Opinion

Adaptation to fluctuating temperatures across life stages in endotherms

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Accelerating rates of climate change have intensified research on thermal adaptation. Increasing temperature fluctuations, a prominent feature of climate change, means that the persistence of many species depends on both heat and cold tolerance across the entire life cycle. In endotherms, research has focused on specific life stages, with changes in thermoregulation across life rarely being examined. Consequently, there is a need to (i) analyse how heat and cold tolerance mechanisms coevolve, and (ii) test whether antagonistic effects between heat and cold tolerance across different life stages limit thermal adaptation. Information on genes influencing heat and cold tolerance and how they are expressed through life will enable more accurate modelling of species vulnerabilities to future climatic volatility.

A more volatile climate at all times of life

Predicting how animals respond to climate change requires a greater understanding of the evolution of thermal tolerance [1,2]. Traditionally, the focus has been on the evolution of heat and cold tolerance as independent traits, with heat tolerance taking recent precedence because of global warming [3]. However, we now know that climate change involves unprecedented temperature volatility [4–7]. In this opinion article we argue that predicting the evolutionary potential of endothermic animals to cope with climate change requires that we (i) integrate work on the evolution of heat and cold tolerance, and (ii) examine thermal vulnerabilities to increases and decreases in temperatures across life stages. With this knowledge, we can identify whether there are genetic conflicts between cold and heat tolerance and between different life stages that may constrain adaptation.

The coevolution of thermal tolerance mechanisms in a fluctuating world

In endothermic species there has been considerable research on the thermal tolerance of adults. This has produced estimates of upper thermal limits measured by establishing the temperatures at which metabolic costs and water loss increase [8,9]. However, increasing temperature fluctuations mean that animals will need to cope with low as well as increasingly high temperatures throughout their life cycles, as temperature stress at any life stage can dramatically reduce organismal fitness. The importance of evolving heat and cold tolerance for population persistence is well recognised [2,10], but how greater temperature volatility will affect fitness at different life stages in endotherms remains unclear.

Increasing temperature volatility generates several challenges for endotherms. A greater range of ambient temperatures caused by higher thermal maxima [4–7] means that animals must evolve a capacity to tolerate hotter temperatures without compromising cold tolerance. But there are reasons why this might not be possible. Higher temperatures can be better tolerated by evolving a reduced metabolic rate or increased heat dissipation. These mechanisms, however, can lower

Highlights

Research on the potential for species to adapt to rapid climatic change has increased in recent years, with new studies examining heritability and evolvability; however, work on endotherms lags behind that on ectotherms.

Increasing temperature fluctuations are expected to generate selection for the evolution of both heat and cold tolerance, which may involve multiple, genetically integrated traits that will shape the speed and direction of evolutionary responses.

Divergent thermal optima across life stages in endotherms may lead to genetic conflicts within thermoregulatory systems, limiting thermal adaptation, and highlighting the need for studies examining multiple life stages.

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cold tolerance by reducing the ability to control body temperatures when temperatures decrease (Box 1). This can potentially cause a trade-off between heat and cold tolerance (Figure 1A) that can limit evolutionary responses to increased temperature fluctuations.

The mechanisms underlying trade-offs between heat and cold tolerances have not, to our knowledge, been examined in endotherms. In ectotherms, work on the vinegar fly (*Drosophila melanogaster*) showed that hot and cold tolerance were positively correlated in populations exposed to experimental evolution for survival at extreme high or low temperatures [11]. The partly shared genetic basis of these traits was reflected at the genomic and proteomic levels, where many genes positively affected hot and cold tolerance, while just a few had opposing effects [12,13]. Experimental evolution using *Escherichia coli* has also identified two prominent pathways influencing increased heat tolerance, one with a fitness cost at lower temperatures and one without [14].

It is unclear whether mechanisms of heat and cold tolerance in ectotherms are relevant to endotherms. Recent work on ostriches demonstrated a negative genetic correlation between reproductive success under cold and hot conditions, indicating that the evolution of increased heat tolerance can come at a cost to cold tolerance in some endotherms [15,16]. There are also heat tolerance mechanisms that should not be directly linked to cold tolerance, and vice versa. For example, mechanisms only activated when hot, such as panting, may be independent of cold tolerance (Box 1). Whether correlations between heat and cold tolerance are contingent upon the types of traits underlying thermoregulation (e.g., behavioural versus physiological), and how they are expressed needs to be established.

Thermal conflicts across life stages

The importance of changes in thermal tolerance through ontogeny have been highlighted by work on resource investment across life stages in insects: juveniles invest in growth while adults invest in reproduction [17,18]. Similar changes in resource investment patterns occur in endotherms, but unlike ectotherms they also need to regulate their body temperature (thermoregulate) as they are generally unable to tolerate changes in core temperature. Endotherms therefore have the additional challenge of physiologically regulating their body temperature as they age. The ability to thermoregulate is influenced by various traits that can change over life. For example, the size and shape of most endotherms differs between juveniles and adults, which alters the surface-to-volume relationship and thermoregulatory demands [2,19,20] (Figure 2).

Both juveniles and adults are vulnerable to high and low temperatures [21,22], but the relative thermoregulatory demands imposed by high and low temperatures may differ across life stages. This may potentially cause a shift in the thermoregulatory priorities across life. The larger size of adult endotherms may offer thermoregulatory advantages under sustained cold conditions, or when there are rapid shifts to cool conditions such as during nights or periods of bad weather. However, the greater thermal inertia of large individuals is expected to render them more susceptible to sustained heat stress [23]. The reverse is likely to be true for juveniles, as their smaller size makes them more susceptible to reductions in temperature but better able to dissipate heat when temperatures increase [24]. For populations to persist, it is therefore important that the mechanisms that promote reproduction under hotter temperatures in adults (e.g., body shapes with low surface area-to-volume ratios) do not compromise the growth and survival of juveniles during cold periods (Box 1).

How selection for thermoregulation under hot and cold conditions changes across juvenile and adult stages will likely differ across habitats (Box 2) and species. By focusing on how key traits, such as

Box 1. Potential for antagonistic thermal selection when hot and cold

The thermoregulatory demand of endotherms and the potential to meet this demand depends on a large range of morphological, physiological, and behavioural traits (Figure I) [8,10,27,60–62]. Some of these thermoregulatory adaptations may operate independently across hot and cold conditions, enabling evolutionary responses to temperature fluctuations. In this box we first describe four traits that may influence heat and cold tolerance independently (Table I). Second, we propose a list of thermoregulatory traits with the potential to have opposing effects on heat and cold tolerance (Table II), potentially limiting evolutionary responses to temperature fluctuations across life stages. Some of these traits may be highly plastic, allowing, for example, changes in insulation by acclimatisation or shape shifting. Such plasticity may relax antagonistic selection on hot and cold tolerance. Whether there is sufficient time to initiate a phenotypic response in a given trait will depend on the frequency of thermal fluctuations (Box 2) and the reversibility of phenotypic responses [30,63].
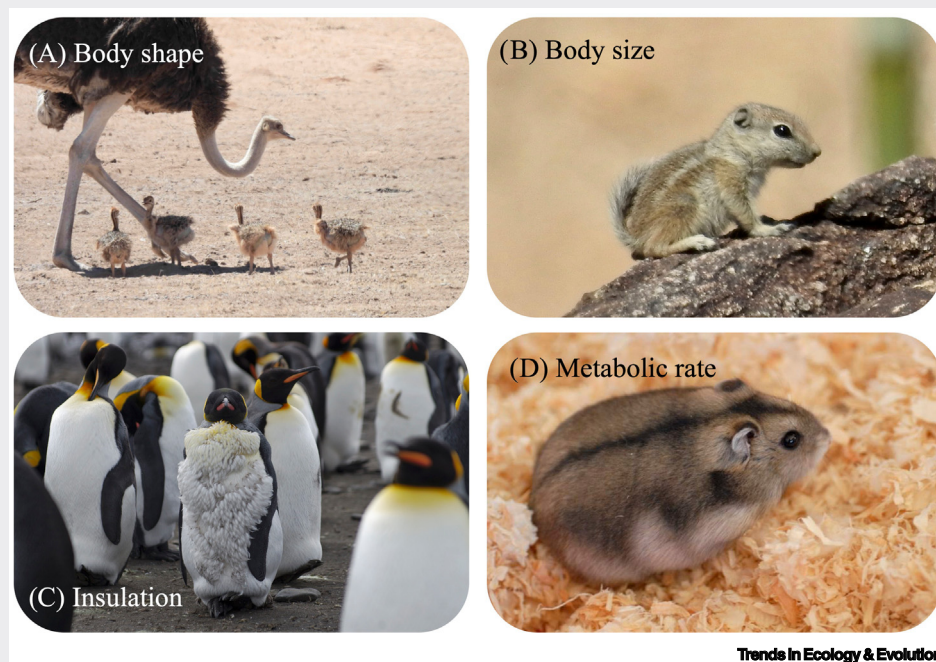

Figure I. Examples of traits related to thermoregulation that can diverge between life stages. (A) Adult and juvenile ostrich (*Struthio camelus*) diverge in body shape and size as they age. (B) Juvenile white-tailed antelope squirrels (*Ammospermophilus leucurus*) are born with a weight of just 3.1% of their mother. (C) Moulting king penguin (*Aptenodytes patagonicus*), drastically change their insulation between juvenile and adult life stages. (D) In the Siberian hamster (*Phodopus sungorus*) plasticity in basal metabolic rate is linked to torpor duration [60]. Photos credits (A) C.K. Cornwallis; (B) dlm1965, licence[ii]; (C) Rob Oo, license[iii]:); (D) Philipp Salzgeber, licence[iv]. All photos have been cropped.

Table I. Traits with potentially independent effects on hot and cold tolerance

| Trait	Thermoregulatory significance
Panting	Improves heat dissipation by evaporative cooling from lungs and mouth. Relies on good access to water and has some energetic costs
Vasoconstriction or vasodilation	Controlling blood flow to poorly insulated areas of the body surface to control heat dissipation and retention when hot and cold, respectively
Facultative hypothermia or hyperthermia	Allows the body temperature to deviate from optimal temperatures when hot or cold respectively. Can conserve energy and water, but may carry fitness costs
Shivering	Shivering can be used to increase the metabolic rate when cold to increase the body temperature, similar to brown fat

Table II. Traits with potentially opposing effects on hot and cold tolerance

Trait	Potential for antagonistic thermal selection	Potential for life stage conflicts
Body shape	Longer appendages allow increased heat dissipation when hot but reduce heat retention when cold	Shape and size of appendages often change across life stages, but there are likely developmental constraints on how much these traits can differ across life stages
Body size	A smaller body is advantageous in hot climates, whereas a bigger body is advantageous in cold climates	Body size is smaller in juveniles than in adults, and body size is not only optimized for thermoregulation but also for feeding, fecundity, and predator avoidance
Insulation	Reduced insulation improves heat dissipation (e.g., by convection) but also lowers the heat retention when cold	Insulation may change across life stages, but moulting can be costly and create vulnerabilities by reducing mobility and thermoregulation
Basal metabolic rate	Higher basal metabolic rate reduces the need to conserve heat when cold, but increases excess heat to dissipate when hot	There is likely flexibility in the basal metabolic rate across life stages but may be costly as adjustments can influence a wide range of other organismal functions

body shape or size, change across life stages it should be possible to predict the magnitude of thermoregulatory conflicts over life. Size differences between juveniles and adults can vary substantially among species, and is most prominent in larger species of birds [25] and mammals [26]. Therefore, changes in selection on thermoregulation between juveniles and adults should be greatest in

Figure 1. Adaptation to cold can limit performance in the heat. (A) African penguin (*Spheniscus demersus*) seeking shade under a boardwalk at Betty's Bay, South Africa. Their thick insulation allows them to feed in cold waters, but is disadvantageous when breeding even in temperate conditions. The African penguin already starts panting at 25°C, and the availability of shelters for their nests are therefore crucial for their breeding success [57]. (B,C) Eurasian blue tits (*Cyanistes caeruleus*) are to our knowledge one of the few species where effects of temperature extremes on growth of juveniles and reproduction of adults have been measured under controlled conditions. (B) Reduction in heat load increases adult reproduction, showing how heat stress limits reproductive success [36]. (C) Small chicks have faster cooling rates than big chicks, making them vulnerable to cold and more dependent on nest temperatures [58]. Photo credits: (A) Mads F. Schou; (B) Andreas Nord, reproduced from [59]; (C) Thomas Hirsch.
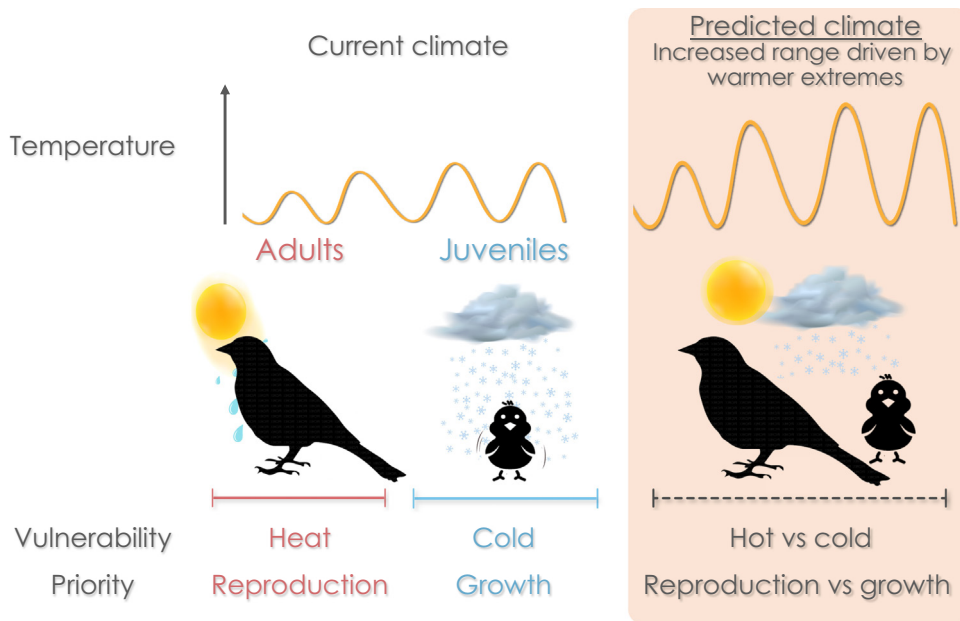
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Figure 2. Temperature fluctuations cause divergent thermal challenges across life stages. Future climatic unpredictability means that animals will need to cope with hotter temperatures while maintaining tolerance to cool temperatures, selecting for thermoregulation over a greater temperature range. Evolutionary responses to such climatic challenges will require different adaptations at different life stages, with any weak spot reducing organismal fitness. Both adults and juveniles are vulnerable to heat and cold, but the change in size from juveniles to adults may lead to different thermoregulatory demands. Large adults are potentially more vulnerable to heatwaves, and small juveniles are potentially more vulnerable to temperature drops. Additionally, adults and juveniles differ in their investment priorities ('reproduction versus growth'), which places different physiological demands on different life stages that may influence thermal tolerance.

the bigger species, all else being equal. For example, both the golden mouse (*Ochrotomys nuttalli*) and the four times larger white-tailed antelope squirrel (*Ammospermophilus leucurus*) produce new-borns of around 3g. The much larger difference in relative body mass in juvenile squirrels (3.1%) compared with juvenile mice (12.8%) should theoretically generate greater divergence in thermoregulatory demands across life stages. However, the magnitude and impact of the resulting selection for resolving such divergence remains unknown.

Thermal conflicts between life stages may be resolved in different ways. Ecological resolutions – such as thermal niche differences between juveniles and adults – may allow juveniles to cope with thermal fluctuations by sheltering in thermal refugia that are accessible due to their smaller size. Life stages may also evolve distinct body shapes: for example, smaller ears or beaks of juveniles relative to their body size. This may increase the cold tolerance of juveniles and heat tolerance of adults by decreasing heat retention across life [27,28]. Many endotherms also have different fur or feather coverage across life stages, reducing heat dissipation in juveniles and increasing it in adults. These mechanisms appear uncoupled across life stages, showing how adaptation to different thermoregulatory demands over life may be achieved [29,30] (Box 1). However, there are likely to be evolutionary constraints on these and other traits [31], and we know from other fields of evolutionary biology that genetic conflicts between juveniles and adults persist and may be difficult to resolve [32–34]. For instance, there is a limit to how small appendages can become without impacting mobility or other key functions [35]. Similarly, energetic investment in increased metabolic rates in juveniles to counter cold stress may reduce investment in growth. Conversely, a reduction in body temperature (i.e., hypothermia) during cold nights might allow juveniles to

Box 2. How will changes in thermal fluctuations across different temporal and spatial scales influence species?

The way climate fluctuations influence the temperatures juveniles and adults are exposed to during development and reproductive periods is likely to vary with species life history and habitat (see Figure 2 in main text). For example, species with slower life histories (longer developmental times and reproductive periods) will experience a greater range of temperatures compared with species with faster life histories, particularly in more seasonal environments (Figure IA). Because of the need to cope with both cold and heat, the potential for evolutionary responses to even small increases in maximum temperatures due to climatic change may be impacted by any genetic association between cold and heat tolerance. However, as seasonal fluctuations are slow, there is also greater potential for phenotypic plasticity as a means of temporarily increasing heat or cold tolerance when most needed. By contrast, in aseasonal environments, the range of temperatures that species experience is less likely to be impacted by their life histories. Instead, diurnal temperature variation, and how this is buffered by habitat type, is likely to be the main determinant of the temperature range that individuals experience, although species with a slower life history are more likely to experience occasional, more extreme fluctuations (Figure IB). Further increases in thermal fluctuations due to climatic change could therefore be particularly challenging for species living in desert environments, as they would need to increase their heat tolerance without sacrificing their cold tolerance.
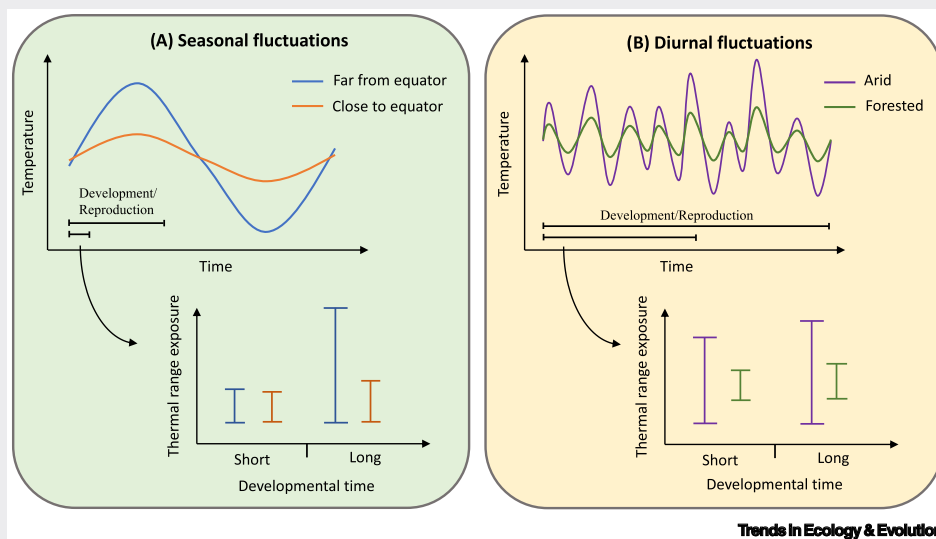

Figure I. Thermal fluctuations can have many shapes. Two major types of thermal fluctuations are (A) seasonal, which predominantly change with latitude [64], and (B) diurnal fluctuations which, among other things, depend on aridity [65,66].

conserve energy, but if this slows growth then it may carry long-term costs. Similar temperature-dependent trade-offs may occur during adult life stages. For example, in blue tits, energetic investment to increase heat dissipation can reduce reproductive investment [36] (Figure 1B), illustrating that changes in physiology to regulate temperature can carry fitness costs.

Quantifying thermoregulation across life

How do we measure heat and cold tolerance across life stages in endotherms? Inspired by the field of thermal adaptation in ectotherms, there has been a recent focus on thermal limits derived from estimates of the thermal neutral zone [37,38]. There are several caveats with this approach: for instance, fitness may be affected before such limits are reached, underestimating the effects of temperature fluctuations on animals [39]. Nevertheless, alternative frameworks for estimating the thermal tolerance of endotherms are currently limited [8]. Fertility limits can be compromised at a narrower range of temperatures than physiological limits, potentially making them a better predictor of species responses to climate change in nature [40]. Because of this, the effect of temperature on reproduction is gaining increased traction in the field, illustrated by the recent foundation of the European Thermal Fertility Network[i].

As thermal fertility limits cannot be measured in juveniles, alternative traits that are related to juvenile fitness, such as growth rates or time to maturation, should be considered. These traits are different from reproductive success in that they cannot be repeatably sampled across years for the same individual, limiting the potential to reliably estimate individual differences in thermal tolerance. That said, they provide insight into the ability of juveniles to translate their thermoregulatory ability into what is most important for fitness: surviving to an age of reproduction. Mechanistic insight from such comparative approaches will always be limited, so there is a need for detailed, species-specific studies. Here, phylogenetic approaches can help to inform which traits and which species are best targeted by future mechanistic studies ('phylogenetic targeting') [41]. For example, species with higher and lower differences in heat and cold tolerance across life stages than the average across clades can be identified for more in-depth studies into the molecular basis of thermoregulation across life.

A deeper understanding of the mechanistic basis of heat and cold tolerance is pivotal to predicting population responses to shifts in temperature regimes [42–44]. A key component of this will be to characterise the molecular regulation of the development of heat and cold tolerance across different life stages. However, previous work on thermal adaptation in endotherms has focused primarily on the physiological mechanisms involved in thermoregulation [9,45], and not how the molecular regulation of thermal tolerance at different ages evolves. For example, we know that many endotherms respond to high temperatures by adjusting blood flow to the skin, increasing convective airflow, panting, using evaporation from the skin, and even selective brain cooling [8]. By contrast, efforts to characterise the genetic basis of heat or cold tolerance in larger endotherms have been restricted to genome comparisons of camels and aquatic mammals [46], population genomics of sheep [47], and gene expression analyses of cattle (e.g., Singh *et al*. [48]). Similarly, information on smaller mammals and birds is limited to genome comparisons and gene expression analyses of poultry [49–51], a few species of songbirds [52], and small rodents [53,54], typically from laboratory experiments and at specific life stages. Hence, many of the genes involved in the evolution of cold and heat tolerance at different life stages in endotherms, including those underlying physiological responses, remain elusive [55].

Studying the genetic basis to thermal tolerance through development requires monitoring large numbers of individuals over prolonged periods of time. This is infamously difficult to do [56], but recent technological developments have made this more feasible. These developments include small bio-loggers that record the ability of individuals to maintain near-constant body temperatures when hot and cold [9]. This approach has the advantage that the trait (body temperature) is directly comparable across life stages. This can potentially be complemented with remote monitoring of fitness-related traits, such as survival and reproductive success, during hot and cold periods, using drones and camera traps. Common to these approaches is that animals are free to move around while fully exposed to temperature fluctuations. Combining this data with individual genotyping will provide insight into the underlying molecular mechanisms of thermoregulation and their evolutionary potential.

Estimates of heritability are often used to infer the evolutionary potential of populations to respond to selection. However, estimates of heritability may be of limited value in forecasting how different populations will respond to new thermal regimes. Heritability measures the proportion of phenotypic variance explained by standing genetic variation in a given population at a given time. Such estimates are therefore population-specific and may not allow extrapolation across environments or species. Furthermore, if much of the genetic variation underlying heritable variation is explained by genes with opposing effects on heat and cold tolerance, then high heritabilities may be misleading. Only if genes involved in heat and cold tolerance operate independently do such

estimates of heritability have a chance of giving reasonable estimates of the evolutionary potential for adaptation to different climatic regimes. In principle, estimating covariances and genetic correlations across traits influencing thermal tolerance to hot and cold may increase the accuracy of predictions, but this requires information on large numbers of individuals that is unrealistic for most species. Consequently, to predict how different populations will respond to new conditions we need to know about the molecular mechanisms regulating thermal tolerance.

Molecular genetic analyses may help identify what genes are involved in cold, heat, or both cold and heat tolerance, and how this changes as individuals age. How genetic variation is distributed across these genes and across populations will provide valuable insight into the evolutionary potential to respond to climatic change, how fast adaptions can arise, and which life stages may be most vulnerable to climatic change. Using molecular genetics to identify homologous thermal tolerance genes across a few species may allow larger-scale inferences across other populations or species. For example, comparative genomic analyses of genetic diversity in homologous genes and their regulatory regions can provide information on the constraints of thermal adaptation in species without the need for large experimental setups.

Concluding remarks

Increases in climate fluctuations will select for tolerance to a greater range of temperatures during juvenile and adult life stages. The potential for species to evolve such thermal tolerance will likely depend on the genomic integration of adaptations to hot and cold conditions expressed throughout life, but this remains uncharted research territory in endotherms. The presence of a trade-off between heat and cold tolerance may generate thermoregulatory conflicts that limit potential evolutionary resolutions within and across life stages. We therefore need to examine tolerance to heat and cold throughout the lifespan of individuals and to identify whether there are antagonistic effects on the underlying molecular machinery. This will tell us whether adaptation to climate change is constrained by divergence in thermoregulatory demands across life stages.

There is a need to do four things (see Outstanding questions). (i) Evaluate the divergence in the thermoregulatory demands at high and low temperatures across life stages, for example using morphological metrics and biophysical models. By integrating work on morphology and physiology (e.g., to quantify the relationship between size and shape and physiological thermal stress) it is possible to estimate the baseline thermoregulatory demands. (ii) Integrate work on cold and heat tolerance to describe the prevalence of trade-offs across species. (iii) Investigate changes in thermal tolerance over life to document thermal conflicts across life stages. This requires repeatedly measuring thermal tolerance, which may be aided by collecting data on survival and growth in juveniles and survival and reproduction in adults in response to increasing and decreasing temperatures. (iv) Examine the role of selection on the regulation of genes involved in heat and cold tolerance (i.e., plasticity in expression of thermoregulatory genes) as a potential mechanism for reducing thermal conflicts between life stages. Including such data on heat and cold tolerance and life stage thermal conflicts in climate models and species distribution models (also known as ecological or environmental niche models) will help predict the vulnerability of species to climate change.

Outstanding questions

Are heat and cold tolerance genetically integrated, or are they free to evolve independently? This can be evaluated by mechanistic studies on specific species, but to understand the evolutionary consequences on the scale of ecosystems comparative approaches are necessary. Measures of thermal tolerance from multiple species are needed for this, making it relevant to assess whether thermal tolerance is best approximated by the ability of animals to maintain optimal body temperatures at extreme temperatures or by repeated fitness measures across variable temperatures.

How much do the changes in thermoregulatory demands across life stages differ among species? With sufficient morphological and physiological data, this can be estimated with biophysical models. It will be challenging to incorporate how behavioural and ecological resolutions to thermal challenges influence variation in physiological thermoregulatory capacity exposed to selection.

How are thermal conflicts across life stages resolved? Selection on the regulation of genes involved in heat and cold tolerance is one potential mechanism for reducing thermal conflicts between life stages. The resolution of genetic conflicts through gene regulation is known from ageing research, although this is not always sufficient to suppress antagonistic effects across life stages.

Are thermal conflicts across life stages resolved, or in a state of ongoing genetic conflict? This may differ among species: for example, because of variation in size differences between juveniles and adults, resulting in different thermal conflicts across life.

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Declaration of interests

The authors declare no competing interests.

Resources

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