding represents one of the most puzzling paradoxes of animal reproduction. It is an area where insight converges with ignorance. So much of what we know about the general mechanisms of reproduction and fertilisation has been developed using amphibian materials that to cite the literature of amphibian reproduction we need simply to refer to any one of the current textbooks on developmental biology.

At the same time, the controlled reproduction of even so common an animal as the American bullfrog *Rana catesbeiana* remains beyond our grasp. It is still impossible with any degree of accuracy to forecast procedures for breeding an untested amphibian species. Although the problems are currently under examination (Rabb, 1973; Lofts, 1974), we cannot at this stage make a reliable prediction as to which will respond to a generally effective hormone – such as human chorionic gonadotrophin – and which may require a hormone unique to its species. Since a knowledge of hormonal responses is critical to the control of both natural fertilisation and artificial insemination, this is a line of research which the prospective breeder is well advised to follow.

When we recall that long before the technique came into wider use, artificial insemination using amphibian materials was routine practice among developmental biologists (Rugh, 1935, 1965), it is pertinent to ask why the methods for maintaining viable frozen amphibian sperm remain to this day undeveloped. Artificial insemination in its application to the breeding of rare and endangered species has outstanding advantages. It may be used to induce reproduction in species which are unfamiliar to the breeder and whose normal courtship patterns are unknown. Furthermore, should an appropriate ♂ be unavailable when a gravid ♀ is at hand, a ready stock of frozen sperm offers an effective solution. There is every reason, as Francoeur (1975) recommended, why artificial insemination should be adapted and applied to policies for the conservation of threatened and sparse populations.

With the possible exception of fish, probably in no other class of vertebrates has purposeful fertilisation of eggs been performed in so many genera as among the amphibia. Yet again we meet the paradox that until only a few years ago it was only the Mexican axolotl *Ambystoma mexicanum* and the African clawed frog *Xenopus laevis* which had undergone sustained captive breeding. Even now the species reproduced with any regularity can be counted on two hands.

Once breeding has been established, however, progeny beyond the needs of captive use should be returned to nature. Is this possible? Amphibians in fact offer good, if perhaps undesirable, examples of both intentional and accidental introductions into new habitats by human activity (Campbell, 1974). For instance, *R. catesbeiana* has been introduced into California, Japan and Taiwan; *Bufo marinus* into Florida and the Pacific islands; and *X. laevis* into California (St Amant, 1975). On the other hand, in the way of specific guidelines, either for maintaining threatened populations (Wright, E. J., 1975), for restocking areas where healthy populations once existed, or for extending populations into apparently favourable habitats (Campbell, 1974;

Zimmerman, 1976), there is relatively little material.

Two attempted introductions known to the author have not been reported elsewhere. One involved transplanting adult genetic mutants of *Rana pipiens* (var. 'Burnsi' and 'Kandiyohi') from a Wisconsin into a Vermont population. Although mutant individuals were sighted over a period of three years, there were no progeny, apparently because the adult implants were not able to follow the migration paths of the native *R. pipiens* to and from breeding and hibernation sites (Mumley, pers. comm.). In the other case, tadpoles of these same dominant Wisconsin mutants were placed in the breeding sites of a threatened Michigan population of the species. Either the number of tadpoles released – several thousand – was not enough, or other factors prevented a 'take'; no mutant juveniles were ever found (Rittschoff & Nace, unpublished).

THE PROBLEM

Clearly, pragmatic and empirical methods have led to some success. Unfortunately, when numbers drop below a critical level, empiricism is a luxury that a threatened species cannot sustain, and we are obligated to follow practices which are based on a solid foundation of theory. It is only now, however, that ecological, physiological and genetic theories are being applied to the preservation of threatened species (Campbell, 1974; Zimmerman, 1976), and so far as amphibians are concerned, such application has received no attention whatsoever.

This omission is hardly surprising when one takes into account the appalling variation of reproductive modes among the amphibia. J. W. Wright (1975), referring to studies by Crump (1974), neatly summarised the variability when he noted that for 81 of the 2800 living species in 285 genera of anurans, Crump

'... found the following reproductive modes:

1. Eggs deposited in ditches, puddles, swamps, ponds, lakes and streams; tadpoles in water – 34 species.
2. Eggs deposited in tree cavity above ground; tadpoles develop there – one species.
3. Eggs deposited in constructed basin of water on ground; tadpoles develop there – one species.
4. Eggs deposited on vegetation above water; tadpoles hatch and fall into water where they develop – 14 species.
5. Eggs deposited in foam nest either on or near water; tadpoles develop in water – six species.
6. Eggs deposited on land; tadpoles carried to water by parent – development occurs in water – five species.
7. Eggs deposited in foam nest on land; tadpoles develop in nest – six species.
8. Eggs deposited out of water; direct development – 14 species.
9. Eggs and young buried in skin pits on dorsum of female; direct development – aquatic – one species.
10. Eggs and young attached to dorsum of female by "gills"; direct development – terrestrial – one species.
11. Mode of reproduction unknown – three species.

Although this list of reproductive modes is impressive, it does not include all of the modes known to be used by frogs. For example, live-bearing frogs are known where complete development occurs within the female and froglets are "born". There are other frogs that brood their eggs and tadpoles in their mouths and in one case brooding takes place in the stomach, where the eggs are swallowed and later small frogs are regurgitated. Contrary to common belief, parental care of eggs, larvae and/or young is widespread and relatively common in frogs'.

And exhaustive as the list may seem, it is only a partial story. It takes no account of the newts and salamanders, and the intricacies of their courtship, reproduction and, indeed, entire life cycles, makes the picture an even more complex one (Arnold, in press).

SUCCESSES AND DEFICIENCIES

The success of the breeding so far accomplished is attributable to three groups: scientists interested in using amphibians as research models (Boterenbrood, 1966; Davidson & Hough, 1969; Kawamura & Nishioka, 1973; Nace *et al.*, 1974) and in studying amphibian biology (Crump, 1974; Arnold, in press); hobbyists fascinated by the diversity and beauty of frogs and the challenge of their varied reproductive modes (Oeser, 1929); and, to a much lesser degree, commercial concerns serving the needs of science and education, as well as those of hobbyists (as in the production of *Hymenochirus*). As far as the author is aware, none of these efforts has been initiated with the express purpose of saving endangered populations, although the potential expansion of commercially significant populations, such as *R. catesbeiana* (USA), *Leptodactylus* (Dominica), *R. tigrinum* (India), is the subject of frequent enquiry. With few exceptions (Rabb, 1973), I know of only incidental attempts by zoos to use reproduction either to maintain their exhibit stocks, or to contribute to the conservation of endangered amphibian species.

Indeed, in their attitude to amphibians in general, zoos appear to have a bad record. Amphibians are usually assigned to reptile or fish houses, and become the stepchildren of curators more interested in the reptiles or the fish. Often there are few concessions made to their amphibian character. The selection of species seems random and exhibits frequently consist of animals received as a 'bonus' with a shipment of other exotics, and of species 'easy' to keep alive in captivity. Local species are seldom shown, and their ecological, commercial, educational, cultural, scientific and biological significance is rarely explained to the public (Conway, 1973). Seldom is there serious effort to illustrate the variety of adaptations developed by these animals – the oldest of the land vertebrates. Seldom are they used to explain to the public biological processes such as reproduction and development, for which science has found them such good models.

As a developmental biologist and educator, I find this hard to understand. With the exception of size, amphibians would seem to offer as exhibits all that a good zoo or aquarium might desire – diversity and beauty; activity both diurnal and nocturnal and, given the right environment, benign but visible behaviour; willingness to take food at almost any time; and great significance in the cultural and religious life of man (Belt, 1975; Brittain, 1975; Emboden, 1975; Sibley, 1975). In a more practical vein, they have also relatively modest space requirements.

There have of course been drawbacks. Although current developments are circumventing these problems, amphibians have often required live food, and their health has seemed precarious. It is small wonder that greater efforts at breeding them have not been made. In addition, amphibian reproduction generally presents difficulties at all stages – during oogenesis, at fertilisation, and during embryonic, larval, metamorphic and post-metamorphic development. What is more, these problems vary from species to species! For a zoo, in particular, the upkeep of the hundreds of tadpoles needed to maintain a viable colony – far too many to be exhibited – is yet another constraint.

There is also a secondary order of difficulty. While in some frogs reproduction of multiple generations is relatively easy, in many other species, such as *R. pipiens*, the process is more complicated. Normal oogenesis and readiness to reproduce is controlled, to a critical degree, by a multiplicity of factors – nutrition, photoperiod, temperature cycles, humidity, and the animal's own temperament. Failure to understand and control these factors has resulted in the failure, in important species, of multi-generational captive reproduction, with an attendant serious loss to science. The reproductive process of amphibians lend themselves to bisexual or parthenogenetic development (Asher, 1970; Nace *et al.*, 1970; Asher & Nace, 1971), cloning, and a variety of other experimental modifications whose application is useful to a deeper understanding of their genetics. Not only can multiple generation breeding improve such understanding. Although the concept of conservation of endangered species – quite rightly – embraces the ideal of preserving the wild type gene pool, the fact that amphibian development and its initiation is so readily adapted to genetic manipulation offers a rich field for the experimental investigator and, at the same time, provides the basis for choosing a gene pool appropriate to the maintenance of the species in question.

GUIDELINES

As breeding procedures will vary according to species and locality, it is not particularly helpful to specify individual routines, and the remainder of this paper will therefore confine itself to outlining the general lines of approach which the author and his co-workers have found effective. Many of these have been detailed in previous publications (Nace, 1968; van der Waaij *et al.*, 1974; Ostrovsky *et al.*, 1976) and brought together in Nace *et al.* (1974), referred to hereafter as *Guidelines*. The material covered will not be reiterated here, but the following notes add to, or update, the published data. It should be pointed out that we regularly conduct multi-generational breeding of *R. pipiens*, *Bombina orientalis*, *Hyperolius* of several species (Richards, in press), *A. mexicanum*, and *Xenopus*. In Japan, Kawamura and his co-workers (Kawamura *et al.*, 1972; Kawamura & Nishioka, 1973) breed a variety of Western Pacific anurans, while in Paris, Gallien (Gallien & Durocher, 1957; Aimar *et al.*, 1974) routinely breeds *Pleurodeles waltl*. There is ample evidence then that, given due attention to detail, the 'laboratory' breeding of amphibians is entirely practicable. Taken with the scattered accounts in the literature of amateur successes, it does suggest that the controlled reproduction of most amphibian species is a feasible proposition.

Housing: Most amphibians are shy. They are ectothermic, which means that they use external heat sources to adjust their temperature. They have photoperiod and temperature cycle requirements. Above all, they vary in their need for water: some species are fully aquatic, some fully terrestrial, and some are truly amphibious. Moreover, their needs for water vary in accordance with seasonal changes in their behaviour. When they are terrestrial, the character of the substratum also becomes important.

The *Guidelines* cover the housing of both adults and tadpoles, but not as it relates to exhibition. Because of the animals' shyness, I would suggest double windows to eliminate sound transmission (especially in the 25–500 Hz range), with a one-way viewing surface to control visual stimuli. Optional 'daylight' and 'dark light' lighting is also advisable. For either holding or exhibit containers, it seems important not to impose prejudged ambient temperatures on the animals. They should be given the option of adjusting their body temperatures (Lillywhite *et al.*, 1973; Kluger *et al.*, 1975). This implies a cool ambient temperature with a localised heat source under which they can bask. Some recent observations suggest that, if provided with a platform activating a microswitch, some species, at least, may learn to adjust their own lighting and temperature. All of these purposes are partially served by providing suitable hideaways.

As regards water depth, one must recall that amphibious frogs seek water to escape stress, to exercise, and to rest. The resting position is with eyes and nose above water, with fore- and hindlimbs extended. Shallow water is like short-sheeting a bed! We find a multi-tiered container ideal. The bottom has relatively deep water with crockery extending above the surface, and the animals can choose the water or move to the crockery or higher terrestrial tiers. From the exhibition standpoint, frogs in the aquatic area are most pleasing. We successfully maintained for four months a mixed exhibit of *R. pipiens*, *B. orientalis* and *R. palustris* in such a multi-tiered container measuring $50 \times 13 \times 25$ cm high (Plates 6–8).

For stock holding purposes, a series of new, highly adjustable containers are at present being developed in our own laboratory and that of Dr Culley (Nace *et al.*, 1974), and should be ready for general use within a few months. As well as incorporating the features already described, they are designed to minimise maintenance and space requirements.

As losses at metamorphosis can be very high, a word on handling juveniles is appropriate. At this stage, species such as *R. pipiens* disperse quickly from their ponds into open fields (Rittschoff, 1975), jumping vigorously as they leave the water. As soon as forelimbs appear, it is thus advisable to move the juveniles to spacious adult-size containers, with no more water than the trickle from the input line to the drain; until the tails have disappeared it is essential that this water should not be chlorinated. Juveniles should not, however, be forced to undergo a triple shift from small 'tail absorption' to 'feeding initiator' and then to 'adult' containers. By avoiding such excessive shifts, we ourselves have reduced losses by 90%.

While there is no evidence that frogs 'scent' their containers, they do seem to become attached to specific familiar surroundings. Our observations are in accord with those of Kingston (1975), working on marmosets, who suggested that when cages are 'changed for cleaning purposes, at least some part ... should be left unchanged. The habit of "sanitizing" everything ... with gallons of highly scented disinfectants is ... undesirable.' This stricture applies to adults as well as juveniles. Although we do not know the biological basis for the attachment, there are grounds for believing that in frogs at least it may relate to some aspects of the pattern of bacterial colonisation (van der Waaij *et al.*, 1974) and defence (Ostrovsky *et al.*, 1976; Ostrovsky & Nace, 1976).

Nutrition: While it is premature to dogmatise about amphibian nutrition, some speculation may be of value. The common belief has been that amphibians are opportunistic feeders, but this is evidently an over-simplification (Cott, 1940). It is more likely that the nutritional requirements of these animals are carefully attuned to the sequence and frequency of their encounters with various arthropods and other food items in the wild, and to the avoidance of distasteful insects, bees, etc. Thus the dietary requirements of a recently ovulated adult may be so adjusted that the food items that she encounters in the spring are precisely those which are necessary for the initial stages of oogenesis. Similarly, the selection of food she meets with in the autumn may contain ingredients essential to the final stages of normal egg maturation.

With few exceptions, such as *B. marinus* which will eat even canned cat food, most amphibians require live food – or at least food which is moving in a correct manner. Although we believe we are close to solving the problem of presentation of non-live food to *R. pipiens*, our experience is incomplete. Consequently, there are no hard data on the nutritional requirements of amphibians, but we have learned some things.

A diet of a single species of arthropod seems ill advised. *R. pipiens* fed on crickets, sowbugs, flies or waxmoths developed quite different absolute and relative organ weights depending on the food items (Lehman, in preparation). Crickets gave the best overall results but in the captive frogs certain organ proportions still varied significantly from those of animals collected in the wild. Frogs such as *Hyperolius*, the African reed frog, develop and reproduce quite satisfactorily on flies alone, but such is not the case for *R. pipiens* (Hejmadi, 1970). Taking all into consideration, a mixed diet seems best. Our focus, however, has been on crickets, since they can be produced in large numbers and their production schedule is readily adjusted to generate a food item of a size appropriate to the amphibian. Just after metamorphosis frogs need small, newly-hatched crickets in quantity, while as they grow larger they feed on intermediate and full-grown ones. Other foods may be used as the occasion demands, but fruitflies and mealworms are uneconomical since many of them die in the highly moist environment of an amphibian container. We find the mosquito *Culex pipiens* (selected because it is easily fed on birds and usually does not carry human or amphibian parasites) easy to raise, well adapted to amphibian containers and useful for young frogs and toads; its larvae are ideal for feeding larval salamanders and newts.

It is hoped that our attempts to feed prepared diets will soon develop sufficiently to allow positive analysis of the nutritional requirements of frogs at different stages in their life cycles and different phases of their egg production.

Records: Almost as important as retaining the genomes of an endangered species, is learning as much as possible about it. Not only does this knowledge facilitate preparations for breeding, in the event of its becoming available, but it is also a permanent record of the biological diversity which, once the species has become extinct, is lost for all time.

I suggest that simple log-book notes and stud records are not enough. The information they contain is often unevaluated and difficult to disseminate, and is seldom on hand when the rare and fleeting opportunity to save and breed an uncommon animal, or to resuscitate a sick specimen, should unexpectedly arise.

Computer hardware and appropriate software is now sufficiently accessible to make this resource available to all. Time-shared, rather than self-owned, facilities are preferable, because they are larger and thus able to handle programmes which are complex in the computer but simple for the user. We described the system we use, called Taxir (Taxonomic Information Retrieval), some years ago (Nace *et al.*, 1973). In the one programme is handled information retrieval and manipulation on demographics, morphometrics, pathology, animal management routines, animal location, correspondence files, sales and accounts, and most other types of alphabetic or numerical information. Since it was described in 1973, it has been greatly improved in respect of both cost and ease of utilisation. Our assistants can start to ask it questions within hours of first introduction and become 'expert' with minimal experience. We can print out a full directory for the location of all 5000 living animals in our standing colonies, with information on the identity of each individual, for approximately $2 per print-out. The expense is thus minimal. Our computer at the University of Michigan is accessible to anyone in the world with a telephone line and a cheap teletype terminal. A similar programme could easily be run on the MTS operating system of the computer at Newcastle-upon-Tyne, in England, and other programmes, which can function on other computers, are also available. There is no need to hire a computer programmer as a permanent member of staff.

We find that information input to the computer is no more time-consuming than it is for a good log-book. Assistants soon learn to take improved pride in the accuracy and completeness of their records because the information is used by others and there is a feedback. While the adage 'garbage in, garbage out' may still be valid, it might be more pertinent to declare 'garbage in, garbage identified'.

Given the will and the assumption of responsibility by a concerned individual, a few basic resources, and sufficient and accurate information, we believe that it is possible to breed amphibians for all purposes – scientific, educational, display, restocking and commercial. The guidelines here described apply both to the breeding of common and of rare and endangered species.

ACKNOWLEDGEMENT

This paper appears as Contribution No. 71 from the Amphibian Facility. The original observations reported here were supported by Grant 1 P06 RR00572 from the US National Institutes of Health.

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Genetic management

[Plate 9]

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At a juncture when most of the species now in zoos are likely soon to appear on the endangered list, the question of genetic management is a timely concern. At the same time it is one which we are singularly ill-prepared to address. At the first Conference on the Breeding of Endangered Species in Captivity, Brambell (1975), speaking of orang-utans, had this to say: 'We need to ensure that the genotype of the species is altered as little as possible by ill-judged selection.... We need to get together and work out how to recognise and eliminate genetic traits that would be lethal in the wild, and then to work out how to allow the remaining genetic pool to mix in captivity much as it might in the wild.'

But the fact remains that for most wild species, sufficient knowledge of their genetic quality (their genotype) simply does not exist. For some indeed, as a careful reading of Dathe (1967) will show, not even the phenotype – the external expression of those genes – has been agreed. In such circumstances, what criteria are we to use in selecting for the 'right' genotype without, as Brambell cautions, degenerating into poodle breeders? This paper aims merely to be an introduction to what is likely to prove an overwhelming task. It is a very personal view of the courses of action open to zoos, and the particular factors governing individual species will need to be evaluated at future meetings. Its emphasis will lie in summarising the few data on wild animals already in our possession; on comparisons with models from domestic species and man; and, primarily, on highlighting those aspects that