The Egg and Its Environment

When the founders of experimental embryology proposed their new science in the late 1800s, they were concerned with both the *internal* factors causing development and the *external* factors that could also induce changes (Nyhart, 1995). At that time, the term "biology" meant something very close to what "ecology" means now—the relationship of the organism to its environment. Although experimental embryology and subsequent developmental biology have stressed the internal factors leading from genes to the adult phenotype, concern over environmental crises has begun to redirect attention towards the relationship between the embryo and the habitat in which it develops (van der Weele, 1995). These investigations have given us new perspectives on older data and have provided us an entire new outlook on how embryos develop "in the real world" outside our classrooms and laboratories.

The egg is often the most vulnerable stage in the animal's life cycle, as it cannot run away or actively protect itself from predation or environmental pollution. However, development has evolved several ways of insuring egg survival. Human interventions in the environment are inadvertently circumventing some of those adaptations and are putting the eggs at more risk.

Ultraviolet Radiation, Natural Sunscreens, and the Ozone Layer

When we go to the beach, we cover our exposed skin with sunscreens to block the ultraviolet (UV-B; 290-320 nm) radiation from mutagenizing our skin cells. UV-B is able to induce the formation of free radicals within cells, and these highly reactive compounds can alter the DNA base pairing. One of the more common effects of UV-B is to condense adjacent thymidines into cyclobutane pyrimidine dimers (CBPDs) which impede DNA replication and transcription.

How can the egg survive all those hours sitting constantly exposed to the sun (often on the same beaches and parks where we sun ourselves)? First, it seems that many eggs have evolved natural sunscreens. The eggs of many marine organisms possess high concentrations of mycosporine amino acid pigments which absorb UV-B. Moreover, just like our melanin pigment, these pigments can be induced by exposure to UV-B (Jokiel and York, 1982; Siebeck, 1988). The eggs of tunicates are very resistant to UV-B radiation, and much of this protection comes from the extracellular coats which are enriched with mycosporine compounds (Mead and Epel,1995). So perhaps the beautiful pigments of marine eggs have a function, after all.

The possibility exists that the global decline of amphibian populations may be caused by increasing amounts of UV-B reaching the Earth's surface in recent years. Populations of amphibians in widely scattered locations have been drastically reduced in the past decade, with some thought to become extinct. While no single cause for these declines has been identified, the fact that these declines have occured in undisturbed areas and throughout the planet has prompted considerations of global phenomena. One possibility that is being studied is that these declines are due to increased terrestrial UV-B irradiation due to the depletion of the ozone layer in the stratosphere. (For more information of declining frog populations, see Phillips, 1994.)

Blaustein and colleagues (1994) have looked at the levels of the UV-damage-specific repair enzyme photolyase (which excises and replaces the damaged thymidine residues) in different amphibian eggs and oocytes. Levels of photolyase varies 80-fold between the tested species and correlated with the site of egg laying. Those eggs exposed more to the sun had higher levels of photolyase.

Table 1

Species	Specific activity of photolyase (10^{11} CBPD/hr/microgram)	Egg-laying mode
P. dunni	<0.1	Eggs hidden/not exposed to sun
X. laevis	0.1	Under vegetation/limited exposure
T. granulosa	0.2	Eggs hidden/limited exposure
R. variegatus	0.3	Eggs hidden/ not exposed
P. vehiculum	0.5	Eggs hidden/not exposed
A. macrodactylum	0.8	Open water/some exposure
A. gracile	1.0	Open, shallow water/exposed
B. boreas	1.3	Open, shallow water/exposed
R. cascadae	2.4	Open, shallow water/much exposed
H. regilla	7.5	Open, shallow water/much exposed

These levels also correlated with whether or not the species was suffering population decline. The highest photolyase levels were in those species, such as the Pacific treefrog (*Hyla regilla*), whose populations were not seen to be in decline, while the lowest levels were seen in those species (such as the Western toad, *Bufo boreas*, and the Cascades frog, *Rana cascadae*) whose populations had dramatically declined.

These investigators tested whether or not UV-B could be a factor in lowering the hatching rate of tadpoles from these eggs. At two field sites, they divided the eggs of three species into three groups. The first group developed without any sun filter. The second group developed under a filter that allowed UV-B to pass through. The third group developed under a filter that blocked UV-B from reaching the eggs. For *Hyla regillis*, the filters had no effect, and hatching was excellent at all three conditions. For *Rana cascadea* and *Bufo boreas*, however, the UV-B blocking filter raised the percentage of hatched tadpoles from about 60 percent to close to 80 percent.

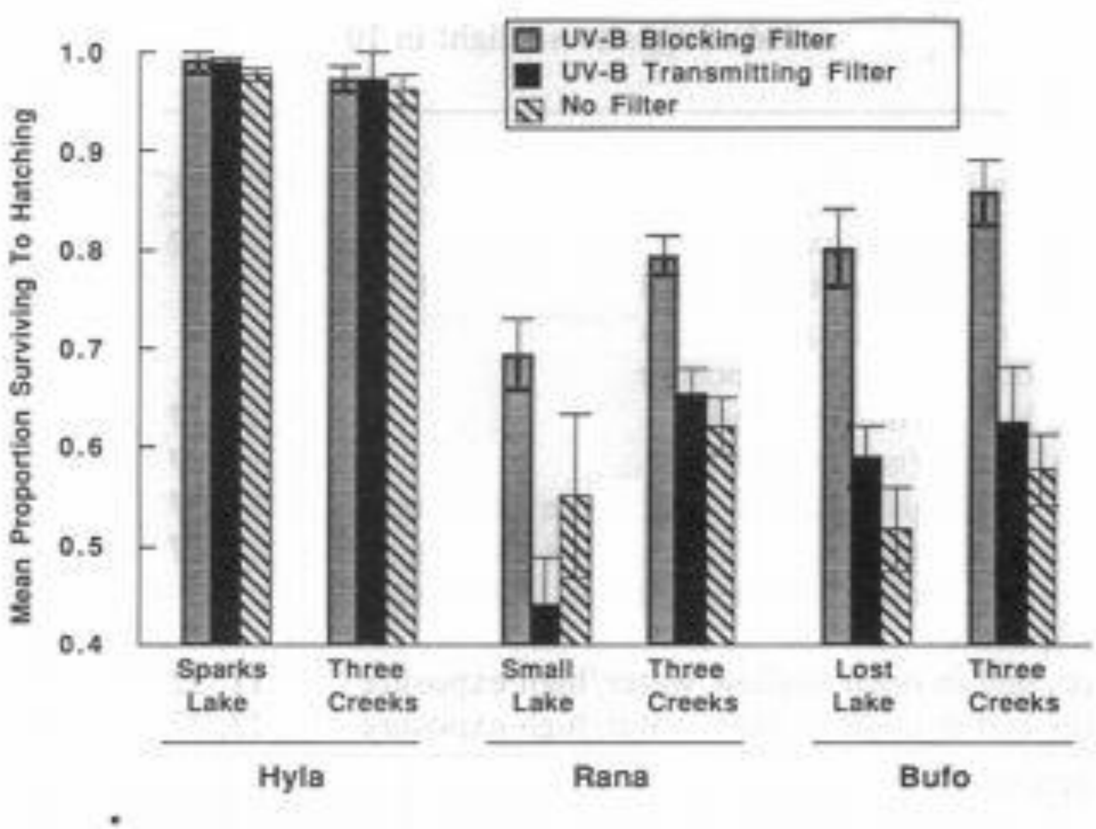

Figure 1 Effects of UV-B on hatching success (+/- standard error) in three anuran amphibians, *Hyla regila, Bufo boreas,* and *Rana cascadea.* Blaustein, 1994)

Protection Against a Strange Environment

In southeast Queensland, Australia, there was a rare aquatic frog, *Rheobatrachus silus*. The female of this species swallowed her newly fertilized eggs (about 20 of them) and brooded the young in her gut. Whereas several tropical frog species had been known to brood embryos in the male vocal sac (which had already become distended to call mates), this frog actually brooded them in her stomach. The eggs develop into larvae, and the larvae undergo metamorphosis all in the stomach, and eight weeks after injection, the small frogs emerge from the female's mouth (Corben and Ingram, 1974; Tyler, 1983).

What stops the eggs from being digested or excreted? It appears that the eggs are secreting agents which stop digestion and the peristaltic contractions in the stomach. During the period of gastric brooding, the gastric musculature is altered, and the cells that are responsible for secreting acid into the stomach are inhibited. After the oral birth, stomach morphology and function returns to normal. The agent that protects the eggs and early embryos is not yet known, but the larvae secretes copious amounts of prostaglandin E2. This compound is capable of inhibiting the acid secretion by the gastric mucosa (Tyler et al., 1983).

This species is now believed to be extinct, as no new individuals have been seen since 1981. Gould [1991] reports that another gastric brooding frog, *Rheobatrachus vitellinus*, had been discovered about 500 miles north of where *R. silus* had lived. It, too, is now extinct.

Protection Against Predators

Organisms have evolved several ways to protect their immobile eggs, and these protective devices can be grossly classified into physical and chemical barriers. Physical barriers include extracellular coats to increase the size of the egg and to provide a hard shell. Chemical barriers often rely on the inclusion of compounds that are distasteful to the particular predators of that species. One of the more interesting examples of chemical protection of the egg occurs in the arctiid moth *Utetheisa ornatrix* (Figure 4).The eggs of this species get a heavy dose of pyrrolizidine alkaloid put into them by both the mother and the father (Dussourd et al., 1988). The mother gets the alkaloids while a larvae, eating the alkaloid-laden plants of the *Crotalaria* genus. These alkaloids do not harm the larvae and continue giving protection to the adult. The female puts these compounds into the eggs. The father also acquires the alkaloids as a larva, and when it is an adult, these alkaloids can be found in its semen. Both the male and female contribution to the egg inhibits the predation of the egg by beetles.

The alkaloid is also made into a pheremone that makes the male sexier. During courtship, the males put this pheremone on combs that touch the female. Males that had been reared on plants that lack the alkaloids were not as successful in courtship as those males who had ingested the alkaloid. In this way, the male advertises that it has eaten the alkaloid-containing plants and can contribute to the survival of the eggs.

Chemical protection against predators was also found to exist in the large yolky eggs of several marine invertebrates. These chemicals made the eggs and their embryos unpalatable to the sea stars, sea anemones, or amphipods that would otherwise eat them. Interestingly, two related species, whose eggs did not contain much yolk, lacked the chemical defenses (Lindqvist and Hay, 1996; McClintock and Baker, 1997). It appears that the large yolky eggs are more likely to be chemically defended than those eggs without much yolk.

Literature Cited

Blaustein, A. R., Hoffman, P. D., Hokit, D. G., Kiesecker, J. M., Walls, S. C., and Hays, J. B. 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? *Proc. Natl. Acad. Sci. USA* 91: 1791-1795.

Corben, C. J., Ingram, M. J., and Tyler, M. J. 1974. Gastric brooding: Unique form of parental care in an Australian frog. *Science* 186: 946-947.

Dussourd, D. E., Ubik, K., Harvis, C., Resch, J., Meinwald, J., and Eisner, T. 1988. Biparental defense endowment of eggs with acquired plant alkaloid in the moth *Utetheisa ornatrix. Proc. Natl. Acad. Sci. USA* 85: 5992-5996.

Gould, S. J. 1991. "Here goes nothing," *Bully for Brontosaurus*. Norton, NY. pp. 294-306.

Jokiel, P. L. and York, R. H., Jr. 1982. Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae. *Bull. Mar. Sci.* 32: 301-315.

Lindqvist, N. and Hay, M. E. 1996. Palatability and chemical defense of marine invertebrate larvae. *Ecol. Monogr.* 66: 431-450.

McClintock, J. B. and Baker, B. K. 1997. A review of the chemical ecology of antarctic marine invertebrates. *Amer. Zool.* 37: 329-342.

Mead, K. S. and Epel, D. 1995. Beakers versus breakers: How fertilisation in the laboratory differs from fertilisation in nature. *Zygote* 3: 95-99.

Nyhart, L. 1995. *Biology Takes Form*. University of Chicago Press, Chicago.

Phillips, K. 1994. *Tracking the Vanishing Frogs: An Ecological Mystery* St. Martin's Press, New York.

Siebeck, O. 1988. Experimental investigation of UV tolerance in hermatypic corals. *Mar. Ecol. Prog. Ser.* 43: 95-103.

Tyler, M. J. 1983. *The Gastric Brooding Frog*. Croom Helm, London.

Tyler, M. J., Shearman, D. J., Franco, R., O'Brien, P., Seamark, R. F., and Kelly, R. 1983. Inhibition of gastric acid secretion in the gastric brooding frog, *Rheobatrachus silus. Science* 220: 607-610.

Voet, D. and Voet, J. G. 1995. *Biochemistry* (Second ed.). John Wiley, NY.

Weele, C. van der, 1995. *Images of Development: Environmental Causes in Ontogeny*. Elinkwijk, Utrecht.