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Q2 Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence

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ABSTRACT

Over the last decade, numerous studies have investigated the role of oxygen in setting thermal tolerance in aquatic animals, and there has been particular focus on arthropods. Arthropods comprise one of the most species-rich taxonomic groups on Earth, and display great diversity in the modes of ventilation, circulation, blood oxygen transport, with representatives living both in water (mainly crustaceans) and on land (mainly insects). The oxygen and capacity limitation of thermal tolerance (OCLTT) hypothesis proposes that the temperature dependent performance curve of animals is shaped by the capacity for oxygen delivery in relation to oxygen demand. If correct, oxygen limitation could provide a mechanistic framework to understand and predict both current and future impacts of rapidly changing climate.

In arthropods, most studies testing the OCLTT hypothesis have considered tolerance to thermal extremes. These studies likely operate from the philosophical viewpoint that if the model can predict these critical thermal limits, then it is more likely to also explain loss of performance at less extreme, non-lethal temperatures, for which much less data is available. Nevertheless, the extent to which lethal temperatures are influenced by limitations in oxygen supply remains unresolved. Here we critically evaluate the support and universal applicability for oxygen limitation being involved in lethal temperatures in crustaceans and insects.

The relatively few studies investigating the OCLTT hypothesis at low temperature do not support a universal role for oxygen in setting the lower thermal limits in arthropods. With respect to upper thermal limits, the evidence supporting OCLTT is stronger for species relying on underwater gas exchange, while the support for OCLTT in air-breathers is weak. Overall, strongest support was found for increased anaerobic metabolism close to thermal maxima. In contrast, there was only mixed support for the prediction that aerobic scope decreases near critical temperatures, a key feature of the OCLTT hypothesis. In air-breathers, only severe hypoxia (<2 kPa) affected heat tolerance. The discrepancies for heat tolerance between aquatic and terrestrial organisms can to some extent be reconciled by differences in the capacity to increase oxygen transport. As air-breathing arthropods are unlikely to become oxygen limited under normoxia (especially at rest), the oxygen limitation component in OCLTT does not seem to provide sufficient information to explain lethal temperatures. Nevertheless, many animals may simultaneously face hypoxia and thermal extremes and the combination of these potential stressors is particularly relevant for aquatic organisms where hypoxia (and hyperoxia) is more prevalent. In conclusion, whether taxa show oxygen limitation at thermal extremes may be contingent on their capacity to regulate oxygen uptake, which in turn is linked to their respiratory medium (air vs. water).

Fruitful directions for future research include testing multiple predictions of OCLTT in the same species. Additionally, we call for greater research efforts towards studying the role of oxygen in thermal limitation of animal performance at less extreme, sub-lethal temperatures, necessitating studies over longer timescales and evaluating whether oxygen becomes limiting for animals to meet energetic demands associated with feeding, digestion and locomotion.

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Abbreviations: MMR, maximum metabolic rate – the maximum rate at which oxygen can be consumed at a given temperature; SMR, standard metabolic rate – the minimum rate of oxygen consumption needed to sustain life in resting, post-absorptive organisms at a given temperature; MMR – SMR, absolute aerobic scope (AAS); MMR/SMR, relative aerobic scope, sometimes also referred to as factorial aerobic scope; OCLTT, hypothesis oxygen and capacity limited thermal tolerance hypothesis; T_{opt} , optimal temperature – the temperature where an organism can achieve maximum aerobic scope (MMR – SMR); T_{pejus} , pejus temperature – the temperature beyond which aerobic metabolism declines rapidly and hypoxemia sets in; T_{crit} , critical temperature – the temperature beyond which aerobic metabolism is no longer sufficient to cover energy demand and anaerobic metabolism sets in; CT_{max} , critical thermal maximum – an empirical endpoint of heat tolerance found in heating trials where the temperature is ramped up, indicating the temperature at which the animal becomes moribund and can no longer escape the adverse temperatures; CT_{min} , critical thermal minimum – as for CT_{max} , but reflecting the cold tolerance.

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1. Oxygen supply and demand in thermal biology

Temperature is a key determinant of species geographic ranges (Addo-Bediako et al., 2000; Root et al., 2003; Calosi et al., 2010; Sunday et al., 2010; Kellermann et al., 2012a,b; Overgaard et al., 2014) and current range expansions and contractions are tightly linked to global climate change (Rosenzweig et al., 2008; Sunday et al., 2012). A thorough understanding of the physiological mechanisms underpinning the thermal tolerance of intact living organisms is therefore essential to predict the impacts of current and future rises in global temperatures (Chown, 2012; Huey et al., 2012). Extreme temperatures directly impact a myriad of organismal functions at all levels of biological organization, with effects ranging from protein denaturation, membrane instability, cell disruption and organ failure. At less extreme levels, altered temperature changes performance, including exercise ability, energy assimilation or reproductive capacities at the whole-animal level (Cossins and Bowler, 1987; Schmidt-Nielsen, 1997; Feder and Hofmann, 1999; Pörtner, 2002; Angilletta, 2009). In the long term, such thermal effects on performance can impact population dynamics (reviewed in e.g., Angilletta, 2009; Chown and Terblanche, 2007). Despite the obvious multifaceted effects of temperature on living organisms, recent studies have focused on insufficient aerobic metabolism as the weakest link in thermal tolerance of ectothermic animals (e.g., Frederich and Pörtner, 2000; Pörtner, 2001, 2002, 2006, 2010; Mark et al., 2002; Klok et al., 2004; Davenport and Davenport, 2007; Pörtner and Knust, 2007; Stevens et al., 2010; Verberk and Bilton, 2011, 2013, 2015; Overgaard et al., 2012; Clark et al., 2013; Ern et al., 2014; Fobian et al., 2014; Norin et al., 2014; Wang et al., 2014; Boardman and Terblanche, 2015; Deutsch et al., 2015; Koopman et al., in press; Lefevre et al., in press). Given the ~15 fold greater energy gains associated with aerobic metabolism compared to anaerobic metabolism, animals depend on a continuous and adequate flux of oxygen from their surroundings to their metabolizing tissue to maintain energy status. In ectotherms, standard metabolic rate (SMR) increases with temperature, reflecting elevated energetic costs associated with maintenance, including for example enhanced protein turnover and increased ion pumping (Hochachka and Somero, 2002). However, the maximum rate of oxygen uptake (MMR) does not always increase with temperature and may plateau or even decrease at high temperatures as shown for several fish (e.g., Fry and Hart, 1948). The difference between SMR and MMR represents excess capacity for aerobic metabolism and hence energy generation, reflecting the ability of organisms to meet energy demands associated with activity, feeding, growth and reproduction, etc. Through its different effects on MMR and SMR, temperature influences both the absolute aerobic scope (MMR – SMR) and relative aerobic scope (MMR/SMR) (Fig. 1).

2. The oxygen and capacity limited thermal tolerance hypothesis (OCLTT)

The oxygen and capacity limited thermal tolerance (OCLTT) hypothesis has been proposed to explain thermal performance curves of animals by integrating various mechanisms from most levels of biological organization into a larger context of animal evolution (Pörtner, 2010; Storch et al., 2014). These mechanisms relate to oxygen delivery (involving both ventilatory oxygen uptake and cardiovascular oxygen transport) and oxygen utilization at the level of mitochondria to maintain aerobic metabolism. One of the central aspects of the OCLTT hypothesis is the thermal dependence of aerobic scope (Fig. 1), which is argued to decline as temperatures deviate from optimum (T_{opt}), where aerobic scope is maximal. Interestingly, several species of fish prefer body temperatures that coincide with maximal performance (e.g., maximal aerobic scope, growth or swimming performance) (Fry and Hart, 1948; Brett, 1971; Pörtner and Knust, 2007), although this generality has recently been contested (Clark et al., 2013). According to the OCLTT hypothesis, beyond threshold temperatures (T_{pejus}),

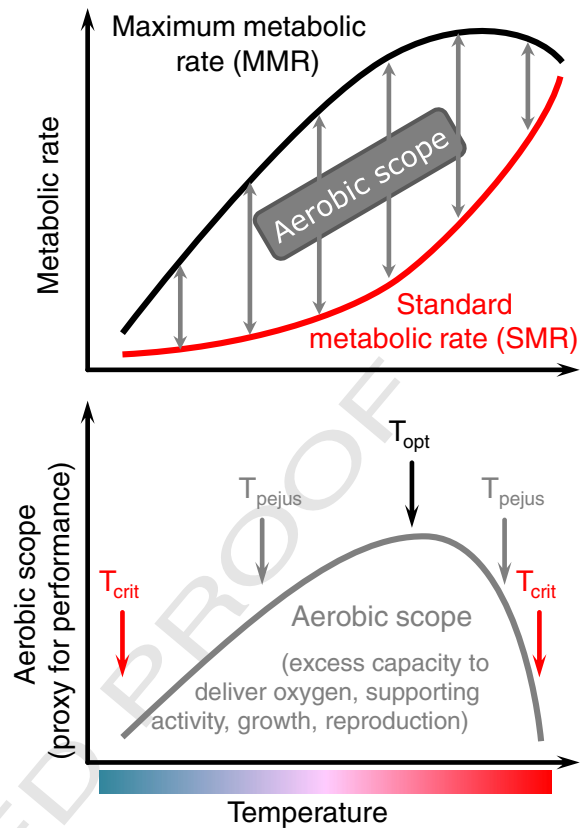


Fig. 1. Thermal dependency of standard metabolic rate (SMR) and maximum metabolic rate (MMR), as well as the difference between both, the aerobic scope. Aerobic scope is maximized at “intermediate” temperatures (T_{opt}) because of the different temperature dependence of SMR and MME (top panel). Aerobic scope is used as a proxy for animal fitness, as it governs aerobic energy available for activity, feeding, growth and reproduction (bottom panel). Aerobic scope declines at T_{pejus} and can no longer be sustained beyond T_{crit} .

aerobic scope is reduced because a mismatch develops between the oxygen supply capacity and oxygen demand. The resulting energy deficiency causes performance to decline, which in the long-term constrains fitness and hence defines the thermal niche of the animal. Under acute exposure to temperatures beyond critical thermal limits (T_{crit}), aerobic metabolism can no longer support energy demand and the animal succumbs, although death may be postponed by compensatory anaerobic metabolism (Pörtner, 2001, 2002, 2010). The idea of oxygen-limited thermal tolerance has historical predecessors (Winterstein, 1905; Fry and Hart, 1948; Brett, 1971), but the OCLTT hypothesis differs by stressing the long term effects of capacity limitations, and by incorporating the role of the mitochondria. As ATP production depends not only on oxygen availability but also on functional mitochondria capable of using the oxygen, the OCLTT hypothesis extends beyond oxygen supply capacity. Indeed, a part of the OCLTT hypothesis deals with how to maintain mitochondrial function and the costs involved in doing so. In relation to cold limits, mitochondrial failure has been emphasized, resulting in falling ATP production rates, which then has consequences for maintaining oxygen delivery as energy demands posed by ventilation and circulation efforts can no longer be met. In relation to heat limits, insufficient capacity for oxygen delivery at the systemic level (i.e., the ventilatory and circulatory systems of the whole organism) is argued to first cause the onset of thermal limitation (e.g., Storch et al., 2014), subsequently resulting in tissue hypoxia and falling ATP production rates. Whether or not oxygen delivery is insufficient depends on the oxygen supply capacity in relation to oxygen (energy) expenditure. Time considerations are important here since dealing with acute thermal challenges will be fundamentally different from dealing with chronic heat stress (e.g., Cossins and Bowler, 1987; 128 129 130 131 132 133 134 135 136 137 138 139 140 141 142 143 144 145 146 147 148 149 150 151 152 153 154 155 156

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