

CHAPTER 6

Thermoregulation and Hydric Balance in Amphibians

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INTRODUCTION

Research on wildlife ecophysiology is accelerating as the urgency of the global biodiversity crisis is recognized (Bovo et al. 2018). Amphibians are an extraordinarily diverse group of tetrapods—with more than 8,000 species living from the sea level to mountaintops up to 5,000 m asl—that managed to adapt to different terrestrial and freshwater environments across the globe (Duellman and Trueb 1994). Despite some differences between the three orders of amphibians, they share important morphological and physiological traits that make them key models to understand central issues of physiological ecology. Salamanders, anurans, and caecilians share a particular link to water (de Andrade et al. 2017). Only through the lens of the interrelations between temperature and humidity can we try to understand the complexity of amphibian ecological physiology. Moreover, as climate change advances, this understanding is crucial to assess amphibian vulnerability and plan their conservation. In this chapter we aim to briefly explain the state of the art on amphibian thermoregulation and hydric balance, their interconnections, and the relation with main threats imposed on these animals in the Anthropocene.

Ecophysiology aims to understand how animals deal with problems and exploit the opportunities offered by environmental conditions (Willmer et al. 2009). The most prominent environmental conditions driving the ecology and physiology of amphibians are temperature and water or moisture regimes. Temperature, because amphibians are ectotherms—i.e., animals that

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do not produce enough metabolic heat to maintain constant body temperatures. And since all cellular processes are temperature-dependent, maintaining a constant internal temperature enhances physiological performance and individuals' fitness (Angilletta 2009, Taylor et al. 2020). Water, mainly because of two facts: larval states are aquatic, and the skin of adult amphibians is highly permeable, turning them profoundly dependable on water and humidity to live and reproduce (Tracy 1976). Moreover, temperature and humidity are tightly related, both environmentally and with regards to amphibian's physiology (Rozen-Rechels et al. 2019).

Despite being interconnected phenomena, thermal and hydric ecology have been traditionally studied separately. Thus, we will begin this chapter by reviewing amphibians' thermal and hydric ecology, with an emphasis on how these animals regulate their body temperature and water balance, to be able to go into depth on both processes separately. Then we will assess the interactions between temperature and humidity, introducing the thermo-hydroregulation framework, and their effects on the biology and ecology of amphibians. Finally, we will briefly comment on the main impacts of human activities in relation with amphibian ecophysiology (more details on amphibian ecophysiology in chapter 3).

Thermal Ecology

As ectotherms, amphibians are highly sensitive to the effects of environmental temperature. Their habitats often experience substantial daily and annual thermal fluctuations (Huey 1982, Huey and Berrigan 2001). Species' environmental physiology can vary considerably, with important consequences for performance and fitness under different environments (Huey and Stevenson 1979, Sinclair 2016). Behavioral thermoregulation is the main strategy of amphibians to buffer climatic variations (Huey et al. 2012, Sunday et al. 2014, Diele-Viegas and Rocha 2018). Thus, we can understand the thermal ecology of one species or population by assessing two main aspects: thermal sensitivity of performance and thermoregulation (Angilletta 2009).

Thermal Sensitivity

Although this chapter focuses on amphibian's thermoregulation, we will briefly introduce thermal sensitivity (or thermosensitivity) to better understand how thermal regulation functions. Thermal sensitivity describes how performance of any biological function, including behavior and relative fitness, depends on environmental temperature. Thermal sensitivity places species and populations in a non-static gradient between thermal generalists—performing under a wide range of environmental temperatures—and thermal specialists—performing under a narrow thermal range (Angilletta 2009). The Australian frog *Geocrinia alba*, for example, shows narrow thermal (and hydric) limits that, living in a drying and warming habitat, make it highly vulnerable to climate change (Hoffmann et al. 2021). At the other extreme of the thermal sensitivity gradient would be, for example, *Bufo bufo*, whose generalist thermal physiology could provide the species a remarkable resilience to climate change (Rosset and Oertli 2011). There is a general trend of specialists reaching higher performance rates than generalists (the “hotter is better” hypothesis),

probably because having a biochemical machinery that performs under different temperature ranges is costly (Angilletta et al. 2010, Richter-Boix et al. 2015).

A function defining thermal sensitivity is called a thermal reaction norm. Some thermal reaction norms, the thermal performance curves (TPC) are commonly obtained to establish and compare the thermal sensitivity of different populations or species. For adult amphibians, it is frequent to make TPCs of locomotion or calling frequency (Bevier 2016), while growth or survival rates are mainly estimated for larval stages (Navas et al. 2008). Locomotion TPCs commonly assess the thermal dependence of swimming burst speed or jumping performance, for aquatic and terrestrial species, respectively (e.g., Careau et al. 2014, Lai et al. 2018, Greenberg and Palen 2021). A typical TPC is left-skewed and bell-shaped, with a minimum temperature value defined as critical thermal minimum (CT_{min}) and a maximum value defined as a critical thermal maximum (CT_{max}). There is an optimal temperature (T_{opt}) for which performance is maximized and a performance breadth that usually covers the temperatures that limit the top 80% of the performance curve (Fig. 1) (Huey and Stevenson 1979, Angilletta 2006). In terms of thermal physiology, temperatures that exceed an ectotherm's critical thermal maximum (CT_{max}) or thermal optimum (T_{opt}) would impair fitness, limit activity, or induce mortality, hence informing on the absolute thermal tolerance range of the species (Sunday et al. 2014). For this reason, and because they are frequently estimated, TPCs are helpful to compare thermal biology of amphibian species and their vulnerability to climate change (Rosset and Oertli 2011, Taylor et al. 2020).

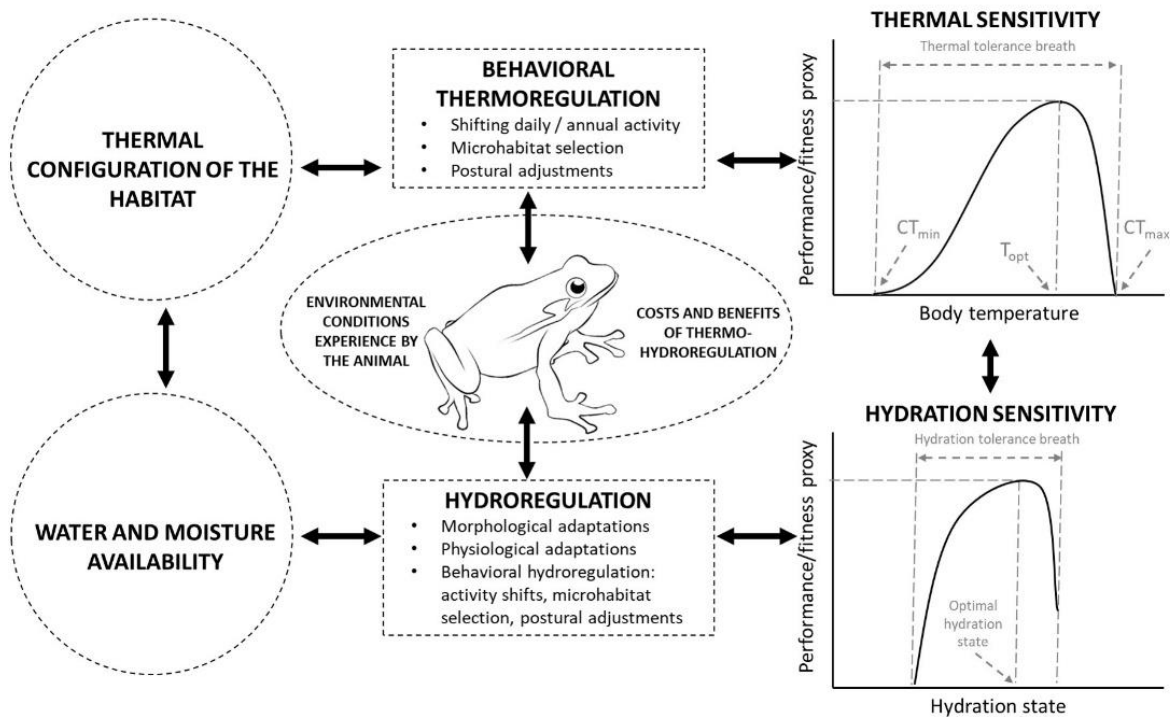


Figure 1. Integrative scheme on how the environment and the organism interact with respect to thermal ecology and water balance of amphibians. The hypothetical situations would be quite different depending on the habitat (aquatic, semi-aquatic or terrestrial) and period of activity (diurnal or nocturnal) species, being the most complex situation that of a terrestrial diurnal amphibian. Abbreviations: CT_{min} = critical thermal minimum; CT_{max} = critical thermal maximum, T_{opt} = optimal temperature.

Variation on thermal sensitivity of amphibian populations can be due to evolution or phenotypic plasticity. These processes interact and, in many cases, it is difficult to assess whether thermal sensitivity differs due to one or the other (Bodensteiner et al. 2021). Critical temperatures usually evolve differently, with CT_{min} evolving at a faster rate than CT_{max} , probably because thermoregulation through microhabitat selection allows animals to actively avoid hot places. This way, thermoregulation may slow evolutionary adaptation of some physiological parameters, a process known as the “Bogert effect” (Huey et al. 2003), as suggested to happen in plethodontid salamanders (Farallo et al. 2018). Although generally evolving slowly, the parameters at the hot part of the TPC, as the T_{opt} and CT_{max} tend to coevolve, allowing thermal adaptation to new conditions. For example, tadpoles of *Lithobates sylvaticus* rapidly evolved, increasing their CT_{max} , when invader beavers modified thermal conditions of their habitats (Skelly and Freidenburg 2000). Moreover, amphibians frequently show events of microevolution and local adaptation to microclimatic conditions, probably due to their low dispersal capacity (Bodensteiner et al. 2021). For example, genetically connected populations of *Rana arvalis* diverged on larval life history and locomotor performance depending on the thermal conditions of ponds (Richter-Boixet et al. 2015).

Phenotypic plasticity can also be reflected into ontological differences on thermal sensitivity or thermal acclimation. Eggs or tadpoles may show different TPCs than adult amphibians, as found in four anuran species—*Hypsiboas crepitans*, *Engytomops pustulosus*, *Rhinella humboldti* and *Espadarama prosoblepon*—in Colombia (Turriago et al. 2015). How other intrinsic (e.g., sex, nutritional state) or extrinsic factors (e.g., altitude, water availability, predation pressure) interact with phenotypic plasticity of thermal sensitivity of amphibians will allow us to better understand the ecophysiology of this group and their responses to human impacts. For instance, research on the treefrog *Hyla versicolor* can illustrate the complexity of plastic responses on amphibian thermal sensitivity, where exposure to predatory chemical cues and pesticides induced interactive effects on the TPC of tadpoles (Katzenberger et al. 2014). In any case, it is important to consider the different aspects of the thermal sensitivity of an amphibian species or population to better understand how they regulate their body temperature.

Thermoregulation

The second key aspect of thermal ecology is temperature regulation or thermoregulation, i.e., the ability to maintain body temperatures with a certain mean and variability, responding to conditions of the external environment. Thus, we can imagine a continuum of strategies from thermoconformer animals—whose body temperatures reflect environmental temperatures—to perfect thermoregulators—whose body temperatures are constant, despite environmental fluctuations. Thermoregulation would evolve to enhance performance on thermally variable environments (Angilletta 2009). Many amphibians are aquatic and/or nocturnal, and, thus, live in quite thermally homogeneous environments with limited opportunities for behavioral thermoregulation. That would also be the case of caecilians that, having less permeable skin than other amphibians and living in moist soils or water, are thought to be quite thermoconformers (Measey and Van Dongen 2006). Diurnal species living in tropical rainforests also experience quite thermally homogeneous environments, even at high elevation (e.g., Navas 1997).

However, diurnal amphibians more linked to terrestrial habitats, as open areas, rely on behavioral adjustments to thermoregulate, allowing them more time for feeding, reproduction, or growth (Brattstrom 1979).

For ectotherms, heat exchange relies on solar radiation (direct and reflected on objects), conduction, convection, and evaporation. Specifically, amphibians would use solar radiation, conduction from the substrate or the water, and convection from the air to gain heat; and would rely on evaporation, conduction and radiation to the substrate, water and/or air, and convection to air to cool themselves. The combination of these sources and mechanisms of heat exchange will depend on the habitat (terrestrial, semi-aquatic, aquatic) and period of activity (diurnal vs nocturnal), as well as the presence of morphological adaptations (Brattstrom 1963) (Fig. 2).

Thermoregulation is usually conceived as a balance of costs and benefits (Huey and Slatkin 1976, Vickers et al. 2011). Benefits are obvious, since achieving a body temperature within a range that maximizes performance will enhance physiological performance of the individual. However, thermoregulation also entails costs, which will depend on habitat traits, thermoregulation strategies and interactions with other organisms (Sears and Angilletta 2015). We can divide costs into two types: energetic and non-energetic costs. Energetic costs consider that energy used for thermoregulation is not allocated to other activities, such as forage or mate. Non-energetic costs include the risk of predation associated with thermoregulation strategies, as well as the loss of opportunities for doing other activities while thermoregulating (Angilletta 2009).

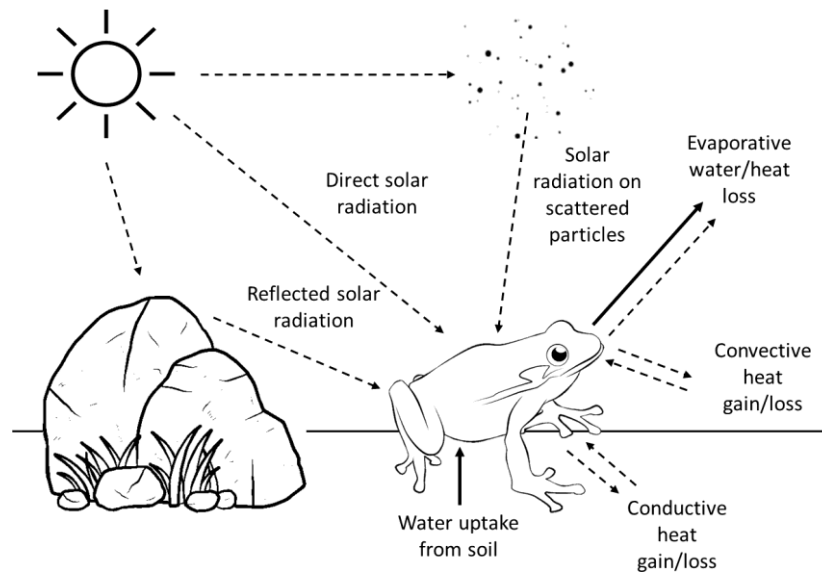


Figure 2. Main sources of heat and water flux for a hypothetical diurnal amphibian. Dashed lines depict heat exchange and continuous lines water exchange. For an aquatic animal (tadpole or adult), heat exchange would be mainly due to convection with the surrounding water, with a possible contribution of solar radiation at the surface of the water. For a nocturnal terrestrial amphibian, heat exchange would rely on convection with air, conduction with the substrate and evaporative cooling, while water exchange would be qualitative similar than this depicted in the figure (evaporative water loss and water uptake from moist soil).

For aquatic amphibians, for example, selecting warmer waters may imply less oxygen availability, thus hindering respiration and osmoregulation (Brattstrom 1979). As with most aspects of the behavioral ecology of amphibians, thermoregulatory strategies are tightly linked to their dependence on water and atmospheric humidity. For aquatic amphibians—or aquatic larval stages of terrestrial species—thermoregulation is limited and mainly behavioral, by means of habitat selection. For terrestrial amphibians, thermoregulation may combine physiology—by means of evaporative cooling—and behavior—by modulating activity, microhabitat selection and postural adjustments (Figs. 1 and 2) (Brattstrom 1963). This way, the inevitable water loss resulting from dermal respiration of terrestrial amphibians is also an important cooling mechanism, and thermoregulation will be only prioritized under suitable hydration or water availability situations (Brattstrom 1979).

Heliothermy (i.e., quickly heat up through solar radiation combining microhabitat selection and postural adjustments) is the main thermoregulatory strategy of many diurnal ectotherms, as lizards. However, the trade-off between cooling through evapotranspiration and maintaining suitable hydration would turn heliothermy too costly for most amphibian species. Nonetheless, some anurans can use heliothermy by being indirect contact with water or by decreasing skin permeability. Some temperate species of *Rana*, *Bufo* and *Hyla* are known to bask under the sun with the ventral part of their bodies in contact with a moist substrate that they actively selected (Brattstrom 1963). Moreover, *Lithobates catesbeianus* combines basking with postural adjustments to keep activity body temperatures within a relatively narrow range (Lillywhite 1970). Different morphological adaptations can allow basking anurans to maintain water balance, such as skin grooves or mucous secretions (Brattstrom 1979). Some amphibians, as *Anaxyrus boreas*, even bask on dry soil, perhaps due to a high water-storage capacity (Lillywhite et al. 1973).

Microhabitat selection and modulation of daily and annual activity patterns are the other two main mechanisms of behavioral thermoregulation (Fig. 1). Plethodontid salamanders are also known to use microhabitat selection to thermoregulate while maintaining water balance (Farallo et al. 2018). While thermal conditions of tropical areas are quite temporally stable, considerable thermal shifts on daily or seasonal activity patterns would be important thermoregulatory strategies for temperate amphibians (Lillywhite 2016). Many frogs and salamanders inhabiting high latitudes or altitudes hibernate when the habitat is below-zero, and some of them have anti-freezing substances in their blood, as is the case of northern populations of *L. sylvaticus* (Costanzo et al. 2013). At not-so-extreme conditions, the toad *A. boreas* is known to thermoregulate by being more diurnal or nocturnal depending on the thermal conditions of the environment (Carey 1978). High mountain Andean populations of *Rhinella spinulosa* use a combination of thigmothermy (i.e., heating up by conduction from the substrate), basking, regulating daily activity hours and microhabitat selection (Sinsch 1989). Thermoregulation through microhabitat selection is not limited to adult amphibians. On the contrary, thermoregulation can begin as early as with the selection of thermally suitable oviposition sites for some species, as documented on *L. sylvaticus* (Freidenburg 2017). For example, tadpoles of *Pseudacris geilla* and *A. boreas* select warmer water both in laboratory and field conditions (Bancroft et al. 2008). Furthermore, tadpoles of high-altitude *R. spinulosa* populations use grouping behavior, or aggregation, to achieve higher temperatures (Espinoza and Quinteros 2008). As we can see, morphological adaptations related to water balance and thermos-hydroregulation behaviors are usually combined in amphibians.

After almost a century of research, we are beginning to understand the complex mechanisms driving the thermal ecology of amphibians. Next steps will elucidate how other important extrinsic and intrinsic factors, such as oxygen availability or personality, interact and shape amphibian ecophysiology. There is also a male bias in studies of thermal traits that needs to be addressed in the next decades to fully understand the evolutionary dynamics and consequences of climate change to these threatened vertebrates (Bodensteiner et al. 2021). If the reader wants to study thermal ecology of amphibians, or to know more about the available methodologies, we refer to a thorough review in Taylor et al. (2020).

Hydric Balance

As many other vertebrates, Amphibians are composed of 70–80% water and need to maintain a stable internal environment for chemical reactions inside cells. The word ‘amphibian’ translates from Greek as ‘both lives’, due to their interphase between aquatic and terrestrial habitats. Amphibians are particular among tetrapods due to their permeable skin, considered an adaptation to terrestrial life (Shoemaker et al. 1992, Toledo and Jared 1993). This, added to the fact that oviposition and larval phases are generally aquatic, makes amphibians a special case regarding their dependence on water. This happens even to the point that the availability of water is an essential driver of the distribution of amphibians, probably even more than temperature (Greenberg and Palen 2021). Aquatic and fossorial species present reduced skin permeability, but terrestrial amphibians possess a skin that is highly permeable to water, equally in both directions (Brattstrom 1963). Main functions of the amphibian skin are osmoregulation and respiration—to the point that some groups, such as plethodontid salamanders, lack lungs. This skin allows water uptake directly from the water, or from moist substrates, but not from air (Brattstrom 1963). Finally, this permeable skin also contributes to thermoregulation via evaporation (Fig. 2) (Toledo and Jared 1993).

The hydration state of the organism also influences performance (Mitchell and Bergmann 2016). Thus, we can think of a ‘hydration sensitivity’ of all biological functions (and, ultimately, fitness) that would be analogous to thermal sensitivity. The relation between hydration state and performance would be more asymmetrical than temperature since performance would drop off sharply under the dehydration extreme of the axis (Fig. 1). This hydration sensitivity would be more evident for semi-aquatic or terrestrial amphibians, since most aquatic phases or species, under normal conditions, would not experience dehydration situations in their habitats. Finally, as different species show a variety of morphological and physiological adaptations to prevent water loss and enhance water uptake, the shape of the hydration sensitivity functions would vary accordingly. In any case, it makes more sense to think of hydration sensitivity as the third dimension of a thermal-hydroregulation framework than to consider it separately (see next section and Rozen-Rechels et al. 2019).

Analogously as we saw for thermal ecology, the other axis of amphibians' hydricecology would be hydroregulation, or regulation of the hydric balance. In addition to behavioral adjustments, some of them similar to those used for thermoregulation— e.g., postural adjustments, being active when humidity is suitable for the species and select humid microhabitats or shelters—many terrestrial amphibians also rely on morphological adaptations to regulate their hydric balance (Fig. 1; also see Chapter 7). Amphibians do not drink in normal conditions; instead, water enters through the skin. Granular skin is more vascularized, allowing rapid water uptake (Canziani and Cannata 1980). Thus, while aquatic species generally have homogeneously smooth skin, terrestrial anurans and salamanders show some parts of granular skin, and the degree of skin smoothness even change within species, being lower on those inhabiting drier environments. Cutaneous grooves are the other most common adaptation enhancing water intake of anurans and salamanders, carrying the water from the moist surface throughout the amphibian body by capillarity. A particular adaptation for water absorbance is the 'pelvic patch', an area concentrating granular skin and/ or cutaneous grooves for rehydration. Other modifications of the skin are adapted to decrease the animal's water loss, such as epidermis with higher lipid content, iridophores, mucus, cocoons that cover the whole animal preventing desiccation on dry seasons, co-ossification and osteoderms of some hylid frogs living inside bromeliad leaves, or a calcified dermal layer (Toledo and Jared 1993). In addition, some behavioral adaptations may be exclusive to prevent water loss during the driest periods, as burying for some species of *Bufo*, who bury themselves deeper the drier is the soil (Ruibal and Hillman 1981). Finally, another morphological adaptation to enhance water balance is to use the bladder for water storage in terrestrial anurans (e.g., Ruibal 1962) and salamanders (e.g., Brown et al. 1977).

Main behavioral hydroregulation strategies imply adjusting daily or seasonal activity periods, looking for moist shelters, and using water-conserving and water-absorbing postures (Lillywhite 2016). These behavioral adjustments are usually combined with morphological and physiological ones (Fig. 1). For example, the desert-dwelling toad *Anaxyrus punctatus* absorbs water by pressing its pelvic patch with the moist substrate (Brekke et al. 1991). Hylid frogs covering themselves with lipids to reduce evaporative water loss show a typical wiping behavior to spread the secretions over the body surface. After wiping, they generally remain immobile for a while, on water-conserving postures, with some species even reducing their metabolism to torpor states (Blaylock et al. 1976, Gomez et al. 2006, Barbeau and Lillywhite 2005). The desert-dwelling frog *Phyllomedusa sauvagei* wipes cutaneous lipid secretions until environmental temperature reaches 30°C, and then, skin water evaporation raises, preventing the animal from overheating (Brattstrom 1979). This example of the use of water evaporation through the skin as a thermoregulatory strategy is widespread among amphibians and links thermoregulation and hydric balance, as we see in more detail in the next section.

Interactions Between Thermoregulation and Hydric Balance

At the planetary level, water availability and temperature are correlated on space and time. At the individual level, body temperature drives biochemical reactions and water balance determines cell

metabolism. Therefore, body temperature and hydration state are correlated physiological axes that will interactively shape performance and fitness (Fig. 1) (Greenberg and Palen 2021). Despite much research on cases where thermo- and hydroregulation interact, an integrative conceptual framework for thermo-hydroregulation is recent (Rozen-Rechels et al. 2019). This framework establishes an integrative panorama where the thermal and water landscapes interact to shape the biophysical properties and behavior of animals, ultimately driving their performance, population dynamics and range distributions (Rozen-Rechels et al. 2019). The adaptation and application of this framework of thermo-hydroregulation for the particular biology of amphibians will be of great interest in future years. Thermo-hydroregulation is defined as an interactive set of behavioral and physiological processes maintaining the organismal thermal and water balance, and thus optimizing performance, survival, and reproduction (Rozen-Rechels et al. 2019). This is obvious for amphibians, whose permeable skin and larval dependence on water bodies make them particularly sensitive to water (Anderson and Andrade 2017). We already explained the main connections between thermoregulation and water balance along the other sections, but here we will briefly summarize the most relevant shared physiological and behavioral mechanisms found in amphibians, to help the reader visualize the integrated framework.

Physiological mechanisms of thermo-hydroregulation are common in amphibians. As evaporation through the permeable skin reduces body temperature, cutaneous adaptations to prevent water loss (see previous section) interact with thermal ecology. Cutaneous resistance to water loss allows arboreal basking frogs to warm up while avoiding hydric stress, and larger frog species (lower surface/volume ratio) may enhance their ability to be away from water sources for longer time than smaller ones (Tracy et al. 2010). Basking *Hyla arenicolor* is known to adapt its evaporative water loss to enhance thermoregulation (Snyder and Hammerson 1993). At the same time, water deprivation can lead amphibians to select for lower body temperatures to avoid further water stress (Anderson and Andrade 2017, Hoffmann et al. 2021). Critical thermal limits are known to change depending on the hydration state of the organism, reducing performance and thermal tolerance as the individual dehydrates (Rozen-Rechels et al. 2019, Hoffmann et al. 2021). In fact, Rozen-Rechels and collaborators (2019) propose to modify thermal performance curves to accommodate hydration state as a third dimension, since there is enough evidence supporting that temperature plus water explain amphibian's performance and fitness better than only temperature (Anderson and Andrade 2017). Although future research will shed more light, and specific differences may exist, the effects of water and temperature on performance are probably interactive rather than additive (Rozen-Rechels et al. 2019).

Main behavioral mechanisms for thermo- and hydroregulation are shared, as the seasonal and daily shifts on activity patterns to match suitable conditions of environmental temperature and water/moisture availability, postural adjustments (that can be different depending on the animal's priority for regulating temperature or water balance) and microhabitat selection (Fig. 1) (Rozen-Rechels et al. 2019). Plethodontid salamanders change the rate of dehydration—by absorbing water

from the soil—depending on body size, air humidity and environmental temperature, and showed different behavioral adaptations to thermo-hydroregulate. For example, *Plethodon ouachitae* and *P. caddoensis* burrowed themselves during hot dry summers (Spotila 1972). In the forest frog *Eleutherodactylus coqui*, postural adjustments throughout the day would lead to optimize thermoregulation while minimizing waterloss at the same time (Pough et al. 1983). With all of this in mind, the model of costs and benefits of thermoregulation needs to be updated to consider the effect of water availability in the habitat. The costs and benefits of hydroregulation may be delayed with respect to those of thermoregulation, since water uptake and loss tend to be slower than heat exchange. In addition, costs of hydroregulation may be more asymmetric, since they would be more associated with a lack of water than an excess of it (Rozen-Rechels et al. 2019). For instance, *Rana temporaria* selects moist and cool habitats in the field (Köhler et al. 2011), and other amphibians seem to also select moist microhabitats over optimal thermal conditions (Greenberg and Palen 2021). In addition, *Lithobates clamitans* that, as many other aquatic frogs, uses jumping as a main mechanism for predator avoidance—and while temperature and moisture interact to shape jumping performance—prioritizes hydroregulation over thermoregulation (Mitchell and Bergmann 2016). Assessing the relative contribution of each environmental variable and their interactions on microhabitat selection of each species will further elucidate how amphibians make these decisions (Ortega et al. 2019).

Relations Between Human Impacts and Amphibian Ecophysiology

Anthropogenic threats, such as climate change (Velasco et al. 2021), habitat destruction (Cordier et al. 2021), and diseases (Brannelly et al. 2021) are causing a global extinction trend in amphibians. Approximately 40% of amphibian species may be close to extinction (Ceballos et al. 2020).

Temperature of the Earth's surface has been changing since the periods of the industrial revolution. Global surface temperature is increasing at the rate of $0.2^{\circ} \pm 0.1^{\circ}\text{C}$ per decade since then and is projected to reach 1.5°C above the pre- industrial period between 2030 and 2052 (Allen et al. 2018). Actions such as pollution, burning of fossil fuels and deforestation have an unequivocal direct influence on climate change (IPCC 2021). Like a cascade, climate change affects several other systems, such as rainfall flow, wildland fire regimes and changes in daily temperature fluctuations (Cheng et al. 2007, Flannigan et al. 2009, Vázquez et al. 2015, Sun et al. 2018). This is not only due to a direct effect on environmental temperature, but also because climate change alters other factors that also impact amphibians' thermo-hydroregulation. For example, frog populations of the Savannah River Site (South Carolina, USA) are declining by the reduction in the amount of rain per year (Daszak et al. 2005).

Vulnerability to climate change depends on physiological traits and environmental conditions (Scheffers et al. 2014). While climate change threatens amphibian species, it remains unclear how they could cope with increasing temperatures, seasonal shifts, and increasing frequency of extreme climatic events (Huey et al. 2012). Climate change episodes may vary among locations, and some

populations might be more affected by climatic events than others (Boyer et al. 2021). For example, temperatures are predicted to increase at higher rates in tropical locations than in the temperate zones. A study carried out in the Brazilian Atlantic Forest showed the increasing occurrence of frosts contributing to the decline of the frog community (Heyer et al. 1988). In addition, Pounds and Crump (1994) noted that a population drop in Costa Rican *Ollotis periglenes* in 1987, which was attributed to the irregular climate, was more likely induced by global warming. Species adapted to cold or extreme environments, for example polar or high-altitude environments, are even more worrying cases (Parmesan 2006, Navas and Otani 2007).

Due to their strong physiological dependence on thermo-hydroregulation, changes in environmental temperature and precipitation deeply affects amphibian's ecophysiology (Li et al. 2013). The effect of climate warming on the toad *Anaxyrus boreas* is known to depend on the interaction of temperature and atmospheric moisture (Bartelt et al. 2010). Moreover, the limited dispersal capability of amphibians makes them particularly vulnerable to habitat modifications (Hoffmann et al. 2021). Species depending on seasonal streams are already experiencing niche contractions due to dryness associated with climate change (Hoffmann et al. 2021). In addition, studying the effect of water availability and temperature on embryonic development is key to assess the impact of climate change (Taylor et al. 2020). Dehydration risk may be the primary driver of amphibian activity and environmental restriction, entailing high fitness costs, and thus being another main driver of amphibians' climate vulnerability (Greenberg and Palen 2021). There is potential for local adaptation of amphibians to adapt to increasing water stress, but we still ignore if this will be enough to face the pace of climate change (Hoffmann et al. 2021). Acclimation and/or plasticity of performance curves will enable some adaptation of amphibians to climate change; and genetic adaptation will depend on the pace and magnitude of climatic change and the generation time of each species (Seebacher et al. 2015). Small body size, low metabolic requirements and behavioral plasticity are also predicted to enhance adaptation and survival to climate change (Lillywhite 2016).

In addition to these threats, epizootic diseases are increasingly affecting wildlife populations, and, to date, it remains poorly understood how the environment shapes most host-pathogen systems. Recently, it has been highlighted that microclimate constraints suppress host thermal behavior that is favorable to disease control. Thus, innate host defenses against these diseases might remain limited in the wild, predisposing to range-wide disease outbreaks and population declines (Beukema et al. 2021). Emerging infectious diseases, such as chytridiomycosis, are associated with population decline and the collapse of amphibian communities, being implicated in the decline of at least 501 species of amphibians worldwide (Scheele et al. 2019). This infectious and fatal disease, caused by a fungus *Batrachochytrium dendrobatidis*, is also related to climate change and amphibians' ecophysiology (Lips et al. 2003, Pounds et al. 2006, Skerratt et al. 2007; see Chapter 5). As global temperatures rise, climatic fluctuations can exceed the limits for certain pathogens, triggering outbreaks and causing some diseases to become more lethal or spread more quickly (Epstein 2001, Harvell et al. 2002). In the specific case of *B. dendrobatidis*, this fungus grows best at moderate temperatures (slightly above 20°C), mainly infecting in winter periods or in environments with mild summers. With the thermal increase due to global warming, these periods may present

ideal temperatures to trigger the spread of the fungus on areas that were too cold for it before (Pounds et al. 2006). In addition, during winter periods the amphibian's immune system response tends to be slower, as these individuals depend on thermoregulation to fight certain pathogens (Wright and Cooper 1981, Woodhams et al. 2003, Pounds et al. 2006). The association of these factors raises great concern about the consequences of the increase in temperature in the development of *B. dendrobatidis*. Furthermore, amphibian decline due to disease can lead to cascading effects, as happened in Panama, where frog's collapse led to a decline in the community of snakes (Zipkin et al. 2020). Paradoxically, the fact that thermal tolerance of the fungus is lower than that of many amphibians can be a solution to mitigate its impact in some regions, providing amphibians with warm microhabitats to avoid infection (Hettzey et al. 2019, but see Cohen et al. 2019). This example illustrates the importance and complexity of ecophysiology for animal conservation.

Loss and fragmentation of suitable habitat is an additional threat for amphibian populations. Habitat connectivity appears to play a key role in regional viability of amphibian populations, where prevalent human land-use changes strongly reduce the richness of amphibians (Cordier et al. 2021). Population connectivity is predominantly affected through juvenile dispersal and the short-term impact of habitat loss and fragmentation increases with dispersal ability. Scarcity of trophic resources, alteration of food web dynamics, increasing of diseases or increasing competition due to shifts on species' distributions will also imply unpredictable and potentially drastic impacts on amphibians' populations (Lillywhite 2016). Conservation strategies would benefit from species-specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes (Cushman 2006). Effective wildlife restoration is a critical requirement of many conservation actions. Outcomes of conservation actions can be optimized through knowledge of species' habitat requirements, but, to date, evidence from local research is not usually used to design habitat management. Furthermore, interventions administered externally from the top down, avoiding those developed with multiple stakeholders including land managers and researchers, run the risk of failing to be effective. Overall, the new habitats constructed or restored should be characterized by ecological research to quantify local habitat requirements and working with commercial land managers to ensure equitable benefits prior to designing conservation actions can promote rapid and efficient recovery of wildlife (O'Brien et al. 2021). The availability of shelters (thermal and hydric buffers as burrows and shadowed areas) will have a major role on restoration ecology, to be able to mitigate the impact of climate change on amphibian populations (Lillywhite 2016).

Conclusions

Amphibians live in different types of habitats—aquatic, semi-aquatic, fossorial or terrestrial—in a wide variety of climates and elevations. In addition, some species show diurnal activity while others are nocturnal. This, and fine-grain behavioral and morphological adjustments, lead amphibian species to experience a great diversity of thermal and hydric environments.

However, amphibians share two key traits that make their ecophysiology particular among other tetrapod groups: they are ectotherms, and they highly depend on water or moisture. Thermal ecology and water balance have been traditionally considered separately, although for amphibians most published studies assessed or commented on the interactive effect of temperature and water availability.

Both processes, thermal ecology and water balance, would have two main axes: physiological sensitivity and regulation. A recently developed conceptual framework of thermo-hydroregulation integrates thermal and hydric sensitivity (which probably interact on most species) with the shared mechanisms for thermo- and hydroregulation. We think that next steps are to develop this framework for amphibians, to gain a better understanding on how thermal and hydration-state performance curves interact on the different species, and how the model of costs and benefits of thermoregulation can be adapted to assess amphibian thermo-hydroregulation. With all of this in mind, we urge herpetologists, behavioral ecologists, ecophysiologicalists and conservation biologists to work together to implement this framework on amphibian conservation with the aim of mitigating the effects of habitat loss, emerging diseases and climate change and incorporate the physiological requirements of amphibians for ecological restoration.

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