Journal of Thermal Biology 38 (2013) 55–63

Contents lists available at SciVerse ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Review

Temperature and respiratory function in ectothermic vertebrates

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ARTICLE INFO

Article history:
Received 7 September 2012
Accepted 7 November 2012
Available online 16 November 2012

Keywords:
Pulmonary ventilation
Gas exchange
Blood gases
Amphibians
Reptiles
Lungfish
Climate changes

ABSTRACT

Pulmonary ventilation is adjusted to maintain balance between O_2 demands and CO_2 elimination, which is essential for acid–base status in land ectothermic vertebrates. Rising temperatures cause increases in O_2 consumption (Q_{10} effect) and decreases in the O_2 affinity of hemoglobin (a rightward shift in the oxygen–hemoglobin dissociation curve). These changes in air-breathing ectotherms are not proportional, i.e., the increased ventilation is relatively smaller than the change in metabolic rate. Therefore, the ratio between ventilation and metabolic rate is reduced, and consequently blood pH changes inversely with temperature. The combination of high temperatures and hypoxia exposure results in an amplified increase of ventilation, which may be explained by the balance between increased O_2-demand and decreased O_2-supply as well as increased O_2-chemoreceptors sensitivity. High temperature also increases pulmonary diffusing capacity. Global warming is expected to have significant impacts on the world's climate, with temperature changes affecting living organisms, in relation to their physiology and distribution. These physiological mechanisms and their capacity to respond appropriately to temperature illustrate the complexity of the relationship between ambient temperature and the respiratory function in ectothermic vertebrates, which are particularly susceptible to change in their environment.

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1. Introduction

Temperature is one environmental factor (among others such as oxygen (O_2) availability, humidity, seasonal cycle) that affects biological processes in vertebrate animals. Most chemical reactions undergo increases in kinetics with rising temperature. Environmental temperature exerts a great influence on ectothermic vertebrates' life and physiology (cf. Dejours, 1981). O_2 is essential playing a key role in ATP synthesis and consequently cell function. Ectotherms may modulate their biochemistry and physiology to compensate for any reduction in performance resulting from the acute effects of temperature change. These processes may differ between species

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0306-4565/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtherbio.2012.11.001

and according to animal size, physiological status, nutrition, thermal history. Responses also vary according to the rate and amplitude of temperature change. Ectothermic vertebrates include a wide variety of species which live in different environmental conditions (Hawkins, 1995). It is important to point out that temperature effects are not limited to the respiratory function (which is the focus of this review), but the effects of temperature change may also be studied in reference to physiology, dispersal capacity and distributional ranges as well as their physiological performance and fitness (locomotor performance), which are highly thermally sensitive (Herrel and Bonneaud, 2012). Another aspect to consider is the effect of seasonal oscillation-related changes in metabolism, which in turn impact respiratory function (da Silva et al., 2008; Toledo et al., 2008; Glass et al., 1997; Bícego-Nahas et al., 2001). Toledo et al. (2008) reported that in tegu lizards (*Tupinambis merianae*), metabolic rates vary seasonally, being higher in spring and summer than in autumn and winter at the same temperatures, regardless of animal size.

In studies of bimodal respiration in fish and amphibians, the relative importance of aerial O_2 uptake can change as a function of various ambient factors such as temperature (Lenfant et al.,1970; Rahn and Baumgardner, 1972; Glass and Wood, 1983; Wood and Glass, 1991; Burggren et al., 1983). Taking into account the aquatic versus aerial environment as respiratory media, there are different aspects to be considered. Due to the amount of dissolved oxygen, water is a very poor environment when compared to the atmospheric air. Two other important variables are the density and the viscosity of both media, in which the water density and viscosity is greater than that of air. This gives an impression on the difficulties faced by the water-breather to achieve the necessary O_2 for its aerobic metabolism, a problem which is partially solved by a highly sophisticated countercurrent system in which the blood passes the gills in the opposite direction of the inspired water flow. Apart from these conditions for respiration, it should be pointed out that the O_2 content in water depends on photosynthesis, which changes on a daily and seasonal basis, although it plays a minor role in fresh water where algae are not abundant. Of interest for the present review is the fact that changes in temperature (among others: water movement, currents, salinity) is determinant for O_2 levels in water (cf. Dejours, 1981). In air-breathing fish this may have a significant impact. For instance, Johansen et al. (1970) stated that increased water temperature is associated with diminished oxygen content and that oxygen deficiency in the water is considered to be the most important single factor favoring selection of air breathing habits in fishes. They found that at 10 °C *Amia calva* (able to breathe air using their swim bladder) is relatively inactive and almost exclusive water-breather. With increasing temperature and activity, the rate of oxygen depletion from the gas bladder increases progressively and air breathing rate increases. At 30 °C, three times as much oxygen is taken from air as from water, but the gills continue to be the principal site for CO_2 elimination (Johansen et al., 1970; Hedrick and Jones, 1999).

Given the great diversity of aquatic environments and of fish species that are subjected to temperature oscillations in their habitat, this review will only focus on some aspects of respiratory function that are influenced by temperature in land ectotherm vertebrates and also will approach the lungfish as an interesting model of studying temperature and respiratory function associated with transition from water to air breathing.

2. Amphibians and reptiles

2.1. Temperature and respiratory control of the acid–base balance

The arterial pH (pHa) of virtually all ectothermic vertebrates decreases with rising temperature (Fig. 1C) (cf. Jackson, 1971, 1978). The negative $\Delta pHa/\Delta T$ can be obtained by adjustments of bicarbonate levels or respiratory modulation of arterial PCO_2. Ectothermic vertebrates are essentially prone to very a labile body temperature (T_b), greatly influenced by ambient temperature (T_a), which causes relatively large variations in their metabolic demands. Ventilation changes in order to balance the CO_2 elimination as well as the O_2 demands. The Henderson–Hasselbalch equation indicates that pH of the blood is greatly influenced by the CO_2

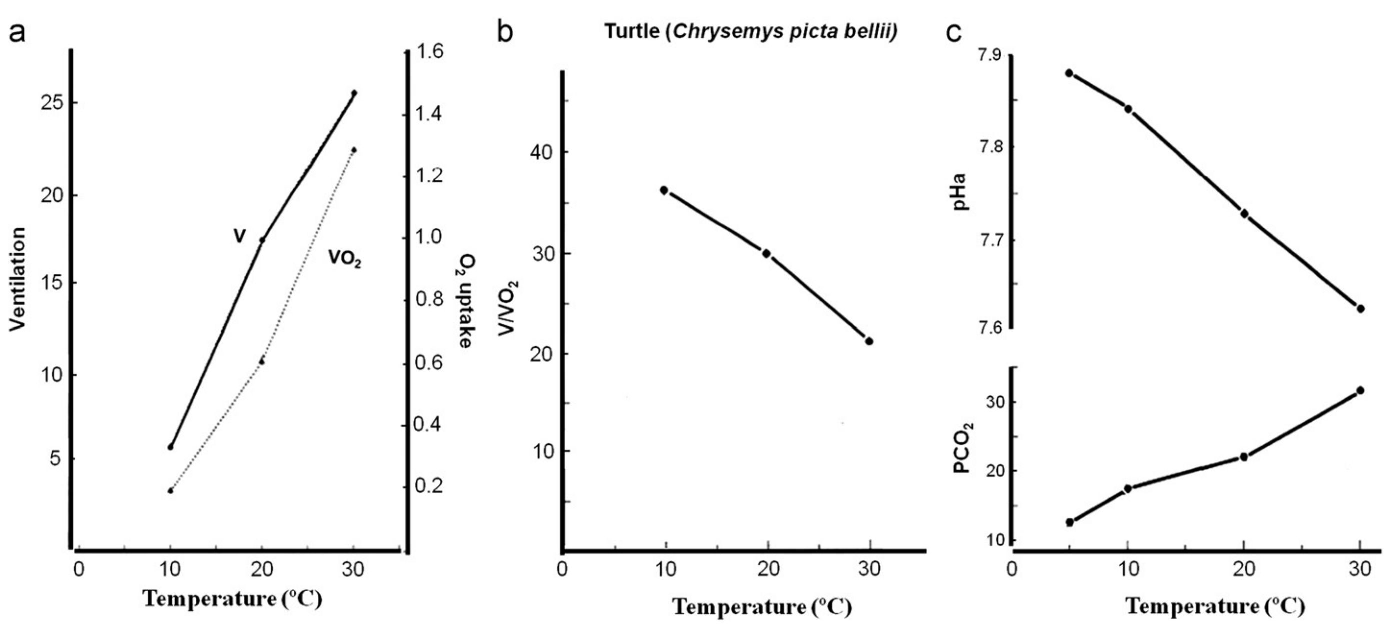

Fig. 1. Temperature effects on pulmonary ventilation and O_2 uptake (panel A), air convection requirement (panel B) and arterial pH and PCO_2 (panel C) in turtle. Notice that as temperature rises (from 10 to 30 °C), there is a non-proportional increase of ventilation and VO_2 (A), which decreases V/VO_2 (B). Consequently PCO_2 increases and pHa falls (C). Modified from Glass et al. (1985).