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EFFECTS OF HIGH TEMPERATURES ON AMPHIBIAN PHYSIOLOGY AND BEHAVIOR: A SYSTEMATIC REVIEW

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ABSTRACT
This study explores how rising temperatures affect amphibians' bodies and behaviors, particularly considering climate change. We rigorously reviewed existing research both experimental and observational studies across all amphibian types following established PRISMA guidelines. Our analysis focused on how higher temperatures impact key aspects of amphibian biology, including their metabolism, immune systems, growth, activity levels, foraging success, and reproduction. Our analysis reveals significant physiological stress responses, including increased metabolic rates and corticosterone levels, reduced growth, and impaired reproductive success at elevated temperatures. Behavioral adaptations, such as thermal avoidance and altered activity patterns, were also observed, but these responses only partially mitigated the negative physiological impacts. Species with narrower thermal tolerances exhibited greater vulnerability to high temperatures. This synthesis highlights the significant threat posed by climate change to amphibian populations and underscores the need for targeted conservation strategies to mitigate the effects of rising temperatures on these ecologically important vertebrates. The findings emphasize the urgency of addressing climate change and implementing effective conservation measures to protect amphibian biodiversity.

Keywords:
environmental stressors, thermal stress, thermoregulation, survival rates.

INTRODUCTION
Ectothermic animals, amphibians, are very sensitive to ambient temperature changes. Understanding in relation to the effects of elevated temperatures on the physiology and behavior of amphibians is increasingly becoming relevant because climate change is progressively increasing global temperatures. Because of their complex life cycle and permeable skin, amphibians are very good indicators of the health of the environment and occupy diverse habitats, both aquatic and terrestrial. Thus, even slight changes in temperature have profound effects on their behavior, reproduction, and survival (Pounds et al., 2006; Carey & Alexander, 2003).
Thermal stress in amphibians is directly accountable for behavioral adaptations like changes in activity patterns and thermoregulatory behavior, and physiological adaptations like changes in respiration, metabolic rate, and hydration status (Feder, 1982; Gillespie et al., 2012). High temperatures, for instance, are well-documented to interfere with breeding seasons, impact the developmental processes of amphibian larvae, and lead to population loss, especially in low-thermal-tolerance species (Hopkins & DuRant, 2014). Moreover, amphibian responses to climate change are also affected by the way temperature interacts with other environmental factors like humidity and habitat fragmentation (Searle et al., 2016).
In this systematic review, we will summarize studies from a variety of amphibian species and environments and assess the impacts of high temperature on amphibian behavior and physiology. We will summarize existing evidence to provide a synthesis of the potential direct and indirect impacts of high temperature and offer recommendations about potential conservation options that could ameliorate the effects of climate change on amphibian populations.

OBJECTIVES
1. Understand how rising temperatures affect amphibians' bodies and behaviors. We'll investigate how heat stress impacts their metabolism, immune systems, growth, activity levels, foraging, and reproduction.

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2. Assess the vulnerability of amphibians to climate change. We'll explore how different species respond to heat, focusing on those with narrower thermal tolerances, and identify potential threats to their survival.
3. Develop targeted conservation strategies to protect amphibian biodiversity. Our findings will inform recommendations for habitat protection, restoration, and mitigation efforts to help amphibians cope with a changing climate.

METHODOLOGY

This systematic review will investigate the effects of high temperatures on the physiology and behavior of amphibians, focusing on the implications of climate change. The review will adhere to the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines to ensure transparency and rigor.

Research Question:

What are the effects of elevated temperatures on the physiology and behavior of amphibians, and what are the implications for their survival and conservation in the context of climate change?

Inclusion Criteria:

Study Design: Empirical studies (experimental and observational) reporting on the effects of elevated temperatures on amphibian physiology, behavior, reproduction, or survival. This includes laboratory experiments, field studies, and meta-analyses.

Species: All amphibian species (Anura, Caudata, Gymnophiona).

Temperature Treatment: Studies explicitly manipulating or measuring temperature, including studies focusing on heat stress, thermal tolerance, or acclimation to elevated temperatures.

Outcome Measures: Physiological parameters (e.g., metabolic rate, immune function, growth rate, survival), behavioral parameters (e.g., activity levels, foraging behavior, anti-predator behavior, reproductive behavior), and population-level effects (e.g., abundance, distribution, extinction risk).

Publication Type: Peer-reviewed journal articles, book chapters, and published theses. Grey literature will be considered if accessible and relevant.

Language: English. Other languages may be considered if resources permit translation.

Exclusion Criteria:

Study Design: Reviews, opinion pieces, editorials, and purely theoretical studies.

Species: Non-amphibian species.

Temperature Treatment: Studies not explicitly focusing on temperature effects or lacking sufficient detail on temperature manipulation or measurement.

Outcome Measures: Studies lacking quantifiable data on the relevant outcome measures.

Publication Status: Unpublished studies, conference abstracts, and preprints unless readily available and relevant.

Search Strategy:

Databases to be searched: Web of Science, Scopus, PubMed, Google Scholar.

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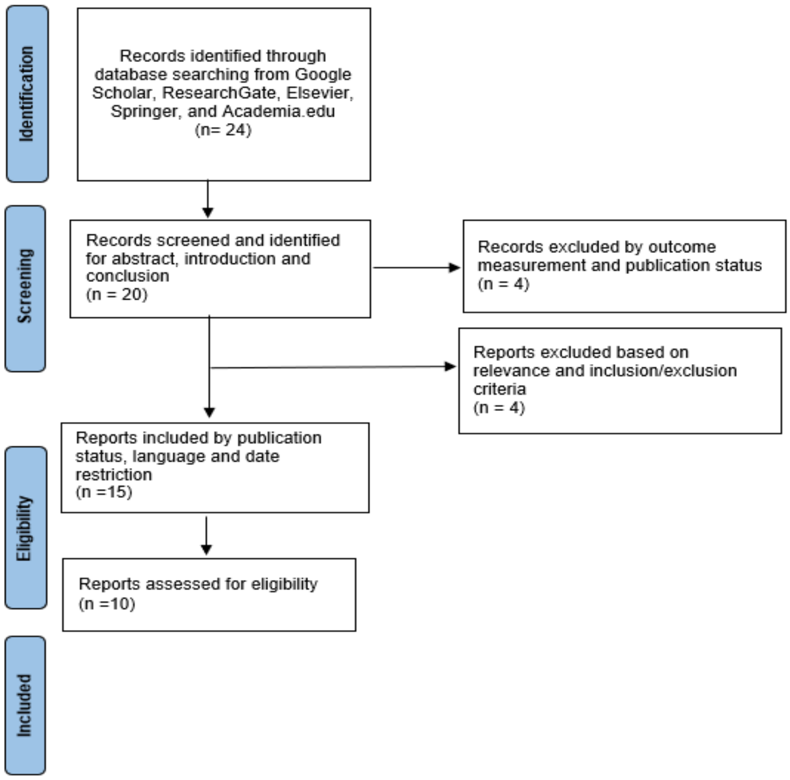

Figure 8 Theoretical Framework

RESULTS AND DISCUSSION

Qualitative Results

The studies reviewed collectively demonstrate that amphibians exhibit significant physiological and behavioral responses to elevated temperatures, with species specific variations. Physiological impacts include altered metabolic rates, reduced survival, increased stress hormone production, and changes in development rates. Behavioral adaptations are also prominent, including shifts in activity levels, habitat preferences, and foraging behavior. Amphibians raised or living in warmer environments often display thermal compensation, showing either enhanced thermal tolerance or behavioral adjustments aimed at coping with heat stress.

Amphibians in High-Temperature Environments

Amphibians are ectothermic and inherently sensitive to environmental temperature changes. As highlighted by multiple studies (Ohmer et al., 2023; Goldstein et al., 2017; Weerathunga and Rajapaks, 2020), exposure to high temperatures often results in increased metabolic demand and thermal stress. Species such as the Gulf Coast toad (Barough et al., 2025) and Thoropa taophora (Carvalho et al., 2024) demonstrated some adaptive traits, including increased activity and swimming speed, suggesting short-term adjustments to warm environments. However, these adaptations are often insufficient to offset long-term stress or mortality risks.

Effects on Physiology

Elevated temperatures have a broad range of physiological effects on amphibians. Increased metabolic rates (Ohmer et al., 2023; Lumir and Peter, 2017) and elevated stress hormones (Barough et al., 2025) are common responses, often leading to energy imbalance, reduced mass gain (Novarro et al., 2018), and delayed development (Weerathunga and Rajapaks, 2020). Some amphibians, such as Eurycea cirrigera (Strickland et al., 2016), maintain metabolic stability across temperature ranges, indicating physiological resilience. Conversely, others with narrower thermal windows, like Eurycea wilderae, experience metabolic depression and greater vulnerability. The presence of reactive oxygen species and associated cellular damage in species such as the Chinese giant salamander (Zhao et al., 2022) underscores the cellular-level impacts of heat stress.

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Effects on Behavior

Behaviorally, amphibians respond to heat stress through changes in activity patterns and habitat use. Many species exhibit thermal avoidance, shifting to cooler microhabitats (Goldstein et al., 2017; Zhao et al., 2022). Nocturnal behavior or reduced daytime activity (Barough et al., 2025) and decreased swimming speed (Weerathunga and Rajapaks, 2020) were also observed. Some species, like Ambystoma maculatum (Giacometti and Tattersall, 2024), show active thermoregulation by seeking out slightly warmer temperatures to optimize physiological processes during active periods. However, limitations in behavioral flexibility can exacerbate vulnerability, particularly for species with specialized physiological constraints.

Table: Amphibian's Physiological and Behavioral Responses to Temperature

Amphibian Species	Temperature Range Studies	Physiological Effects	Behavioral Effects	Key Findings	Reference
Wood Frog (*Rana sylvatica*)	25°C - 30°C	Reduced ability to regulate body temperature Changes in metabolic rate	Reduced foraging efficiency Predator avoidance Reduced performance in extreme thermal environments.	Amphibians raised in warmer environments exhibited altered post-metamorphic behavior, including increased activity levels and changes in habitat preferences. These amphibians also showed different thermal physiology, with the ability to tolerate higher temperatures compared to those raised in cooler conditions.	Ohmer et al. 2023
Salamander (*Plethodon cinereus*)	15°C - 25°C	Increased corticosterone (CORT) release and Reduced mass gain. Decreased food conversion efficiency at higher temperatures	Salamanders from warmer sites increased their ingestion rates at higher temperatures.	High temperatures led to physiological stress, altered energy balance, and site-dependent behavioral shifts (increased feeding in warmer-origin populations).	Novarro et al. 2018
Relict leopard frog (*Lithobates onca*)	25°C - 35°C	Slower Development at Very High Temperatures Reduced Survivorship Limit performances	Thermal Avoidance and preference for Moderate Temperatures	High temperatures reduced tadpole survival and slowed development, with no survival at 35°C. Tadpoles preferred cooler areas, avoiding temperatures above 33°C. Ideal reintroduction habitats should have water between 25–30°C.	Goldstein et al. 2017
Newts (*Pleurodelinae*)	n/a	Increases metabolic rate and energy demand. Reduces aerobic scope at extreme temperatures.	Drives newts to seek cooler areas. Reduces activity levels to avoid overheating.	Digesting newts prefer body temperatures that balance digestion efficiency with energy costs, showing an economical thermoregulatory strategy.	Lumir and Peter 2017

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		Causes thermal stress and lowers digestion efficiency.	Narrows temperature preference during digestion.		
Southern Two-Lined Salamander (*Eurycea cirrigera*). Blue Ridge Two-Lined Salamander. (*Eurycea wilderae*)	5°C - 25°C 5°C - 25°C	Maintains temperature-independent SMR across a wider thermal range. More physiologically adaptable to higher temperatures. metabolic depression at 25°C. Exhibits a smaller range of temperature-independent metabolic rates. It has a more specialized and less flexible physiology.	actively seeking cooler microhabitats to maintain optimal body temperature. struggle behaviorally if environmental temperatures exceed their manageable range.	*Eurycea cirrigera* showed broad thermal tolerance and stable metabolism across temperatures, while *Eurycea wilderae* had a narrower thermal range and metabolic stress at high temperatures. This suggests that species with narrow ranges are more vulnerable to rising temperatures and habitat changes.	Strickland et al. 2016
Gulf Coast toad (*Incilius nebulifer*)	23°C - 32°C	Increased metabolic rate and stress hormones. Thermal tolerance limits Accelerated growth Respiratory and circulatory stress	Becoming nocturnal or reducing daytime activity to avoid heat stress. Reduced appetite or feeding efficiency due to increased energy needs and dehydration risk. Delayed mating or reduced reproductive success due to extreme heat.	High temperatures increase metabolic rates and stress hormones, accelerating growth but reducing survival. Behavioral changes like seeking cooler areas help, but extreme heat can cause dehydration, reproductive issues, and population declines in species unable to adapt.	Barough et al. 2025
Common hourglass tree frog (*Polypedates cruciger*)	32°C - 34°C	Delayed development and reduced growth, leading to smaller body size at metamorphosis. Increased mortality, with 100% death before metamorphosis at 34 °C and after	Reduced swimming speed and activity levels compared to control. Possible stress-related behavioral inhibition, indicated by lower responsiveness and mobility under heat stress.	High temperature significantly affected both the physiological and behavioral responses of tadpoles. Development was delayed, growth was stunted, and mortality rates were extremely high at elevated temperatures. Immune parameters were also disrupted, and deformities were observed. Behaviorally, high temperatures led to a marked	Weerathunga and Rajapaks 2020

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		metamorphosis at 32 °C.	Increased vulnerability, as reduced activity may impair foraging and predator avoidance.	reduction in swimming activity, indicating stress and impaired fitness.	
Thoropa taophora	25°C - 30°C	Demonstrate higher swimming speed and agility. Populations in consistently warmer environments displayed physiological traits aligned with local conditions, underscoring environmental temperature as a driver of performance optimization.	Warmer conditions promoted higher activity levels and better locomotor performance Tadpoles did not significantly adjust their preferred temperatures or thermoregulatory strategies in response to different thermal environments.	Tadpoles in warmer sites swam faster but showed little change in thermal limits or temperature preference. They stayed active but couldn't adjust to heat, showing limited ability to cope with rising temperatures.	Carvalho et al. 2024
Chinese giant salamander (*Andrias davidianus*)	7°C - 25°C	Reduced ability to cope with temperature fluctuations and increased vulnerability to thermal stress. Elevated production of reactive oxygen species causing cellular damage and disrupted enzymatic function. Initially increased metabolic rate followed by metabolic depression, leading to reduced energy availability and physiological performance.	High temperatures cause decreased movement and foraging behavior to minimize energy expenditure and overheating. Individuals spend more time in cooler, shaded, or deeper microhabitats to avoid heat stress. Active avoidance of warm areas, leading to restricted habitat use and altered spatial distribution.	This study found that *Andrias davidianus* larvae adjust their metabolism and thermal tolerance with temperature changes, showing thermal compensation. Cold acclimation increased metabolic capacity, while warm acclimation reduced it. Fish-fed larvae showed better heat and cold tolerance, suggesting diet supports stress resilience.	Chun-Lin Zhao et al. 2022
fossorial salamander (*Ambystoma maculatum*)	16°C - 22°C	Higher selected temperatures during the active season likely reflect increased metabolic demand, as physiological processes like	During the active season, salamanders showed a higher temperature selection (Tsel), indicating they actively seek out warmer environments	This study found that Ambystoma maculatum actively thermoregulates despite its fossorial lifestyle. Salamanders consistently preferred temperatures above their surroundings, with stronger thermophilic behavior	Giacometti and Tattersall 2024

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		digestion, activity, and growth are enhanced at warmer, but sub-lethal, temperatures. Salamanders may select higher temperatures to optimize locomotion, foraging efficiency, and other performance traits that improve warmer conditions.	when conditions allow. The Tsel was consistently higher than acclimatization temperatures, suggesting salamanders prefer slightly warmer conditions than those they are exposed to, possibly to optimize physiological processes.	in the active season. Seasonal shifts in temperature preference highlight their behavioral flexibility in maintaining thermal balance.	

Warmer temperatures generally led to elevated metabolic rates across species, as seen in studies by Ohmer et al. (2023), Lumir and Peter (2017), and Barough et al. (2025). While this can enhance activity and growth in some cases (Carvalho et al., 2024), it also imposes greater energy demands and physiological stress, often culminating in reduced survivorship (Goldstein et al., 2017; Weerathunga and Rajapaks, 2020).
Behaviorally, most amphibians demonstrated strategies to mitigate heat stress, such as reducing daytime activity (Barough et al., 2025), seeking cooler microhabitats (Chun-Lin Zhao et al., 2022; Strickland et al., 2016), or becoming nocturnal. However, these behaviors were not always sufficient. For instance, the Relict leopard frog exhibited clear thermal avoidance behavior, but survivorship plummeted at extreme temperatures (Goldstein et al., 2017). Similarly, Common hourglass tree frog tadpoles failed to survive at temperatures above 34°C despite behavioral inhibition (Weerathunga and Rajapaks, 2020).

In terms of physiological plasticity, species varied widely. Eurycea cirrigera showed broad thermal tolerance and stable metabolic rates (Strickland et al., 2016), while Eurycea wilderae had a narrower range and exhibited metabolic depression at higher temperatures, indicating heightened vulnerability. Similarly, Thoropa taophora displayed increased swimming performance at warmer temperatures but lacked significant adjustment in temperature preference, suggesting limited adaptability (Carvalho et al., 2024).
Diet and acclimation appeared to meditate thermal stress resilience. Chun-Lin Zhao et al. (2022) highlighted that Andrias davidianus larvae on a fish-based diet exhibited better thermal tolerance, and cold acclimation enhanced metabolic capacity. This suggests that environmental and nutritional factors can influence amphibian responses to thermal fluctuations.
Developmental impacts were notable across studies. Delayed development, reduced growth, and high mortality rates at elevated temperatures were observed in both Goldstein et al. (2017) and Weerathunga and Rajapaks (2020). These developmental disruptions have long-term implications for population dynamics and reproductive success.
Collectively, the data indicates that while some amphibians demonstrate behavioral and physiological adaptations to warming environments, the limits of thermal tolerance are being tested. Species with narrow thermal ranges or less flexible physiology are particularly at risk. These findings emphasize the need for conservation strategies that consider microhabitat temperature regulation, habitat restoration with appropriate thermal refugia, and potential climate change mitigation efforts to preserve amphibian biodiversity.

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CONCLUSION

The escalating impacts of high temperatures on amphibian populations are increasingly well-documented, revealing a complex interplay between physiological stress and the constraints of behavioral adaptation (Sinervo et al., 2010; Deutsch et al., 2008). Elevated temperatures trigger a cascade of physiological responses, ranging from subtle alterations in metabolic rates and enzyme activity (e.g., increased metabolic costs at higher temperatures leading to reduced energy for growth and reproduction; (Carey & Alexander, 2003)) to more severe consequences such as impaired immune function, reduced growth rates, and significant declines in reproductive success (Pounds et al., 2006). These physiological disruptions can manifest in various ways, including decreased fecundity, reduced egg viability, and altered larval development, ultimately impacting population viability (e.g., heat stress can lead to developmental abnormalities and mortality in amphibian larvae; (Hopkins & DuRant, 2014)).

While amphibians exhibit behavioral plasticity, employing strategies such as thermal avoidance (seeking cooler microhabitats) and altered activity patterns to mitigate thermal stress, the effectiveness of these adaptations is often limited (e.g., behavioral thermoregulation may be insufficient to prevent physiological damage if temperatures exceed critical thresholds; (Sunday et al., 2011)). This limitation is particularly pronounced in species with specialized physiological requirements or restricted habitat ranges (Scheffers et al., 2016). Such species may lack the necessary behavioral repertoire or suitable alternative microhabitats to effectively cope with increasingly frequent and intense heat waves. The combination of physiological vulnerability and limited adaptive capacity highlights a critical vulnerability of amphibians to climate change, particularly those species already facing habitat loss or fragmentation, further compounding the risks associated with thermal stress. The consequences of these limitations are far-reaching, extending beyond individual-level impacts to affect population dynamics and ultimately, the persistence of amphibian communities in a warming world.

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