

The impacts of global warming on animals and their response to climate warming

Hejunru Zha*

Southwest Forestry University, Kunming, China

*Corresponding author: zhahejunru@163.com

Abstract. This paper reviews on animals' thermoregulations under climate change. There are aspects of animals' thermoregulation that encompass behavior, physiology, and life history. Among these, behavioral thermoregulation is mostly studied and reported in the early years, which is usually about the strategic selection of optimal timing and locations, facilitating efficient evaporative and conduction heat dissipation, modifying their dietary preferences, and increasing shuttle behavior. The field of physiology involves hormonal regulation, such as secreting more glucocorticoids to achieve better balance control, changing body temperature to be more efficient in heat loss, energy allocation (e.g., metabolic rate) to select optimal strategy between growth and reproduction, and oxidative stress injury. In parallel, life history traits encompass rising growth rate, shrinking lifespan, changing body posture, and declining survival rate. Global warming is the main feature of climate change, with both of the average temperature rising and frequently heat waves occurring being the major characteristics simultaneously. Consequently, there come two scientific questions of this review: (1) What are the impacts of global warming on animals?(2) How do animals respond to climate change?

Keywords: climate change, warming, thermoregulation, behavioral flexibility, physiological plasticity

1. The impacts of global warming on animals

Climate-driven changes in temperature and precipitation affect the distribution of organisms, since species are inclined to live in areas where climate conditions are most suitable.¹ Besides, organisms' habitats tend to rise in elevations.² Meanwhile, migration of species not only is a response, but also the search for suitable microclimate in habitats. While warming may reduce macroclimate suitability, microclimate importance varies with such large-scale fitness.³ Like the meadow pipit (*Ochotona princeps*), the pika's heat stress can be indeed reduced through increased relative humidity, reduced sunlight exposure and solar radiation provided by this microhabitat.⁴

Yellow armadillos (*Euphractus sexcinctus*) reduce their diurnal activities under the warmer climate. Furthermore, their nocturnal activity patterns become more pronounced above 30°C.⁵ For those diurnal animals that are unable to evaporate amounts of water (e.g. Those living in the water-scarce environment or experiencing excessive cooling costs), changing their circadian rhythm from diurnal to nocturnal might offer them opportunities to be active which however are limited by continued warming. For example, golden spiny mice (*Acomys russatus*) living in hot and arid rocky deserts reduce their diurnal active time and exhibit bimodal activity characteristics, thereby reducing midday activity.⁶ There is another interesting research on the behavior of nesting birds Kentish plovers (*Charadrius alexandrinus*) during warming. Some behavioral thermoregulations like standing, gaping, panting, ptiloerection, wing-dropping and belly-soaking among hatching time have been reported to be significantly connected with the temperature rising.⁷ Additionally, polar bears (*Ursus maritimus*) rely on sea ice to hunt for seals, but recent rapid warming has shrunk the region, enforcing pole bears to change their diet mainly to terrestrial breeding birds and their eggs, finally seriously influencing the reproduction success of the hunted birds.⁸

Body core temperature and metabolism rate of organisms increase in response to higher temperatures, controlling body temperature above the ambient level, which leads to thermal gradient resulting from difference in heat loss to the environment and reduces gaining heat from surroundings. It may also bring benefit for the endangered Patagonian lizards (*Phymaturus tenebrosus*), which

exhibit the greatest body locomotor performance when their body temperature is similar to surroundings.⁹

Besides, there is a positive relationship between the resting metabolism rate of South American rattlesnakes (*Crotalus durissus*) and temperature, with different behaviors under diverse gradients.¹⁰ The same trend is also discovered in Mesquite lizards (*Sceloporus grammicus*) on their resting metabolism rate and body mass, which habituate in mountainous region.¹¹ Only under acute heat stress, antioxidant capacity (e.g. superoxide dismutase, SOD and glutathione S-transferase, GST) of the bald notothen (*Pagothenia borchgrevinki*) is significantly risen.¹² The SOD levels of fresh water molluscs (*Bellamyia bengalensis*) also increase when exposed to warmer conditions.¹³ This phenomenon has been observed in chicks as well, although extreme heat load can lead to SOD inhibition and variations in oxidative extent across different tissues.¹⁴

It is common to discover the decline in species population, but warming can even lead to worse situations like extinction. Some species may persist despite habitat loss or recent climate change rates, but simultaneous occurrences of these two factors can push them towards extinction due to the inability of their evolutionary rate to keep up with climate change and the significant reduction in their adaptation rate caused by habitat loss.¹ Although global warming may enhance and extend the reproductive period of North American lizards (*S. undulatus*), thereby compensating for the decreased survival rate of embryos and juveniles.¹⁵ Meanwhile, all the sizes of the pike (*Esox lucius*) fertility increase, while there is a trade-off between energy allocation to reproduction and somatic maintenance.¹⁶ Besides, the hibernation period shrinks with warming, and the survival rate declines as well. Another report showed a decline of lifespan among 15 species, due to the MDA injury caused by respiration and efficient rate of mitochondria.¹⁴

2. Animals' response to climate warming

Under the influence of global warming, endotherms and poikilotherms employ distinct adaptive strategies. In terms of poikilotherms, behavioral thermoregulation is typically achieved through shuttling between sunlight and shade, which is also observed in endothermic species. While behavioral plasticity and flexibility can buffer the impacts of climate warming to some extent, coping with the current situation still remains a serious challenge. Consequently, corresponding adaptations in animal physiology and life history are imperative. In short, there are three aspects of animal adaptation, namely adaptation in behavior, physiology and life history.

2.1. Behavioral flexibility

2.1.1 Evaporative heat loss

In the presence of water, animals dissipate heat through sweat gland activity, panting, wetting feathers, and licking. However, these thermoregulatory mechanisms also incur physiological costs such as dehydration and reduced locomotor performance.

When exposed to thermal pressure, the Double-crested Cormorant (*Nannopterum auritum*) slightly opens its mouth and exhibits regular vibrations. The rapid and repetitive movement of the hyoid bone occurs independently from the respiratory airflow, facilitating heat dissipation through the moist membranes of the oral cavity, pharynx, and esophagus.¹⁷ Animals belonging to the Bovidae family present varying degrees of sweat gland activity in response to heat exposure. As ambient temperature increases, sudden and rapid escalation appears in water loss from the skin, which eventually reaches a steady state. Specifically, cattle achieve equilibrium at 40°C.¹⁸ Red kangaroos (*Osphranter rufus*) exhibit various physiological responses to different stimuli, including increased sweating during exercise, panting and salivation when at rest, and adaptive mechanisms in response to severe heat stress. With the decreased sweating rate of kangaroos and the increased respiration rate following cessation of exercise, they engage in licking behavior on their well-vascularized forelimbs.¹⁹ Notably, evaporative cooling also poses an increased risk. Great skuas (*Stercorarius skua*) employ feather wetting as a means to thermoregulate, yet this breeding behavior may potentially impede juvenile

production and consequently compromise reproductive success.²⁰ The cost of evaporative cooling in desert birds may moderately influence the behavioral traits of this species. With recent climate warming, avian evaporative heat dissipation has increased by 18.8% according to statistics. It is anticipated that future evaporative heat dissipation in dry and hot desert regions will rise by 50-78%.²¹ Studies have revealed that evaporative cooling efficiency of eight resident Palearctic songbirds maintains a positive correlation with rising ambient temperatures beyond the upper threshold. Moreover, smaller species demonstrate a steeper decline in body mass relative to evaporative water loss, thereby increasing their susceptibility to potentially lethal dehydration.²²

2.1.2 Heat loss by conduction

Previous studies have traditionally considered evaporative cooling as the primary mechanism for heat dissipation in endotherms. However, it is limited in low moisture or high humidity environments.

The arboreal koala (*Phascolarctos cinereus*) actively seeks out tree trunks with lower temperatures than the surrounding environment and engages in tree-hugging behavior to conduct heat conduction. Thereby, utilizing tree trunks as suitable microclimates for heat dissipation is a novel discovery in arboreal animals.²³ Baboons (*Papio hamadryas ursinus*) residing in arid savanna regions adopt sand baths as a means of dissipating heat. The practice of utilizing sand sourced from deep, cool regions and elevating it towards the abdomen depending on wrist movements does not demonstrate efficacy in preventing insect bites, as ticks predominantly attach themselves to the head and ears.²⁴ Additionally, dust bathing behavior has also been observed in Asian elephants (*E. maximus*), and the frequency of this behavior significantly increases with rising ambient temperatures exceeding 13 °C.²⁵

2.1.3 Selection of suitable habitats

Animals not only seek out suitable long-term habitats, but also select microclimates. However, these behaviors may incur certain costs.

In high summer temperatures, moose (*Alces alces*) often choose to rest in the shade of trees or in the mud beside the beach. Such habitats can be regarded as heat shelters, revealing that animals can adapt to different environmental conditions by using environmental characteristics.²⁶ It also reflects a seasonal migration of mountain ungulates to higher elevations during the hot summer months.²⁷ However, this behavior also is accompanied with a trade-off. In elevated temperatures, moose (*A. alces*) exhibit a preference for high canopy density areas with decreasing their food consumption.²⁸ Nevertheless, not all animals opt for long-distance migration. The American pika (*O. princeps*) occupies microclimate in mossy low-altitude terrain with dense vegetation and dark basaltic formations. These conditions contribute to elevated relative humidity, reduced sunlight exposure and solar radiation attenuation, thereby providing insulation properties and facilitating evaporative cooling.⁴

2.1.4 Selection of the right time to be active

When available habitats fail to provide adequate thermal balance for animals, they might select optimal temporal and spatial conditions to engage in active behaviors, although these choices may involve trade-offs. In addition, animals may also be in a state of micro-torpor in summer as a result.

As ambient temperature increases, captive white-tailed deer (*Odocoileus virginianus*) demonstrate a preference for cooler and shaded feeders. In a separate investigation of unshaded feeders, deer were observed to selectively consume food during dusk rather than daytime, thereby minimizing their exposure to elevated temperatures. Additionally, they allocate more time towards being active during lower temperatures as they exhibit torpor during the daytime. These behaviors are considered as a strategic mechanism to mitigate detrimental impacts.²⁹ Mountainous ungulates such as the Chinese muntjac (*Muntiacus reevesi*) and tufted deer (*Elaphodus cephalophus*) not only respond to warming through migration but also appear alterations in their diurnal activity patterns, often displaying heightened activity levels at dusk.²⁷ Additionally, being torpor is also a way to reduce heat production. Certain small endotherms adopt this strategy to control their balance. Malagasy bats (*Macronycteris*

commersoni) regulate their metabolism by short micro-torpor bouts during the hottest days, but elevated temperatures may pose a threat to their survival.³⁰

2.1.5 The changing of foraging strategy

Due to limited water intake and budget constraints associated with foraging in arid environments, animals may alter their food acquisition strategies, including rates and types. Besides, this may also be due to the nutritional need in warmer conditions.

Warmer climatic conditions can lead to a decrease in the relative proportion of herbivorous and predatory invertebrates within the diet of common lizards (*Zootoca vivipara*), potentially attributed to an increased nutritional demand for higher protein degradation, consequently prompting changes in the feeding ecology of lizards.³¹ Furthermore, in order to optimize their energy intake, European tree frogs (*Hyla arborea*) adjust their dietary ratio with increasing herbivore consumption.³² The composition of food significantly impacts the cost of cooling consumption in hot and arid regions, particularly due to water intake. In contrast to herbivorous and omnivorous species, carnivorous birds (including insectivorous species) exhibit infrequent independent water drinking behavior and rely more on their prey during periods of dry heat. Consequently, the additional demand for prey intake increases cooling costs. Larger avian species exhibit an increased foraging requirement, yet they are adept at mitigating predation risks by targeting larger and more widely dispersed insect prey. Conversely, smaller birds demonstrate enhanced water regulation capabilities, potentially adapting their feeding behavior to include larger and moisture-rich prey as a means of reducing reliance on hydration from insects.²¹ To enhance water intake, common brown lemurs (*Eulemur fulvus*) modify their dietary composition, particularly during arid periods by increasing the proportion of fruits consumed. During times of limited water availability, lemurs allocate a significant portion of their time to consuming juicy salix (*Lissochilus rutenbergianus*) in order to maintain water balance; whereas during other periods, the consumption of salix is considerably lower.³³

2.1.6 Shuttling through bright and shade

Ectotherms often regulate their temperature balance through shuttling, while this behavior is also observed in smaller endothermic organisms.

The shuttle behavior of *Eremias argus* and *E. multiocellata* lizards significantly increases when exposed to diurnal heat stress.³⁴ Cape ground squirrels (*Xerus inauris*) also exhibit such behavior, utilizing cave retreats to dissipate heat and sustain daily activity.³⁵

2.2. Physiological plasticity

2.2.1 Hormonal regulation

Cortisol and its analogue act on a variety of tissues to recruit the body's resources to allow an individual to maintain or restore homeostasis in the face of current challenges.

As temperatures increase, there is a corresponding elevation in fecal glucocorticoid metabolite (FCM) levels observed in polar bears (*Ursus maritimus*). Gender and age demonstrate an interactive effect on FCM secretion. Among adolescent bears, FCM secretion rises below the critical temperature threshold but declines above it. Furthermore, limited evidence of FCM secretion exists among older individuals, particularly those surpassing their natural lifespan.³⁶ The baseline cortisol levels in European sea bass (*Dicentrarchus labrax*) stabilize subsequent to an initial increase in response to warmer climate conditions, while prolonged heat exposure is associated with higher baseline levels.³⁷ For amphibious animals, an elevation in temperature leads to an increase in corticosterone (CORT) content. Temperature exerts a significant influence on the hormonal profiles of leopard frog tadpoles (*Lithobates pipiens*), as there exists a correlation between accelerated metamorphosis and earlier CORT upregulation under warmer conditions.³⁸

Among reptiles, there is an increase in the secretion of green sea turtles (*Chelonia mydas*) and tawny dragons (*Ctenophorus decresii*), with secretion levels reaching near the upper critical threshold and maintaining a stable trend.³⁹

2.2.2 Body temperature regulation

For all the species, only if the body temperature approaches to ambient level, the ratio of metabolic heat production and evaporative heat loss will be closer to one. This is an efficient way of heat loss.

Within a specific temperature range, lizards regulate their body temperature to maintain it within the defined threshold.³⁴ Birds like the scaly-feathered weaver (*Sporopipes squamifrons*), sociable weaver (*Philetairus socius*) and white-browed sparrow weaver (*Plocepasser mahali*) typically demonstrate a consistent body temperature, surpassing the constant level, whereby their body temperature gradually increases with each rise in ambient temperature. The accelerated rate of change in body temperature at extremely high ambient temperatures substantiates the inference that birds have indeed reached their maximum tolerable environmental temperature (T_a) and are no longer capable of maintaining a stable internal body temperature (T_b).⁴⁰ An increase in T_b ensures songbirds to maintain a favorable gradient of $T_b > T_a$, which allows passive heat dissipation and saves body water by delaying water loss from heat evaporation.²⁷

2.2.3 Metabolic rate

With warming, the rate of metabolism is also getting higher, which is thought to be an adaption to temperature-dependent selection for a faster pace of life.⁴¹

Three types of weavers including the scaly-feathered weaver (*S. squamifrons*), sociable weaver (*P. socius*) and white-browed sparrow weaver (*P. mahali*) have been investigated and found to manifest significantly higher resting metabolism rates once they reach the upper threshold temperature.⁴⁰ Resting metabolism rates in songbirds increase with warming, significantly rising above the upper critical temperature.²⁷ The zebrafish (*Danio rerio*) exhibit an elevated metabolic rate under warmer conditions.⁴¹ Like other heterothermic mammals, such as pronghorns (*Antilocapra americana*), also represent this characteristic, displaying a noticeably higher resting metabolic rate when exposed to high temperature.⁴² Furthermore, the resting metabolism rate of South American rattlesnakes (*C. durissus*) exhibits a positive correlation with temperature and varies across different gradients.¹⁰ Similarly, Mesquite lizards (*S. grammicus*), which inhabit mountainous regions, also demonstrate this trend in their resting metabolism rate and body mass.¹¹

2.2.4 Oxidative stress

The extent of oxidative stress is associated with the degree of oxidative damage (e.g. malondialdehyde, MDA), antioxidant capacity (e.g. superoxide dismutase, SOD), immune capacity, telomere length, and so on.

A previous study revealed that the MDA content of lizards (*E. multiocellata*) in the warmer group significantly increased, while IgM expression was remarkably lower in the warmer group compared to the control group (indicating decreased immune capacity), suggesting that temperature warming could lead to immunosuppression and oxidative damage.⁴⁵ The desert agama (*Phrynocephalus przewalskii*) also provides evidence, since a significant reduction occurs in its telomere length after long-term exposure.⁴³ For mammals like mice, applying the MitoSOX red probe (a fluorescent indicator to monitor superoxide in mitochondria) indicates an increase in ROS content during heating.⁴⁴

2.3. Life history traits

2.3.1 Maternal effect

Maternal effect not only happens in insects, but also in other kinds of animals. That means what occurs in intra-maternal will also express in embryo, and may persist in adulthood.

Generally, it takes about six generations of zebrafish (*D. rerio*) to exhibit the characteristic. Research has manifested a significant difference in standard metabolism rates between the control and warming groups in the first generation. However, by the sixth generation, no statistically significant differences have been observed between these two groups. After undergoing long-term training, maternal effects influence the phenotypic traits of offspring.⁴¹ The offspring of maternal

untrained multiocellated racerunners (*E. multiocellata*) in warmer climates, which have not been trained in heat resistance since embryo, are in poorer body condition compared to the trained offspring. However, the survival rate remains the same for both individuals trained in warm climate and untrained in present climate.⁴⁵ This may suggest that their growth performance is maximized when matched with parental temperatures.

2.3.2 Reproduction

Birds, like black-tailed godwits (*Limosa limosa limosa*), often encounter un conspicuous advanced phenomenon of the laying date.⁴⁶ The breeding season of the rock sparrow (*Petronia petronia*) lasts longer, resulting in larger average clutch sizes.⁴⁷ The successful reproduction of amphibians, like pond frogs (*Pelophylax nigromaculatus*) is not straightforwardly significantly associated with temperature, but rather with the food resources that are influenced by temperature.⁴⁸

2.3.3 Body size and posture

Ground squirrels (*X. inauris*) regulate their core temperature using their tails as parasols, which helps mitigate the harmful effects of warming and allows them to extend their diurnal foraging time outside. However, when the temperature exceeds the upper limit, they have to retreat into their burrows.³⁵ Koalas (*P. cinereus*) change their posture to enhance conduction heat loss, stretching themselves during climate warming while huddling up in mild days.²³ The posture change also occurs in the American pika (*O. princeps*) which can curl into an oval shape in winter, and adopt an elongated oval shape in summer.⁴ In colder temperatures, the asp viper (*Vipera aspis*) experiences less weight loss, which may be attributed to its lower metabolism rate, resulting in energy conservation. This suggests that during warmer winters, increased mortality is caused by body weight loss, as a thin body cannot sustain the required energy.⁴⁹ In recent years, with climate warming, the body sizes of desert birds have declined because larger bodies require more cooling costs and increased water intake, which cannot be fulfilled in warmer conditions.²¹ Due to the difference in thermal conductivity between air and water, changes in body size vary among marine and terrestrial animals. Consequently, it appears that terrestrial animals exhibit significant discrepancies, while marine animals only show minor differences.⁵⁰

2.3.4 Growth rate and survival rate

Under climate warming, lots of animals enhanced growth rate, but at a cost to survival, likely due to trade-offs among the competing requirements of life-history traits (growth vs. survival) that cannot be maximized simultaneously.

Tadpoles such as leopard frog tadpoles (*L. pipiens*) grow faster in warmer conditions.³⁸ Iberian painted frogs (*Discoglossus galganoi*), European tree frog (*H. arborea*), and Mediterranean tree frog (*H. meridionalis*) are similar in this regard, resulting in a shorter metamorphosis stage for all three types when exposed to warming.³² Meanwhile, bluehead chub (*Nocomis leptcephalus*) and creek chub (*Semotilus atromaculatus*) are also the same.⁵⁸

In addition, the growth rate varies across distinct developmental stages.

Going through six generations in lab demonstrated by a DEB model of pike (*E. lucius*) shows decreased somatic growth and increased fecundity with smaller body size in warming conditions. In compensation for this optimized energy ratio, the maximal size in future becomes smaller. In conclusion, there is a change in pike in groups, which is shrinking somatic size to enlarge survival rate, and conversely, augmenting body size to increase fecundity.¹⁶ Calves of red deer (*Cervus elaphus*) in heat stress experience a negative growth rate, with a sex-specific difference. Moreover, it makes a difference in adults. Calves are unable to maintain homeothermy without sacrificing growth due to insufficient energy resources.⁵⁹

The survival rates of Iberian painted frogs (*D. galganoi*) and Mediterranean tree frogs (*H. meridionalis*) decline with warming.³² Three types of animals including bluehead chubs (*N. leptcephalus*), creek chubs (*S. atromaculatus*) and mottled sculpins (*Cottus bairdii*) also manifest the same traits under warming.⁵⁸ The North American lizards (*Sceloporus undulatus*) have decreased

survival rates of embryos and juveniles.¹⁶ Besides, among rodent populations, the hibernation period shrinks with warming, and the survival rate declines as well.¹⁷

3. Summary

The influences of climate warming vary among species due to factors such as their species, distribution, and life history. Organisms in tropical or polar regions may be more sensitive to climate change. In the initial stage of life called infancy, there is a stage significant influenced by maternal effect. And this can result in either a positive or negative impact on the future development of all species.

This review provides scientific evidence for wildlife conservation and forecasting global biodiversity in the face of frequent warming and heat waves occurring worldwide.

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