

CORRESPONDENCE

Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology

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The Commentary by Pörtner, Bock and Mark (Pörtner et al., 2017) elaborates on the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis. Journal of Experimental Biology Commentaries allow for personal and controversial views, yet the journal also mandates that ‘opinion and fact must be clearly distinguishable’ (<http://jeb.biologists.org/content/article-types#comms>). We contend that Pörtner et al. (2017) do not meet this requirement, and that they present a biased account of the OCLTT hypothesis. We raise two main points: (1) Pörtner et al. (2017) do not do justice to the growing number of empirical studies that failed to support the OCLTT hypothesis when specifically testing its predictions, and (2) in response to these studies, and without new empirical evidence to support OCLTT, Pörtner and colleagues have gradually redefined the core assumptions of the hypothesis so that it is increasingly difficult to test and has lost predictive power.

Overlooking evidence against the hypothesis

Pörtner et al. (2017) portray the OCLTT hypothesis as a widely accepted consensus theory with great predictive power and depth. This impression is created by selective sampling of the literature (Pörtner is an author of 46 of the 98 references in Pörtner et al., 2017), and failure to acknowledge and incorporate studies that do not support the OCLTT hypothesis. In reality, the ecophysiological community is divided over the validity and utility of the hypothesis.

The controversy mainly revolves around whether OCLTT mechanisms are prevalent across ectotherms during warming, especially in response to long-term climate change. We agree that tissue oxygen limitation has been reported in some species during

acute thermal challenges, and that oxygen limitation may be the direct cause of deterioration in whole-animal performance in some animals in some contexts. However, a multitude of studies not cited in Pörtner et al. (2017) do not support oxygen limitation as the main factor limiting performance at high temperatures in ectotherms, emphasising that the OCLTT hypothesis is far from universally accepted (see discussions and references in Clark et al., 2013a,b; Jutfelt et al., 2014; Lefevre, 2016; Schulte, 2015).

There are a number of problems associated with the OCLTT hypothesis, including the points in Box 1 and the following findings. For marine ectotherms, a meta-analysis of aerobic metabolic rates failed to find a clear optimal temperature for aerobic scope in the majority of species during acute and long-term thermal exposures (Lefevre, 2016), contradicting a foundational assumption of the OCLTT hypothesis. In fish, the thermal profiles of aerobic scope and cardiac performance (following acute and long-term exposures) often do not align with ecologically relevant temperatures encountered by the species, and do not match the profiles of other important performances such as growth and reproduction (e.g. Gräns et al., 2014; Norin et al., 2014). Manipulations of ambient oxygen levels usually fail to alter acute thermal tolerance until severe hypoxia is reached (Brijs et al., 2015; Ern et al., 2016; Verberk et al., 2016), and altered tissue oxygenation capacity and aerobic scope generally have little effect on acute thermal tolerance (Brijs et al., 2015; Ekström et al., 2016; Wang et al., 2014). In arthropods, a review of the scientific literature demonstrated that oxygen limitation during acute warming is not universal but instead is restricted to certain groups (Verberk et al., 2016).

Box 1. Outstanding issues with the OCLTT hypothesis

1. Low testability of many claims means that unequivocal evidence for OCLTT mechanisms is lacking and confidence should be withheld.
2. Vague terminology and poorly defined concepts make measurements of these parameters prone to biased interpretations (e.g. pejus temperature, aerobic power budget).
3. Continuously changing y-axis labels on the famous bell-shaped thermal profiles (Fry curve or aerobic scope curve). In Pörtner et al. (2017) they read: 'Aerobic window (steady state)' in box 1 and 'Steady-state routine performance levels (—) at different metabolic rates (e.g. —)' in box 2, and the text refers to 'aerobic power budget' (Pörtner et al., 2017).
4. High reliance on schematic (aspirational) diagrams rather than empirically derived data to support the OCLTT hypothesis (e.g. see fig. 2 in Pörtner et al., 2017).
5. Although the OCLTT hypothesis is presented as mechanistic in Pörtner et al. (2017), most of the evidence supporting the hypothesis is indirect and derived from correlations among processes (i.e. negating the ability to attribute cause and effect).
6. The claim that tissue hypoxia is the first and most important cause of the downstream effects during warming (effects on growth, reproduction, foraging, immune competence, behaviours and competitiveness) has been asserted, not demonstrated.
7. Incorrectly considering aerobic scope or oxygen delivery capacity as the 'energy' available to animals, when in fact it is only a permissive factor compared with other constraints (e.g. food availability).
8. Overreaching conclusions and bold climate change-related extrapolations of results from acute, non-steady-state thermal challenges.

It is concerning that Pörtner et al. (2017) argue that studies using acute thermal challenges and 'non-steady-state' experiments are unsuitable for testing the OCLTT hypothesis, despite these authors using the same acute and non-steady-state approaches to initially devise the hypothesis and to continue to support their assertions. Results from studies based on acute and chronic thermal and hypoxic challenges that have failed to support the OCLTT hypothesis are of no lesser value than those claiming to support the hypothesis. If Pörtner et al. (2017) wish to develop the OCLTT hypothesis in accordance with available evidence, these critical studies should not be misrepresented, dismissed or ignored, but instead they should be weighed equally as those favouring the hypothesis.

The changing nature of the hypothesis

We are concerned with the way the OCLTT hypothesis continues to morph, despite the absence of new supportive data. Pörtner et al. (2017) modify the hypothesis compared with the many previous reviews of the subject, from the original focus on maximum metabolism and aerobic scope to a new emphasis on routine metabolic rates. While the relevance of the OCLTT hypothesis in a long-term ecologically relevant context remains unresolved, the added reservations for the 'aerobic power budget' and 'functional reserves' make the hypothesis much less testable. Indeed, oxygen limitation is readily testable at maximum physiological function (e.g. maximum oxygen uptake rate, or critical thermal maximum), yet it is difficult to investigate the existence or avoidance of local tissue oxygen limitation during routine activity. Moreover, the concept that oxygen might be limiting at routine levels of activity

seems illogical; it is hard to imagine why animals would allow tissue hypoxia to become severe enough to inflict performance declines at moderate levels of activity when possessing the functional capacity to significantly increase oxygen delivery to tissues. That assertion in Pörtner et al. (2017) is possibly untestable with available techniques and technologies.

To conclude, counter to the impression given in Pörtner et al. (2017), there is no consensus in the field on the generality of OCLTT mechanisms. While there is empirical support for the OCLTT hypothesis in certain contexts, there are substantial datasets contradicting predictions derived from the hypothesis. Moreover, the theoretical basis of the hypothesis appears to have shifted markedly. We encourage Pörtner and colleagues to consider all tests of the predictions originally made by the OCLTT hypothesis, and to provide a balanced assessment of these tests to draw conclusions about its generality. It is crucial that the OCLTT hypothesis retains clear and testable predictions, so that empirical scientists can evaluate in which animals and contexts the hypothesis might have predictive value. We would appreciate a clear guide on the experimental approaches deemed satisfactory for testing the current OCLTT hypothesis, and we welcome an open collaboration to conduct this research.

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Connecting to ecology: a challenge for comparative physiologists? Response to ‘Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology’

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Science is built on skepticism. We therefore appreciate the high interest in our paper (Pörtner et al., 2017) and welcome a debate that has been going on for some time. Our commentary started as a draft correspondence with specific criticism of a paper, and was then invited by the journal editor to address misunderstandings about the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis. Here we express some general concerns and the need to widen the debate as well as to eliminate an overly normative tone.

Further debate needs to be based on an interdisciplinary effort towards bridging the historic disciplinary divide between physiology and ecology. At present, this most-needed connection is prevented by a gap between many experimental findings and ecological reality. We assume, however, that agreement exists on the need to better understand the molecular, biochemical, physiological and anatomical factors that shape behavioral patterns, biogeographic distributions, abundance and biodiversity of ectotherms. Comparative (ecological and evolutionary) physiology needs to meet this challenge in order to contribute to projections of climate-related responses at the local community to ecosystem levels. Failure to embed physiological studies in a wider context can lead to the marginalization of experimental one-species studies as ‘simplistic’ (Boero et al., 2004), whereby the physiological (functional) background is left out in explaining ecological patterns and theory (Killen et al., 2014; Gaylord et al., 2015) owing to lack of realism (P. W. Boyd, S. Collins, S. Dupont, K. Fabricius, J.-P. Gattuso, J. Havenhand, D. A. Hutchins, U. Riebesell, M. S. Rintoul, M. Vichi et al., unpublished). This also applies if the conceptual approach is not sufficiently comprehensive, e.g. if constrained to molecular markers or behavioral change. Physiology needs to contribute to explaining demographic and vital rates, movement and shifts in species interactions – across multiple scales.

This challenge exposes classical physiological testing to scrutiny. In brief, fitting physiological patterns to related field phenomena using the OCLTT hypothesis has emphasized the relevance of (1) routine (i.e. long-term sustainable) performance and (2) subtle functional constraints at their onset, as well as the physiological and molecular indicators of those constraints and, only then, (3) time-dependent (short-term) tolerance to extreme challenges such as heat waves as captured by critical temperature of OCLTT and critical thermal maximum (CT_{max}) (Pörtner et al., 2017). Importantly, investigations of (1) to (3) need to precisely consider the species-specific ecological background. Furthermore, the temperature-dependent long-term performance window is mirrored in relevant gene expression patterns (e.g. Windisch et al., 2014). We have assessed several papers identified as candidates for evidence against OCLTT and found that some approaches used do not meet relevant requirements (Pörtner et al., 2017). For example, we caution against testing the role of oxygen in OCLTT using CT_{max} (too insensitive) and with an inward look into classic physiological knowledge. Insofar, we argue that such studies are at high risk to fail and indeed,

we interpret many of their findings differently. This is a natural process of scientific debate, which will ultimately push the field forwards.

Importantly, and often miscommunicated, the OCLTT hypothesis reaches beyond aerobic scope for exercise (AS) to include various routine performances fueled by the more comprehensive aerobic power budget (and underlying food intake). As a result of trade-offs within the total energy budget, individual physiological processes such as growth and exercise may or may not have different thermal optima. The OCLTT concept takes into account the fact that subtle physiological constraints at the onset of thermal limitation are already connected to ecological change. Pejus temperatures (T_p) indicate the onset of limitation and are most relevant on ecological terms in sensitive life stages, also seen in an air breather (e.g. Smith et al., 2015), and during routine activity. Accordingly, we conclude that the title chosen by Jutfelt et al. is factually and conceptually misleading.

The methods used to develop the OCLTT hypothesis are all available and provide relevant data with new avenues for their interpretation. The challenging of conventional methods implies that more sophisticated methods and indicators may need to be developed (as for an insect study, Teague et al., 2017). Importantly, to connect closely to ecological change, studies need to consider the long-term consequences of subtle functional constraints for performance capacity and competitive strength in an experimental setting that would not disrupt the ecological context for the respective life stage (e.g. salmon migration, Farrell, 2016). Indeed, such requirements are rarely met in purely physiological studies. Pushing the OCLTT hypothesis back to early stages of the concept does not support further progress. The request for a detailed guide on how to investigate OCLTT is unusual as our studies of different levels of biological organization and field phenomena are repeatable and thereby, in addition to supporting our conclusions, fulfil relevant requirements associated with scientific publishing. That said, jointly developing a best practice guide would, in fact, be rewarding.

The OCLTT hypothesis also strives to integrate levels of biological organization from gene to cell and organism to ecosystem. As no alternative integrative concept is presently available, we anticipate that the OCLTT hypothesis will continue to evolve and be useful for those working in an ecological context as closely as we are trying to do. We also reiterate that the OCLTT concept considers the evolutionary context, beyond the testing of as many individual species as possible (Pörtner et al., 2017). We need to understand the constraints and changes that have affected key physiological functions over evolutionary time. ‘Stamp collecting’ many species at an adult stage does not help here, if the ecology and life history of each species as well as temperature-induced constraints on critical life stages are not considered in the interpretation (e.g. Marcus and Boero, 1998; Farrell, 2016; Boardman and Terblanche, 2015; Pörtner et al., 2017). In light of

the need to carefully match hypotheses and data, one wonders whether the database of the careful meta-analysis referred to can provide evidence for or against OCLTT.

Finally, we thank Jutfelt et al. for the offer of collaboration, which we happily accept. At the same time, we encourage everybody to develop alternative concepts equally powerful in bridging the gap between physiology and ecology that we can then test together. We need a healthy competition of concepts with a perspective to build linkages to other disciplines rather than an inward-looking overly narrow normative debate, which, if successful, would constrain future inter- and transdisciplinary research. We might then also miss a chance to enhance the contribution of experimental biology to addressing questions of high societal relevance, such as the impacts of climate change (e.g. Urban et al., 2011; Pörtner et al., 2014; Poloczanska et al., 2014). In light of the difference of opinion regarding the applicability of the OCLTT hypothesis, perhaps now is the time to move the debate to a more flexible forum than journal correspondence, which is restrictive in its length and therefore its scope.

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