

Respiratory allocation and standard rate of metabolism in the African lungfish, *Protopterus aethiopicus*

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Abstract

This paper quantifies the relationship between respiratory allocation (air vs. water) and the standard rate of metabolism (SMR) in the primitive air-breathing lungfish, *Protopterus aethiopicus*. Simultaneous measurements of oxygen consumed from both air and water were made to determine the SMR at ecologically relevant aquatic oxygen levels for juveniles 2 to 221 g. Total metabolic rate was positively correlated with body mass with a scaling exponent of 0.78. Aerial oxygen consumption averaged 98% (range=94% to 100%) of total respiratory allocation under low aquatic oxygen levels. Measurements of oxygen consumption made across a gradient of dissolved oxygen from normoxia to anoxia showed that *P. aethiopicus* maintains its SMR despite a change in respiratory allocation between water and air.

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1. Introduction

Air breathing in fishes has a rich evolutionary history, having evolved independently numerous times in several different phylogenetic lineages and with various structures for gas exchange (Randall et al., 1981; Graham, 1997; Perry et al., 2001). Air-breathing in fishes dates to the Late Silurian, based on fossil traces of lung-like structures in Placoderms and Ostracoderms (Gardiner, 1980; Little, 1990; Coates and Clack, 1991; Gordon and Olson, 1995; Long, 1995; Graham, 1997; Perry et al., 2001). Early evolution of lungs and evidence of their widespread occurrence among ancient fishes is supported by the observation that bimodal breathing is present in extant representatives of mostly extinct groups, through the use of either paired lungs (ancestral condition) or a single lung as the primary air-breathing organ (Randall et al., 1981; Burggren et al., 1986; Ultsch, 1996). The lungfishes are of great interest because of their probable relationship as the sister group to

tetrapods (Tohyama et al., 2000). Recent evidence suggests that ventral lungs and a 2-cycle air-breathing circuit evolved within the Sarcopterygii, supporting the homology between lungfish and tetrapod lungs (Perry et al., 2001). Their use of lungs as the primary site of oxygen exchange and apparent increased physiological dependence upon aerial respiration across ontogenetic stages provides an excellent opportunity to study the physiology of these ancient fishes along an evolutionary vector similar to that which tetrapods might have initially experienced during the transition to a terrestrial existence. However, very little is known about the energetics of these air breathers under ecologically relevant dissolved oxygen levels or the relationship between respiratory allocation (water vs. air) and body size.

The majority of early research on the African lungfish, *Protopterus aethiopicus*, and lungfishes in general, focused on cardio-respiratory adaptations in larger fish (Sawaya, 1946; Johansen and Lenfant, 1968; Lahiri et al., 1970; Lenfant et al., 1970; McMahan, 1970). The few studies that explored ontogenetic variation in respiratory strategies reported shifts in respiratory allocation with body size. For example, Johansen et al. (1976) found that immediate post larval and early juvenile *Protopterus amphibius* depended on aquatic respiration for 70% of their oxygen demand, while fish between 300 and 500 g

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obtained as little as 10–15% of their oxygen from water. For *Protopterus annectens*, Babiker (1979) found that small specimens <200 g utilized less than 10% aerial respiration to meet metabolic demands, whereas individuals >400 g utilized aerial respiration for 83% of their total oxygen uptake. Johansen and Lenfant (1967) found that one juvenile *Lepidosiren paradoxa* (150 g) used aquatic respiration to meet 64% of its metabolic demand. And, Oduleye (1977) found that 4 to 150 g juvenile *P. annectens* acquired about 94% of their oxygen aerially, however allocation was not reported in conjunction with size classes. These studies contributed to a physiological portrait of the Lepidosirenidae and Protopteridae as animals characterized by two distinct respiratory life stages, with small juveniles primarily dependent on aquatic respiration and an increased dependence on aerial respiration with growth (Jesse et al., 1967; Lenfant et al., 1970; McMahon, 1970; Johansen et al., 1976; Babiker, 1979). However, in these earlier studies, measurements of oxygen consumption in juvenile *P. aethiopicus* were made under conditions of near-saturated aquatic oxygen levels, an environment not reflective of observed natural ambient conditions at this life-history stage.

In the field, nestling *P. aethiopicus* have been observed to begin air breathing at a length of 23 to 27 mm while still possessing external gills (Smith, 1931; Greenwood, 1987). At this size, they are associated with either floating mats of papyrus roots or found amongst heavily vegetated patches within the swamp (Greenwood, 1987). In lakes Victoria and Nabugabo (East Africa), Goudswaard et al. (2001) reported that *P. aethiopicus* smaller than 40 cm were very rare in open waters and almost exclusively associated with the fringing swamp. In this swamp habitat, dissolved oxygen concentration can be extremely low (Chapman et al., 2002a,b). Both Greenwood (1958) and Johnels and Svensson (1954) suggested that the shallowness of *P. aethiopicus* nests might be connected with the air-breathing behavior of the nestlings. In these nests, young had been observed resting on the roots near the surface (Greenwood, 1987). Dissolved oxygen measurements made by Greenwood (1958) at the surface and at the bottom of the nests ranged between 1.01 and 1.71 mg L⁻¹, and between 0.98 and 2.66 mg L⁻¹, respectively. Although the smallest size of aestivating individuals is unknown, *Protopterus dolloi*, a West African lungfish species, has been found in cocoons at lengths of 40–50 mm (Johnels and Svensson, 1954). The fact that individuals this small are capable of aestivation suggests that they are capable of sustaining themselves solely on aerial respiration. In conditions such as these, and with the capacity to acquire oxygen aerially, it would appear that small, juvenile lungfish might use aerial respiration in their natural environment to an extent previously unrecognized.

The objective of this study was to examine the energetics of *P. aethiopicus* across a range of body sizes to detect ontogenetic shifts in respiratory allocation and to measure standard rate of metabolism. We hypothesized that based on their distribution in the hypoxic wetlands, juvenile lungfish would respire primarily aerially, regardless of size. We focused on juvenile lungfish over the size range typically found in the marginal hypoxic wetlands in the Lake Victoria

basin (nestlings to 40 cm TL, Goudswaard et al., 2001). We measured rate of oxygen consumption and relative allocation to air and water breathing across a range of aquatic oxygen levels reflective of the natural habitat.

2. Materials and methods

2.1. Study site

Specimens of *P. aethiopicus* were obtained from a natural population within the Lwamunda Swamp that surrounds Lake Nabugabo, Uganda (31°50'E; 31°56'S; to 0°20'E; 0°25'S; see Randle and Chapman, 2004 for site map). Lake Nabugabo lies just south of the equator and is a small satellite lake (surface area=24 km², mean depth=4.5 m) that was isolated from Lake Victoria approximately 4000 years ago (Greenwood, 1965). The lake lies within the extensive Lwamunda Swamp that was formerly a bay on the western shore of Lake Victoria (Worthington, 1932; Greenwood, 1965; Ogutu-Ohwayo, 1993). The dense interior of the swamp is characterized by numerous small lagoons and channels. These serve as important habitats for *P. aethiopicus* (<40 cm total length, Goudswaard et al., 2001). Dissolved oxygen concentrations within the swamp are severely hypoxic throughout the year. In a study of a small lagoon within the Lwamunda Swamp measurements were made during both wet and dry seasons at several microsites. Over a 1-year period monthly dissolved oxygen measurements in the upper 20 cm of water averaged 1.5 mg L⁻¹ (≈26.8 mm Hg) in the morning and 1.8 mg L⁻¹ (≈32.9 mm Hg) during the afternoon (Chapman et al., 2002b). Water temperatures at the sites averaged 22.3 °C in the morning and 23.8 °C in the early afternoon (Chapman et al., 2002b).

2.2. Collection and maintenance of *P. aethiopicus*

Individuals were live-captured using baited minnow traps set at various places within the lagoons of the Lwamunda Swamp and left overnight. Traps were collected the following morning and each captured lungfish placed in separate holding containers. This method was appropriate for catching individuals ranging in mass from 10 g to ~250 g. Smaller individuals (<5 g) were obtained by dip netting vegetated areas within the lagoons and in all cases were caught in dense vegetation mats.

Individual lungfish were held in 1.2-L buckets with lids while in Uganda and then transported to the University of Florida (UF). Once at the University, individual lungfish were held in partitioned 208-L tanks with no two lungfish occupying the same space within a tank. Water temperature was maintained at 23±0.5 °C, with a 12/12 photoperiod. Dissolved oxygen concentration averaged 8.16±0.05 mg L⁻¹ (147.2±0.9 mm Hg). Temperature, dissolved oxygen, pH, conductivity, ammonia, and nitrite levels were measured weekly to maintain water quality. Individual fish were held under these conditions up to 1 year before experimental trials. Fish were fed once a week on fresh chicken or beef liver and, in the case of the smallest individuals, blood worms.

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