Physiological Ecology of the Mudskipper: A Synthesis

Donya Saied

Writer's comment: Scanning the list of topic choices for our term papers, I saw the mudskipper and thought, "Writing about an animal featured on the *Ren & Stimpy* cartoon show…? YES!" Navigating through the literature, I discovered three fellow mudskipper enthusiasts and outstanding scientists whose writing inspired me. In acknowledgement of their influential works, I would like to thank Heather J. Lee and Jeffery B. Graham of the Scripps Institute of Oceanography and Ivan Polunin of the University of Singapore.

—Donya Saied

Instructor's comment: Donya was asked to create a research synthesis that linked ecological pressures to physiological mechanisms that contributed to the fitness of an animal in the wild. Not only did she supercede the requirements of the task, she created an essay that placed the reader into the unique environment this fish calls home. Furthermore, she masterfully translated complex physiological mechanisms into easily understood concepts. Assimilating a precise and comprehensive scientific account in a format that is as interesting as it is clear requires a special skill set that few posses. In my opinion, the most important and sometimes most difficult task required by scientists is the translation of their ideas into a universally understandable format. Donya has done this and deserves the recognition she is receiving.

—Scott Lankford, Wildlife, Fish, and Conservation Biology

1. Meet the Mud

Peering at the creature, one gets the impression she is being privileged with a glimpse back in time to when animals first crawled out from the sea. The four-inch long creature appears to be a chimeric blend between the front end of a frog and the tail end of a fish. It uses its sturdy pectoral fins like crutches and its circular pelvic fin as a suction cup. It feeds primarily on small mollusks such as snails and resides in a 10–20 inch deep mud lair, sometimes complete with a turret as perhaps a sunroom or lookout post (1). The animal can live submerged indefinitely, though it feeds, courts, and defends territory on land (1). Among its banes are the heron, snake, and—odd for a fish—the mosquito (1). Only high-speed winds and temperatures colder than 15 Celsius keep this predator from the hunt (2). Breeding season brings its territoriality to a peak, stirring the male to staunchly defend his underground mud lair in fierce mouth-to-mouth combat. An amorous suitor, he displays his vivaciousness with incredible leaps into the air twice his own body length. A mesmerized female will follow the suitor home, and when she slips inside his place he shuts the "door" behind her with a mud plug (1). They implant their fertilized eggs into the walls of the burrow. At birth, the hatchlings drop into the burrow water. The juveniles drift to the open ocean, living a planktonic existence sustained by a small yolk sack. At 45 days the juvenile has morphed into an adult and returns to land to vie for a place among its kind along the tropical shores (3).

These fascinating animals are the mudskippers, a group of 24 Old World amphibious fish species inhabiting tidal mudflats and mangroves throughout the Indo-Pacific from West Africa to Papua New Guinea. These animals, the best studied amphibious air-breathing fish, are classified into four genera: Scartelaos (4 species), Boleophthalmus (5 species), Periophthalmus (12 species), and Periophthalmodon (3 species). These four genera are among the ten belonging to Subfamily Oxudercinae, itself falling under the fish family Gobidae (3).

2. Tricks of the Trade

From a physiologist's perspective, the air-breathing of the mudskipper is its most phenomenal feat. It is not alone in this capacity (49 fish families have members that air-breathe to some extent) but no fish is as terrestrial as the mudskipper which completes courting, feeding, hunting, and territorial defense on land (1,4). Its air-breathing capacity is thought to have evolved in response to drought-generated shallow, hypoxic waters at land-water interfaces where aerial oxygen exploitation would significantly heighten fitness (4). Air-breathing has given mudskippers not only a survival advantage in low-oxygen waters, but also reduced its competition for prey and habitat with purely aquatic species, and even lessened its exposure to pollutants in water. Spied when coming ashore, the mudskipper's appearance may convince one she is looking at the closest living ancestor to terrestrial vertebrates, but most scientists believe that distinction belongs to the Sacropterygii (lobe-finned fishes such as the coelocanth) (3). Mudskippers are actually very distantly related to the fish that gave rise to terrestrial vertebrates.

3. What a Big Mouth You Have!

The mudskipper is specialized for its lifestyle by modifications to its fins for terrestrial locomotion, its eyes for aerial vision, and its metabolism for aerial respiration. Its sturdy, highly dexterous pectoral fins are jointed, enabling it to "crutch" itself along, climb over mangrove roots, skip across mudflats, and even climb up small trees (1). Its stalked eyes have reduced lens curvature to compensate for the added refraction of air, and have skin folds beneath them which hold fluid to bathe the eyeballs when they are rotated down (4). Its respiratory-related modifications to the skin and gill chambers are numerous. These include reduced gill area, increased volume in pharynx and opercular chambers, and specialized epithelia with alveolar-like spaces interspersed with strips of muscle on the buccal, pharyngeal, branchial, and opercular chambers (4). Additionally, the mudskipper has an inhalant aperture created from a curtain-like membrane between first gill arch and hyomandibular bone (4). Another membrane surrounding the gills controls the air volume and exhalation. When the animals head for shore they carry water in their gill chambers, sort of a fish version of a scuba tank (4). An interesting conundrum for the mudskipper is that, after a successful hunt, swallowing discharges the water and air from its gill chambers and forces the fish to slip back into the water (1).

One experiment found that mudskippers (species *Periophthalmus sobrinus*) can be sustained in air for a maximum of 37 hours in 70-80% relative humidity (5). The fish passively lost water at rate of 1.8% of initial body mass per hour until they lost 22% of initial body weight (5). How did they manage to hang on so long? The scuba tank approach is not the sole way mudskippers sustain themselves out of water. Problems of gill desiccation and collapse encountered during land excursions have been limited by modifying the skin into a respiratory surface, minimizing the gill exposure in air. Diffusion distance is reduced by placement of the capillaries in the epidermis rather than in the dermis as with most fish, and capillary density is greater in the mudskipper's skin than any other Gobi (4). The skin and gills provide tandem respiratory function in both water and air, but while in air the skin facilitates 60-70% of the respiration (gills just 40-30%) compared with 40% performed by the skin when in water (4), (5).

Breathing out of water is not the only challenge for the mudskipper. At high tide, when escaping predators, while guarding eggs and even during its own development, the animal's water-filled mud lair turns hypoxic (low in oxygen). Physiologists report that under similar experimental conditions (5% O_2) the mudskipper responds with a tremendous inspiration rate of 580% Vm (ventilation minute), while simultaneously reducing oxygen consumption to 33% VO_2, one third of normal (6). No energy or glycogen change could be detected at this early stage even though the animals displayed signs of oxygen debt (6). Maximal endurance (measured to metabolic arrest) in hypoxic water was 6 hours (6). Interestingly, the response of the animals to anoxic (zero oxygen) waters varied significantly depending on whether the exposure was acute (survival was 5-10 minutes) or gradual (survival ranged from 1-2 hours) (4). Recent research at the Scripps Institute of Oceanography using cutting-edge artificial burrows revealed the animals create air pockets in the lair (holding anywhere from 55 to 4000 mL of air), leading researchers to speculate that the storage of fresh air bubbles in the burrow may enhance anoxia tolerance and perhaps help fulfill the fish's daily requirement of 100 mL of O_2 (6). The air pocket is also thought to be crucial to developing eggs and to mated pairs sharing a burrow during high tide (3). Estivation, another avoidance behavior, has also been reported in mudskipper though it is not well documented (4).

4. Details, Details

The biochemical basis of the mudskipper's terrestrial sojourns have also been a subject of interest to physiologists. In fish, ammonia (waste nitrogen) is formed in mitochondria. It diffuses to the tissue and plasma, then is shuttled out through the gills to the environment. As long as ample water is available this method is effective since ammonia is a highly soluble toxicant (4). But mudskippers spend much time in air, and precious water cannot be spared excreting ammonia. How do these fish thwart being poisoned by their own metabolites? Research suggests the fish resort to storage during aerial exposure, then excrete the ammonia as normal, preliminary studies pointing to accumulation in the liver (5). Further, reduced locomotory activity and diminished protein and amino acid catabolic rates have also been reported (5). Together these responses minimize the need for energy-intensive detoxification pathways (5).

The energy metabolism of mudskippers has itself also been adapted for air-breathing. Liver and muscle enzyme activity analysis suggests these animals have a well-developed capacity for anaerobic glycolysis (4). Higher PK (pyruvate kinase) and LDH (lactate dehydrogenase) levels coupled with a high LDH to MDH (Malate dehydrogenase) ratio in its muscle suggests these tissues have a high lactate production capacity, while its liver is geared toward NADH (nicotinamide adenine dinucleotide) oxidation. Additionally the muscle is optimized for lactate oxidation and not gluconeogenisis (4). Since the tissues and blood have limited oxygen storage capacity, it appears the mudskipper has evolved the ability to abruptly reduce metabolic activity, though its limitations are unknown. A number of LDH isomers, particularly in the heart, are suspected to hold further clues to these mechanisms (4).

5. Time Machine Not Required

Study of the mudskipper gives us a glimpse into the myriad of challenges aquatic Sacropterygii had to overcome to conquer land, most importantly the development of air-breathing. Their study further demonstrates the challenge of achieving homeostasis notwithstanding the interconnectedness of body systems with each other and the environment. For instance, switching from water to air for oxygen extraction required not only lungs in place of gills, but also necessitated the evolution of an alternative route of ammonia excretion. Lucky for us, our ancestors did just that so we can watch the ostentatious mudskipper mating displays along the shoreline and glimpse into the past.

References

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