



## Implications of Pathogenic Fungi for Life-History Evolution in Amphibians

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### Implications of pathogenic fungi for life-history evolution in amphibians

Pathogens are easily overlooked, and their significance has been repeatedly underestimated during the history of biology as a science, although their profound importance in fields such as population dynamics, population genetics and sexual selection has been recognized in recent years. Pathogenic fungi can have major effects on host populations and community structure (e.g. Carroll & Wicklow 1992; De Rooij Van Der Goes 1995; Carey 1996). However, their importance in amphibian ecology has, until now, been little appreciated.

The infection of amphibian eggs by aquatic Saprolegniaceae fungi is widespread in the temperate world (Beebee 1996). Many authors have assumed these fungi to be saprophytes exploiting embryos that die from other causes (e.g. Tejedo 1992), but recently it has been demonstrated that pathogenic infections of *Saprolegnia* cause high rates of embryonic mortality in some populations of anuran amphibians, and that egg masses laid communally suffer higher mortality than those laid away from other egg masses (Blaustein, Hokit & O'Hara 1994; Kiesecker & Blaustein 1997). Infection can spread either by direct contact through growth of hyphae or by colonization via the free-swimming zoospore stage (Smith *et al.* 1985; Wood & Willoughby 1986).

As far as I know, no one has previously considered explicitly the effects that pathogenic fungi have had on the evolution of amphibian life histories, and no one has previously commented on the effects of pathogenic fungi on the eggs of urodelan amphibians. Among the aquatic urodelans, oviposition in clumps is the primitive condition. Single oviposition appears to have evolved polyphyletically in the Sirenidae and Salamandridae (Duellman & Trueb 1986; Larson & Dimmick 1993). In my opinion, single oviposition may have been selected to reduce fungal infections. Single oviposition appears to reduce embryonic mortality by pathogenic fungi in the Old World newts *Triturus* (Salamandridae), which oviposit singly, wrapping the eggs in the leaves of water-plants (Miaud 1993), although they may lay strings of up to 15 eggs when denied suitable oviposition sites (Bell & Lawton 1975).

Casual observation on *Triturus* newts breeding in aquaria shows that eggs frequently become infected with Saprolegniaceae water moulds, and that the moulds often spread to and kill neighbouring eggs (A. J. Green, personal observation, and J. Baker, personal communication). *Saprolegnia* can also infect wounds in larval and adult salamandrids (Walls & Jaeger 1987; A. J. Green, personal observation). Infected

eggs become covered with a visible crown of white hyphal filaments, and never survive to hatching. Furthermore, experimental manipulation shows that Smooth Newt, *T. vulgaris*, embryos suffer higher mortality when touching infected eggs than when separated from them by 1 cm.

In 1987, I collected female Smooth Newts from Oxfordshire ponds and housed them in aquaria (as described by Green 1991) where they laid eggs singly on nylon stocking material. Individual eggs were often infected by *Saprolegnia*. Two eggs (one infected and one uninfected, identified with the unaided eye) were placed together in each cell of embryo trays. In one experimental treatment, the two eggs were placed touching each other and the cell perimeter. In the other treatment, the two eggs were placed at opposite sides of the cell, 1 cm apart. This 1 cm distance is similar to the distances observed between eggs when females oviposit freely in the laboratory (A. J. Green unpublished data). Egg pairs were randomly assigned to treatments in three groups of 9, 12 and 12 replicates per treatment established on 20 and 30 April and 12 May, respectively (i.e. total  $N = 33$  for each treatment). Uninfected eggs had not passed the neural fold development stage (Horner & Macgregor 1985) when the experiment was started. The development stage of infected eggs was unclear. The embryo trays were kept at room temperature on a natural daylight schedule with 1-cm depth of dechlorinated tap water in each cell. The experiment was terminated when all previously fresh eggs had either hatched or died from fungal infection, which took 6–12 days for each group.

From a total of 33 fresh Smooth Newt eggs for each treatment, 10 healthy larvae hatched from the 'separated' treatment compared with only one from the 'touching' treatment. All eggs that failed to hatch were infected by water moulds. There was no evidence to suggest that infection was not the direct cause of mortality in every case. The effect of treatment on embryo survivorship was highly significant (Yates corrected  $\chi^2_1 = 6.98$ ,  $P < 0.01$ ). There were no significant differences in results between the three replicates ( $\chi^2_2 = 0.68$ , NS).

Thus, single oviposition can markedly reduce cross-infection by water moulds, and healthy embryos are more readily infected by mycelial spread from an adjacent, infected neighbour than by zoospores. The dispersal of eggs in space and time via single oviposition and egg wrapping behaviour in *Triturus* newts have previously been interpreted as strategies to reduce predation (Miaud 1993, 1994). Although egg mortality by predation does appear to be high in the field (Bell & Lawton 1975; Miaud 1993, 1994), I am unaware of any evidence that egg dispersal reduces predation rates, and egg clumping in amphibians can

in fact reduce predation (Kaplan & Sherman 1980; Beebee 1996). It has been shown experimentally that egg wrapping in plant leaves reduces predation of *Triturus* eggs (Miaud 1993, 1994). However, this behaviour may also reduce fungal infections by shading eggs from radiation, since there is a synergistic effect between UV-B radiation and *Saprolegnia* that enhances embryonic mortality (Kiesecker & Blaustein 1995). Single oviposition may also allow eggs to be placed more easily towards the top of the water column, where higher temperatures facilitate more rapid development (Miaud 1994). Faster embryonic development is likely to reduce mortality from both fungi and predation (Banks & Beebee 1988; Beattie, Aston & Milner 1991), although this requires further investigation.

As well as partly explaining the evolution of single oviposition in aquatic urodelans (Duellman & Trueb 1986), embryonic mortality caused by pathogenic fungi has probably been an important selective force driving life-history evolution in other amphibians. In anurans, this may be one reason why females of many species divide their eggs into several small packets separated in time and space instead of laying them all in a single mass (see Duellman & Trueb 1986 for review of anuran reproductive strategies). For example, Pacific Treefrogs *Hyla regilla* divide their eggs into packets of about 25 eggs and suffer much lower mortality from *Saprolegnia* than sympatric populations of Western Toads *Bufo boreas* and Cascades Frogs *Rana cascadae* that produce large egg masses (Kiesecker & Blaustein 1997).

In addition, the repeated evolution of parental egg care in all three amphibian orders (Crump 1995) may partly have occurred to reduce mortality by pathogenic fungi. Even in terrestrial environments, amphibian eggs are attacked by lethal pathogenic fungi (Villa 1979). In both aquatic and terrestrial breeders laying clumped eggs, carers prevent the spread of fungal infections by eating dead eggs (Tilley 1972; Forester 1979; Simon 1983). In terrestrial species, carers move eggs around mechanically, destroying fungal hyphae (Forester 1979; Crump 1995). Oviviviparity and viviparity occur in relatively few species of anurans and urodelans (Duellman & Trueb 1986), and have classically been explained as a means of circumventing predation of eggs and larvae. However, they could also have evolved to avoid fungal attacks on embryos and larvae (Bragg 1958, 1962).

The evolution of the hard reptilian egg shell has classically been explained by the selective benefits of exploiting drier terrestrial environments and by the increase in egg size permitted by the shell (e.g. Carroll 1988). However, I propose that the shell may have originally evolved partly because of the protection it provides against fungal infections. This is suggested by the fact that reptiles typically lay eggs in clumps, yet parental egg care is much rarer than in terrestrial

amphibians (Shine 1988; Mateo & Cuadrado 1998). Pathogenic fungi attacking reptilian eggs have yet to be described, although it seems likely that they exist, since female Five-Lined Skinks, *Eumeces fasciatus*, have been reported to turn their eggs to prevent fungal growth, and to eat spoilt eggs (Shine 1988).

Clearly, the influence of pathogenic fungi is only one of several factors likely to have been involved in the evolution of amphibian reproductive strategies such as those discussed here. Others include predation, competition, the influence of numerous abiotic factors on embryonic mortality and growth rates, and the exploitation of different habitats that vary greatly, e.g. in their predictability in time and space. As Lawton (1996) says, 'for many phenomena, there are likely to be several contributory mechanisms, and the question is not so much about which mechanism is correct, but about the relative contributions of a plurality of mechanisms.'

Previous authors addressing the evolution of reproductive strategies in amphibians have often ignored the potential importance of pathogenic fungi (e.g. Magnusson & Hero 1991; Resetarits 1996). Further research, including comparative studies, is needed to assess the relative importance of pathogens in amphibian life-history evolution.

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