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PARENTAL TRADE-OFFS

FIELD NOTES

Exceptional Parents

A frog species that defies the rule

By Sinlan Poo and David P. Bickford

Most animals encourage independence in their offspring at the earliest possible date. Invariably, the goal is to minimize energy output and maximize offspring survival. Parental investment tends to evolve only when attentive parenting can mitigate environmental threats, such as hungry predators, scarce or hard-to-get food supplies, or a harsh climate or terrain. In the case of amphibians, the majority of species abandon their large clutches of eggs in wet or moist habitats shortly after fertilization occurs. A few species of frogs, however, do look after their eggs, and sometimes they even care for their young after the eggs have hatched. In those cases, the adaptation of extra parental care offsets high mortality rates in what tend to be harsh, often terrestrial environments.

Here at the Sakaerat Environmental Research Station, situated on the edge of Thailand's Khorat Plateau about 200 miles northeast of Bangkok, we have found a small tree frog, *Chiromantis hansenae*, that straddles a middle ground between abandonment and attentive parenting. For instance, *C. hansenae* cares for its offspring by covering its egg mass with its body, a behavior that would seem to suggest a harsh, terrestrial breeding environment. Yet *C. hansenae* breeds on leaves or twigs above ponds, a relatively comfortable environment for a frog, and it lays over 200 eggs per clutch, an extremely large number for a care-providing frog species. So what distinguishes the environment of *C. hansenae* to the extent that parents risk their own lives to offer extended care?

Amphibians are an excellent class in which to investigate the costs, benefits, life-history trade-offs, and evolutionary drivers of parental care. As the Amphibian Survival Alliance points out, "There are over 6,500 species of amphibians, and they inhabit all continents except Antarctica, living in varied habitats such as rainforests, rivers and streams, deserts and alpine environments." They have remarkable diversity in reproductive ecologies and show a wide array of parental care behavior. Notably, of all classes of vertebrates, they are at the greatest risk of extinction in the coming decades.

Eight different modes of parental care are generally recognized in amphibians: egg attendance, egg transport, egg brooding, tadpole attendance, tadpole transport, tadpole brooding, tadpole feeding, and froglet transport. Predation seems to have the strongest impact on parental care in terrestrial-breeding species, whereas harsh environments appear to be the determining factor for arboreal-breeding species. In other cases, limited food supply for tadpoles has been associated with so-called trophic feeding, in which adults purposefully deposit unfertilized eggs as a food source to sustain tadpoles. Egg attendance—a parent remaining with the egg mass at a fixed location—represents by far the most common mode of amphibian parental care. By investing in egg attendance, amphibians can increase offspring survivorship by reducing or preventing developmental abnormalities, predation, and egg dehydration. In addition, attendance by adults may reduce the incidence of fungal infection of embryos. Parental care in amphibians has been associated with five life-history traits: breeding in small bodies of water, such as tree holes or bromeliads; breeding in moving water; having fewer eggs; having large eggs; and direct development—embryos hatch as miniature versions of the adult frog, without entering a free-swimming tadpole stage.

The Thai treefrog, *Chiromantis hansenae,* deviates from all of the above patterns of life history and parental care. *C. hansenae* breeds above large temporary ponds during the mid- to late rainy season, from

Thai tree frog, Chiromantis hansenae, *cares for its offspring longer than most amphibian parents.*

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Female C. hansenae *guards a clutch of approximately 200 eggs, protecting them from drying out and from being eaten or disturbed by predators.*

July to October. Eggs are deposited in a hemispherical gelatinous mass, containing a large number (150–250) of very small eggs (only one or two millimeters per capsule) compared to those of other amphibians that offer parental care. Egg clutches are attached to vegetation overhanging water; after three to five days, the eggs drop into the pond below and hatch into tadpoles. In addition to some of those peculiar life-history characteristics, egg attendance appears to be performed by females. (Males perform the majority of egg attendance in frog and toad species whose offspring go through a tadpole stage.) In addition to exploring the ecological significance of maternal versus paternal care, the study of *C. hansenae* offers a look at a geographic outlier among amphibian caregivers. The majority of research on amphibian parental care has occurred in the Neotropics, in Sub-Saharan Africa, and in Melanesia, with a few cases in Europe and East Asia. By comparison, in Southeast Asia, an area encompassing four major biodiversity hotspots, only a handful of the more than 700 species are reported to have some form of parental care. Moreover, existing reports lack data quantifying any benefits to offspring survival, or any costs to adult fitness, of the apparent parental investment. These few Southeast Asian species with parental care represent an opportunity to test theories developed from observations in other regions for their broader validity, as well as to add to the breadth and depth of data for future analysis to enhance our understanding of the evolution of parental care.

In 2011, we began a field study of 126 clutches. Initially, we observed mating frog pairs and recorded new egg clutches between 3:00 A.M. and 6:00 A.M. to ensure that clutches were located immediately after they were laid, which usually occurs between 9:00 P.M. and 3:00 A.M. We continued to observe clutches four times a day until all embryos had hatched, died, or disappeared. We recorded the distance between clutches and the surface of a pond and the type of material to which clutches were attached. Offspring survivorship was assessed by the simple presence or absence of dead embryos. We didn't count them because we wanted to minimize disturbance of attending adults and living embryos. Causes of death in eggs included predation, submergence, dehydration, and lack of fertilization. Parental investment was quantified by the amount of time an attending adult was present. To verify the benefits of parental care for offspring survivorship, we removed attending adults from some clutches. Those experimental clutches were paired with control clutches in the same habitat conditions. Furthermore, we confirmed the sex of caregiving adults by observing males and egg-bearing females collected from the field and paired in open-air laboratory settings (following procedures approved by the Institutional Animal Care and Use Committee). Once embryos hatched and observations of parental care were concluded, tadpoles and adults were returned to their original locations.

Field observations indicate that males attract females by calling to them; the females then carry males on their back to a chosen egg-laying site. After all eggs are laid and fertilized, males leave; females continue to secrete mucus to form a thicker layer of gel covering the exposed surface of the entire clutch. Females are generally in close contact with clutches, covering part or all of the exposed clutch surface with the posterior part of their body and hindlimbs. Occasionally, females will make trips down to the pond, presumably to soak up more water, and return to secrete liquid from their cloacae and extend their hindlimbs backward to glaze the substance over the clutch. In addition, females were observed in a few instances to be resting on the opposite side of the leaf or grass blade from the egg mass. Female attendance was observed at all stages of embryonic development, until the eggs had hatched and become tadpoles. Although *C. hansenae* adults are nocturnal, females can remain with clutches during the day and maintain their guard duty while resting.

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Three to five days after being deposited, the eggs will drop or be washed by rain from the vegetation into a seasonal pool of water below and hatch into tadpoles. At that stage the mother C. hansenae *leaves them to fend for themselves.*

We conducted a total of 1,448 observations of the 126 clutches. Nearly 63 percent of egg clutches died during the embryonic period, with predation, the primary cause, resulting in about half of those deaths. Predators included katydids, ants, snakes, and spiders. Mortality due to egg dehydration totaled less

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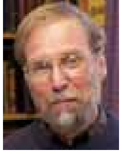
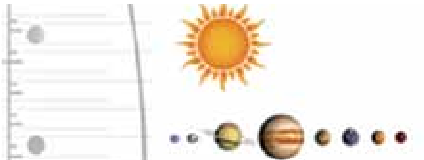


BOOKSHELF BY LAURENCE A. MARSCHALL



How Big is Big and How Small is Small

The Sizes of Everything and Why
by Timothy Paul Smith
Oxford University Press, 2014;
264 pages, $39.95

Over several decades of teaching physics and astronomy, I have found one of the hardest modes of thinking to instill in students to be a sense of universal scale. The mind of a seasoned scientist contains a sort of organizational chart of the natural world, so that he or she intuitively knows the approximate order of magnitude of a calculation even before doing the detailed arithemetic. A neophyte, in contrast, may be perfectly satisfied and blissfully ignorant when flawed mathematics and unwarranted assumptions produce, say, a distance to the moon measuring less than the diameter of an atom, or a time span for a ray of sunlight to reach the Earth that lasts longer than the age of the universe.

A fine new book by physicist and science writer Timothy Paul Smith provides a remedy for this all-too-prevalent form of innumeracy. Measuring 8.5 × 5.6 × 0.9 inches and weighing in at 12.6 ounces, the diminutive book conceals a wealth of information packed into 264 pages. Within it you will find diagrams illustrating the range and ratios of lengths, times, energies, and forces in the real world. Descriptions of the tiniest entities, the quarks that make up nuclear particles, less than 10^{-18} meters across, coexist with chapters on the largest structures, superclusters of galaxies that span hundreds of millions of light years, 10^{42} times larger than quarks. You learn that bacteria live the shortest lives (based on the times between cell divisions)—twenty minutes—and that the longest-living things are Great Basin bristlecone pines, *Pinus longaeva*, at almost 5,000 years. And you will find that a ton of TNT can produce an earthquake registering 2 on the Richter scale, while the largest earthquake on record, the 1960 Chilean temblor, registered a Richter level of 9.5.

So many facts and figures! Yet Smith's little book never feels hopelessly dense or mindlessly boring. That's because, in addition to a good head for numbers, Smith has a raconteur's talent for wrapping a good story around raw details. One chapter, for instance, on the minuscule size of molecules and the vast numbers we find in even a liter of gas, begins with a simple problem: pour a cup of wine over the rail of a boat; wait until ocean currents, winds, and rain, diffuse it throughout every ocean in the world; then fill a cup with ocean water again. How many of the original wine molecules are in that cup? The answer itself, around 250, allowed Smith to calculate that the cup also contains "some of the wine used to launch Cleopatra's barge." Of far greater consequence than the aforementioned factoids, Smith addresses atomic theory (recounting details of a classic problem introduced by the nineteenth-century physicist Lord Kelvin), and provides a lengthy and lucid explanation of how Avogadro's number was discovered and what it means—a puzzle to all high school chemistry students.

Despite some gripping exposition, Smith's book would be too much to digest in a short sitting. Best taken in small samples, it's a book not for a luxurious armchair but for a small seat on a subway commute.

LAURENCE A. MARSCHALL is a professor of physics at Gettysburg College in Pennsylvania. His most recent books, coauthored with Stephen P. Maran, are Pluto Confidential: An Insider Account of the Ongoing Battles over the Status of Pluto *and* Galileo's New Universe: The Revolution in Our Understanding of the Cosmos *(both Ben Bella Books, 2009).*

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than 6 percent. On average, adults were present during 64 percent of observations. Considering all other factors—clutch height, breeding substrate, and weather conditions—only parental attendance was significant in determining offspring survivorship.

By comparing offspring survival between natural egg masses and egg masses whose parent frogs had been experimentally removed, we found that although *C. hansenae* breeds very close to water sources, in the absence of parental care, nearly 70 percent of egg clutches died of dehydration. The rest died as a result of predation. Therefore, the tending behavior of the females is essential to the life-sustaining moisture of their eggs and the survival of their offspring.

Our study, the first to investigate parental care in a frog of Southeast Asia—a region with the third-highest amphibian diversity in the world—is still in the early stages. We aim to further explore the mechanisms, adaptations, and driving forces of this behavior in *C. hansenae* in order to yield a more comprehensive understanding of parental care across the spectrum of life.

SINLAN POO is a PhD candidate in the Evolutionary Ecology and Conservation Laboratory at the National University of Singapore. She is studying with DAVID BICKFORD, an assistant professor in the Department of Biological Sciences, also at the National University of Singapore. Bickford focuses on terrestrial vertebrate ecology, evolution, and conservation, with an aim to protect biodiversity in Southeast Asia.