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Making a difference: the role of comparative biology in tackling climate change

Two endangered polar species, the polar bear (*Ursus maritimus*) and the Eastern Greenlandic narwhal (*Monodon Monoceros*). Photo credits: Anthony M. Pagano and Terrie M. Williams.

For many, 2020 was notorious for the COVID-19 pandemic, but for climate scientists, the year is also infamous for tying with 2016 as the hottest since records began. 'Nine of the warmest years on record have occurred since the last JEB special issue in 2010 on the things that are changing as a consequence of Earth's growing population and our impact on the global system', says JEB Editor-in-Chief, Craig Franklin. With the ice caps and glaciers melting, devastating bushfires scorching arid regions, and hurricanes and typhoons battering coastal communities, the impact on local ecosystems has been catastrophic. Estimates suggest that 3 billion animals died in the blazes that engulfed Australia in 2020. Although many impacts of climate change are not as dramatic, they are no less profound. As temperatures gradually increase, rainfall patterns alter and ocean currents shift; species that once survived in comfort are forced to relocate or are taken to the brink of extinction.

'Physiologists can play a critical role in the conversation around climate change', says Franklin, explaining that knowledge of physiology ideally positions comparative physiologists to predict the impact of climate change on species and to inform conservation policy and action. 'We have a series of tools and underlying theories and concepts that really do add a lot of power to the conversation', says Franklin. With this in mind, Craig Franklin and Hans Hoppeler (JEB Editor-in-Chief, 2004–2020) commissioned a series of review articles dedicated to strategies for, and predictions of, the impact of climate change on ecosystems across the globe. Spanning the animal kingdom from symbionts and reptiles to insects and charismatic megafauna, the collection discusses our current understanding of the physiological impact of the climate crisis and the lessons that will inform biodiversity management and conservation in the coming decade.

Predicting the future

In his review, Hans-Otto Pörtner from the Alfred Wegener Institute, Germany, and co-chair of the Intergovernmental Panel on Climate Change (IPCC) Working Group II, discusses the physiological and ecological impact of increasing temperature in ectothermic animals, differences in vulnerability to high temperatures through different life stages and the impact of temperatures on geographic distributions (jeb238360). In addition, Pörtner cautions that endotherms, including humans, are vulnerable to the damaging effects of high temperature when the humidity is high – limiting heat loss by evaporative cooling – leaving humans and other mammals vulnerable as heat waves become increasingly severe. Warning that current temperature changes are too fast for endotherms and ectotherms currently living close to their thermal limits to adapt successfully, Pörtner says, 'Evolutionary adaptation limits may leave geographical shifts (migratory movements) as the only option to respond'. However, he is optimistic, saying 'Uncovering the basic interdependencies of relevant systems, as well as using the right levers to mobilize political and societal action will be key to mastering the climate crisis'.

While many scientists resort to simulations of future climate scenarios in the lab, Sarah Diamond and Ryan Martin from Case Western Reserve University, USA, use urban heat islands associated with cities to investigate the impact of climate change in the real world (jeb229336). Focusing on the impact of local temperatures on common woodland ants (*Lasius americanus*) colonising pockets of urban woodland in Knoxville, Tennessee, USA, the pair investigated the physiological differences between rural populations and populations at higher temperatures in the city (~3.6°C warmer). Although the urban ants were more tolerant of warm conditions, they struggled at low temperatures. Turning to the scientific literature, the duo found that the resilience of many urban species results from a combination of evolutionary responses and shorter term individual flexibility, and is similar in scale to the physiological differences between organisms living at different latitudes. The lessons learned from comparisons with urban populations will allow scientists to identify vulnerable species that require particular conservation attention.

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An urbanization gradient, Cleveland, Ohio, USA. Photo credit: Case Western Reserve University.

However, Christian Hof (Technical University of Munich, Germany) warns that a lack of integration between scientific disciplines is holding back our ability to predict the impact of environmental change on biodiversity. Identifying four key factors that impact species' survival – climate change, land-use, physiology and species mobility (dispersal) – Hof challenges whether all of these factors are given sufficient emphasis when researchers consider the impact of climate change on biodiversity (jeb238352). From a total of almost 80,000 publications assessing the impact of climate change on biodiversity, he found that only 591 studies jointly incorporated the roles of physiology, species mobility and land use together. 'The research field of physiology appears to be more separated from the other studies than those dealing with dispersal and land-use change', says Hof, who attributes the lack of integration to structural stratification within the scientific system. Proposing a series of solutions – including an interdisciplinary approach to education, broader acceptance of interdisciplinary research by journals and reducing disciplinary funding barriers – Hof is optimistic that more scientists will embrace the rewarding opportunities of a broader integrative approach if these challenges are met.

Reviewing the roles of fecundity and survival in the ecological and evolutionary responses of organisms to environmental change, Lauren Buckley (University of Washington, USA), Sean Schoville (University of Wisconsin, Madison, USA) and Caroline Williams (University of California, Berkeley, USA) argue that 'understanding systematic shifts in fecundity and survival, and how organism-environmental interactions produce these shifts, can improve predictions of ecological and evolutionary responses' (jeb228031). Observing how fecundity is restricted at high altitudes and latitudes – where energy is limited and offspring must develop fast – whereas survival may be more limited at low latitudes – where ectothermic creatures may already be living on the physiological edge – they say, 'Environmental constraints on individuals, populations, species and communities along a spatial environmental gradient can inform predictions of how environmental change leads to differential shifts in fecundity and survival'. Modelling the impact of climate change on the fitness of montane butterflies (*Colias* spp.), the trio shows how the insect's fecundity will peak at higher elevations while their survival will decline ominously.

Prediction case studies: reptiles

Reptiles that depend on the nest temperature to determine the sex ratio of their offspring are particularly vulnerable to the effects of climate change as environmental temperatures increase. A. L. Carter and Fredric Janzen from Michigan State University, USA, outline the challenges that researchers have faced over the past five decades investigating temperature-dependent sex determination (jeb236018). Explaining that estimates of nest temperature based on present and future climate predictions are currently insufficiently accurate to predict their impact on reptile embryonic development, the pair recommend monitoring of alternative nesting sites that could provide refuges for reptiles that are no longer able to reproduce successfully in their current locations. They are also optimistic that recent breakthroughs will lead to a better understanding of the role of temperature in sex determination, which will allow more accurate predictions of the physiological outcomes of different climate scenarios for a number of reptile species.

Diving ectotherms – turtles, crocodiles, frogs and iguanas – are also at risk as environmental temperatures rise, limiting dive duration. Yet the extent of these restrictions remains unclear. Reviewing the literature spanning 20 species, Essie Rodgers (University of Canterbury, New Zealand), Craig Franklin (The University of Queensland, Australia) and Daniel Noble (The Australian National

A saw-shell turtle (*Elseya latisternum*) by Fitzroy River in Queensland, Australia. Photo credit: Cameron Baker.

University) have concluded that every 1°C rise in water temperature reduces dive durations by 11% – meaning there could be a 44% fall in time spent diving if water temperatures rise, as predicted, by 4°C (jeb228213). Unfortunately, species that supplement their oxygen supply through the skin, mouth or cloaca will be as vulnerable to environmental temperature increases as animals that depend solely on inhaled oxygen, and large creatures are unlikely to have much of an advantage over small divers. As many diving animals will probably be unable to adapt and extend dive durations, Rodgers and colleagues are concerned by the detrimental effects of more time spent at the surface; including the increased risk of predation, the cost of additional descent and ascent, and the loss of foraging time while submerged.

Prediction case studies: mammals

Although endothermic creatures do not depend on their environment to maintain a stable body temperature, the ability of mammals that populate dry habitats to maintain their body temperature within a narrow range is challenged as temperatures soar and drought limits the availability of food and water. Andrea Fuller from the University of Witwatersrand, South Africa, and

An aardvark starved by drought foraging during the day to reduce the energetic cost of maintaining its body temperature. Photo credit: Wendy Panaino.

colleagues discuss the impact of rising temperatures and drought on the physiology of species such as aardvarks, flying foxes, koalas, camels and Arabian oryx (jeb238113). 'The lack of water makes it harder for them to maintain a normal body temperature on hot days', says Fuller. Although smaller mammals can seek shelter from the heat in small crevices and resort to torpor to conserve energy, larger animals may be more resilient to dehydration and able to remain active during the heat of the day. Fuller and colleagues are also concerned by the risk of starvation during drought when food is scarce and mammals are unable to maintain their temperature on cold nights. She says, 'we need to consider how food and water are changing to predict how dryland mammals will cope with climate change, as well as consider how a mammal's body size will influence its responses'.

Mammals in the Polar Regions also face an uncertain future as unprecedented warming drives catastrophic loss of sea ice. Anthony Pagano (San Diego Zoo Global, USA) and Terrie Williams (University of California, Santa Cruz, USA) discuss the impact of environmental change on two iconic species: the polar bear and narwhal (jeb228049). Reviewing how polar bears are being driven onto land after losing access to sea ice and the highly calorific seals that live upon it, Pagano and Williams also consider how unpredictable shifts in sea ice have led to the loss of the reliable breathing holes that narwhals depend on, trapping and suffocating the mammals. 'We found that major ice loss translated into elevated locomotor costs that range from 3- to 4-fold greater than expected for both species', they say. In addition, the narwhal's slow pace of life leaves them vulnerable to attacks by killer whales in open water. The pair warn that the decline of both apex predators will 'lead to rapid changes in the Arctic marine ecosystem'.

Prediction case study: birds

Desert birds frequently experience heat in excess of their own body temperature, leaving them no choice but to regulate their body temperatures by evaporating water – either through the skin, by panting or by gular fluttering – to remain cool. In a bid to predict the impact of increasingly frequent heat waves on desert bird survival, Andrew McKechnie (University of Pretoria, South Africa) Alexander Gerson (University of Massachusetts, USA) and Blair Wolf (University of New Mexico, USA) analysed the heat tolerances and evaporative cooling abilities of 56 bird species from arid regions of the US southwest, Australia and southern Africa (jeb229211). Identifying that smaller species are at greater risk of overheating and dehydration than larger birds, the researchers also noticed that passerines are more likely to be vulnerable to extreme heat waves than columbids and caprimulgids, thanks to less efficient heat loss by panting. They add that 'the metabolic costs of heat dissipation pathways, rather than capacity to increase evaporative water loss above baseline levels, appear to represent the major constraint on the upper limits of avian heat tolerance'.

A heat-stressed southern red-billed hornbill (*Tockus rufirostris*) in December 2020 in Kruger Park, South Africa. Photo credit: Marc Freeman.

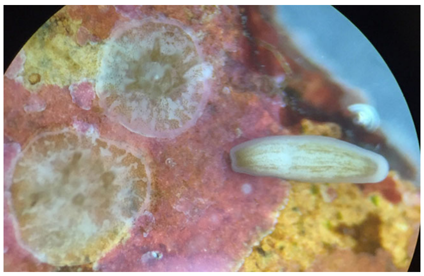
Prediction case study: insects

While the threats posed to many ectotherms by climate change are becoming better documented, the impact on the insect parasitioids that regulate insect populations by killing their hosts has been less well scrutinized. Reviewing how parasitoids are more vulnerable to extreme climate events than their hosts – resulting in the loss of biological control and pest outbreaks – Cecile Le Lann and Joan van Baaren from Université de Rennes, France and Bertanne Visser (UCLouvain, Belgium) discuss how parasitoids that used to wait out winter as diapausing eggs three decades ago now no longer do so, remaining in sync with their insect hosts, which now remain active during warmer winters (jeb238626). The researchers also warn that strategies that allowed parasitoid populations such as *Anaphes victus* in Canada to endure extreme cold conditions may no longer protect them as winters warm and the insulating blanket of snow is lost, fatally chilling the next generation of parasitoids and removing the brake on host populations. 'To better address the consequences of climate change for both hosts and their parasitoids, further studies should focus on short-term phenotypic responses to predictable and unpredictable variation in temperature, such as phenotypic plasticity and bet-hedging', they say.

Prediction case studies: aquatic species

In recent years, two theories have been at the forefront explaining the impact of temperature on the growth and performance of fish, both underpinned by oxygen delivery restrictions at higher temperatures. However, laboratory measurements of the effect of temperatures on aerobic scope – the difference between the maximum metabolic rate and basal metabolic rate – vary greatly between species, 'indicating that oxygen- and capacity-limited thermal tolerance is unlikely to be a universal mechanism', says Sjannie Lefevre (University of Oslo, Norway), Tobias Wang (Aarhus University, Denmark) and David McKenzie (University of Montpellier, France) (jeb238840). In the hope of identifying alternative physiological factors that are better suited to predict the impact of temperature on fish growth and performance, the researchers propose two alternatives: growth rates at different temperatures and the increase in metabolism associated with digestion. Although Lefevre and colleagues acknowledge that recording both parameters over a range of temperatures can be more challenging than the measurements required to determine aerobic scope, they argue that digestion and growth are more holistic values that better reflect the real life situations of animals in the wild and will lead to better predictions of the impact of climate change on fish populations.

Reviewing the responses of aquatic ectotherms to multiple stressors – temperature, salt, UV, toxins and radiation – Inna Sokolova from the University of Rostock, Germany emphasises how energy metabolism is the lynchpin for survival as ectotherms redress physiological imbalances caused by stress (jeb236802). Listing the impact of protein synthesis, ion and salt homeostasis, mitochondrial proton leak and detoxification mechanisms on the energy budget of aquatic ectotherms, Sokolova also reviews the metabolic factors that can be used to detect when situations are stressful for these animals, which also determines the geographic ranges they can occupy. ‘The conserved nature and high energy cost of the general cellular stress response underscore the usefulness of bioenergetics in assessing the effects of the multiple stressors and predicting their ecological consequences for populations’, says Sokolova.



Pocillopora acuta larva and newly settled juveniles. Photo credit: Hollie Putnam.

Concluding this collection of reviews, Hollie Putnam (University of Rhode Island, USA) describes corals as ‘a clear canary in the coal mine’, that warn of future losses as climate change gathers pace. Yet corals are more responsive to the challenges they face than was previously appreciated. Each community component – from coral hosts to their dinoflagellate symbionts and the microorganisms that colonise the coral tissue and skeleton – is capable of responding to environmental change, which can offer protection from stressors in a matter of weeks or months. In addition, beneficial adaptations can be inherited from previous coral generations through genetic and non-genetic means (jeb239319). Putnam points out that the presence of corals in apparently inhospitable environments – such as CO_2 vents in the seafloor and following thermal stress – provides ‘a ray of hope’ for the future of reefs. ‘Now, more than ever, it is critical to engage in collaborative cross-scale and multi-omics approaches to push our knowledge of coral holobiont biology forward’, she says.

Protecting biodiversity in a changing world

Looking to the future, Franklin is optimistic. ‘Physiologists and experimental biologists can make valuable contributions to our understanding of threats to biodiversity’, he says, adding that comparative physiologists can make pivotal contributions to the dialogue surrounding conservation. Understanding the interactions between animals and their environments and how those will change as temperatures rise, climate patterns change and population distributions shift, is essential for building policies to protect keystone and vulnerable species alike. From Diamond and Martin’s review detailing the lessons that we can learn from urban heat islands to Putnam’s hope for the future of corals, this collection of reviews provides a foundation for comparative physiologists to build on as the vanguard in the battle to protect biodiversity. ‘We see this as an important special issue. We know we are imperilled by climate change, but this collection of articles talks about what we should be doing in the future to protect the planet’, says Franklin.

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