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Chapter 20 *Least Oxygen Dependent*

ANDY RASMUSSEN

Department of Entomology & Nematology
University of Florida, Gainesville, Florida 32611-0620

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Apneustic insects (those with closed tracheal systems) rely solely on dissolved oxygen and show the least oxygen dependence. Midges (Diptera: Chironomidae) are common and widespread apneustic aquatic insects and are often the only insects to occur in low oxygen habitats such as profundal sediments in highly productive lakes. The midge Chironomus plumosus *typifies least oxygen dependence and is declared champion.*

Insects, like other multicellular animals, require oxygen for efficient cellular metabolism. Insects obtain oxygen from their environments and convey it to cells in many ways, and hence have adapted to nearly all terrestrial and aquatic habitats. The morphological, physio-logical, and behavioral adaptations of insect respiration must be examined to understand how insects can survive in a wide array of oxygen environments. This paper discusses how insects have adapted to low-oxygen environments, identifies the insect group that has most successfully adapted, and names a representative from this group as champion.

The Candidates

Two groups of insects that have successfully invaded low oxygen environments are endo-parasitic and aquatic insects. These insects have developed a wide array of strategies to obtain oxygen from their respective environments. These respiratory strategies can be grouped into two general categories: 1) insects obtaining oxygen from atmospheric sources, either through a direct connection with the atmosphere or indirectly through an intermediate source; 2) insects relying solely on dissolved oxygen of a particular microhabitat. The insects requiring the lowest oxygen concentrations and demonstrating the least dependence on atmospheric oxygen (i.e., insects in the second category) are apneustic, meaning the tracheal system is closed with no functional spiracles. These insects generally obtain oxygen by diffusion of oxygen through the body cuticle into the tracheae where oxygen comes out of solution and can be more readily transported as a gas to the areas of need.

Apneustic endoparasites

Examples of apneustic endoparasites include the larval forms of a number of parasitic Hymenoptera (e.g., braconids, ichneumonids) and parasitic Diptera, such as the cryptochetids which parasitize scale insects (Borror et al. 1989). The spiracles of these endoparasites remain closed and non-functional until larvae mature and are ready to leave the host. Until that time, apneustic endoparasites are strictly dependent upon cuticular diffusion of oxygen, either dissolved or gaseous, from host oxygen supplies. The braconids facilitate gas exchange by everting their hindgut to form a caudal vesicle that then functions as an additional surface for cuticular diffusion of oxygen from host tissues (Chapman 1982). In the case of the cryptochetids, one species, *Cryptochaetum iceryae*, possesses two long caudal filaments containing tracheae which become entangled with the tracheae of its host. Atmospheric oxygen diffuses from the host tracheae into the tracheae contained in the caudal filaments of the *parasite (Thorpe 1930).*

Apneustic Aquatic Insects

The differences between terrestrial and aquatic environments, in terms of oxygen availability, are striking. Approximately 20% of atmospheric air is composed of oxygen whereas water, even when saturated, contains less than 0.4% (by weight) of free oxygen. Therefore insect respiration, utilizing dissolved oxygen in water, requires that far more water be processed for an equal amount of oxygen. Additionally, because water weighs more than air (of equal volume), more energy must be expended by aquatic insects in moving water past respiratory surfaces than expended by atmospheric breathers. In response to the intrinsic difficulties involved with aquatic respiration, aquatic insects have evolved a variety of morphological, physiological, phenological, and behavioral adaptations enabling them to become widespread in aquatic habitats with variable supplies of dissolved oxygen (Eriksen et al. 1996).

Gas exchange in aquatic insects with closed respiratory systems requires that oxygen be absorbed through the cuticle of the insect's body wall. In insects with a membranous, highly permeable cuticle and a high surface to volume ratio, diffusion of oxygen through the general body wall is sufficient in providing oxygen. Respiration is strictly cutaneous in many of the smaller worm-shaped dipteran larvae, including chironomids, ceratopogonids, simuliids, chaoborids, as well as gill-less trichopteran and plecopteran larvae. In insects without these morphological attributes, cutaneous respiration is supplemented by tracheal gills (thin, highly permeable and tracheated outgrowths of the body wall).

The Champion

The dipteran family Chironomidae is widespread and abundant in extremely low oxygen environments where other insects would quickly die or enter anoxybiosis. Although many chironomids are tolerant of low oxygen conditions, the species *Chironomus plumosus* perhaps best typifies least oxygen dependence. This well studied species is a common and abundant inhabitant of oxygen depleted lake sediments.

Discussion

Chironomids are often the only insects found in lake sediments of the profundal zone where hypoxic (oxygen concentrations less than 3 mg l^{-1}) and even anoxic conditions sometimes occur (Pinder 1995). The chiro-nomids inhabiting lake sediments are there throughout most of their larval and pupal stages. The pupae, just prior to eclosion, rise to the surface where the adults emerge. The terrestrial adult stage is relatively short-lived with mating constituting the activity of primary biological importance. The larvae, which pass through four larval instars, occur on the bottom sediments at population densities sometimes numbering thousands m^{-2}.

Chironomids, occurring in sediments of high organic matter and very low oxygen content, have been uniquely successful in exploiting these environments as a result of behavioral and physiological adaptations. The larvae and pupae of most species occurring in low oxygen sediments construct burrows and fixed tubes of sediments held together with silky secretions. Tube and burrow dwellers are able to ventilate their tubes with fresh water by dorso-ventral undulations of the body, thereby facilitating gas exchange during times of low ambient oxygen. In *Chironomus dorsalis*, tube height above the sediment bed has been shown to be dependent on oxygen concentrations, with larvae extending the tubes above the sediment bed as oxygen concentrations at the sediment bed level decrease (Konstantinov 1971). Other species, such as *C. plumosus*, construct burrows within the sediments which are interconnected and ventilated in a mutualistic effort (Jonasson & Kristiansen 1967). The undulations, in addition to ventilating the tubes and burrows, draw in food from nearby organic sediments, thereby reducing activities related to food gathering. During periods of anoxia, chironomid larvae become inactive and some species are able to survive for extended periods of time. In a laboratory study of resistance to anoxia, Nagell and Landahl (1978) found that *C. plumosus* survived anoxic conditions about twice as long as *C. anthracinus*. The corresponding LT_{50} values were ca. 205 and 100 days.

In addition to the aforementioned behavioral adaptations, many of the tube- and burrow-dwelling chironomids that appear bright red (e.g., Chironominae) possess hemoglobins which play a vital physiological role in increasing respiratory efficiency. The hemoglobins found in chironomids have a very high affinity for oxygen, unlike vertebrate hemoglobins, and serve as a temporary store for oxygen absorbed through the cuticle until it is needed for metabolism. Walshe (1950) determined that hemoglobin present in *C. plumosus* is capable of storing oxygen sufficient to meet the metabolic needs of the resting larva for approximately 9 minutes. Hemoglobin is also considered vital in the transport of oxygen to the various tissues. Typically, chironomids in tubes or substrate burrows alternate periods of ventilation movements, causing the hemoglobin to become saturated, with periods of feeding or rest when oxygen stored in the hemoglobin is released and used for metabolism.

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