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Inside JEB

SURVIVAL IN A CHANGING WORLD

In August 2009, the International Union of Physiological Sciences (IUPS) held its 36th Congress in Kyoto in the same convention centre where the historic Kyoto Protocol was drawn up 12 years earlier. The symbolism of this coincidence was not missed by Malcolm Gordon, the Chair of the IUPS's Commission on Comparative and Environmental and Evolutionary Physiology. For Gordon, a long standing advocate of the importance of ecological and environmental physiology, the meeting in Kyoto was an ideal opportunity to bring together many of the leading voices in the environmental physiology community to look at one of the most pressing issues currently facing the planet: climate change and its ecological and physiological impact. Contacting his IUPS colleague and Editor-in-Chief of *The Journal of Experimental Biology* Hans Hoppeler, Gordon suggested publishing a collection of review articles addressing the issue of survival in a changing world. Teaming up with Brian Barnes, a leading researcher in Arctic animal physiology, Gordon and Hoppeler have drawn together reviews addressing issues ranging from the impact of climate change on a wide range of terrestrial and aquatic species, to the effects of environmental change on ecosystems and populations, disease distributions and the ability of species to adapt to the environmental changes that they encounter.

The opening review by Glen MacDonald discusses the impact of climate change on a major ecological niche; the Arctic (p. 855). With CO_2 levels currently at a 600,000 year high and 100 p.p.m. above previous records, MacDonald warns that future CO_2 levels could reach 500 to 900 p.p.m. by 2100. This coupled with a surface warming pattern unlike any seen before including warmer winters and the phenomenon of Arctic amplification – where northern latitudes warm faster than other regions – leads MacDonald to predict that by the turn of the next century the Arctic 'will be a brand new world for the plant and animal species of the region'. Reviewing the effects of increased temperatures, relatively warm winters and higher atmospheric CO_2 levels on the growth of the boreal forest and tundra, MacDonald points out that increased temperatures and moisture stress could be major factors in limiting the growth and distributions of some species while increasing that of others. According to MacDonald, the Intergovernmental Panel on Climate Change projections suggest that large areas of tundra could be replaced by boreal forest by as early as 2100. Although the speed of such replacement remains debatable, MacDonald notes that not only would such a displacement impact regional animal populations but also it could ultimately lower the reflectivity of the planet, consequently accelerating climate change.

EFFECTS OF CLIMATE AND ENVIRONMENTAL CHANGE ON ECOSYSTEMS

Now that the majority of the scientific community has accepted the reality of global climate change, interest has shifted towards assessing the impact that these unprecedented changes are having on populations and ecosystems. Frank La Sorte and Walter Jetz from Yale University describe observed and projected changes in bird distributions in response to climate change and the impact that this is having on their migration strategies and community structures (p. 862). With the huge amount of data that are available on bird distributions, La Sorte and Jetz explain that correlative distribution models (where distribution predictions are based on associations between birds and the climate zones they inhabit) can apply these data to make predictions of the effects that climate change will have on bird populations. However, correlative distribution models are relatively inaccurate, so La Sorte and Jetz propose the development of more sophisticated models that 'attempt to capture the mechanistic link between species' distribution and the environment' to achieve more accurate predictions. While these models will be extremely powerful in the management of well-studied temperate bird populations, La Sorte and Jetz point out that significantly less is known about species in the tropics. The tropics contain approximately 85% of the world's bird species, and the duo explain that we must find out more about these species as they are at greatest risk from the effects of climate change.

Ectothermic creatures, dependent on their environment for thermoregulation, would seem to be even more susceptible to climate change. Ary Hoffmann from The University of Melbourne, Australia, explains that their vulnerability is probably 'dictated by the proximity of the environment to their physical limits,' and the ectotherm that he focuses on is the humble fruit fly: *Drosophila melanogaster* (p. 870). According to Hoffmann, species can be vulnerable to environmental change at a number of levels: the individual, population or species/lineage. Outlining *Drosophila*'s ability to cope with temperature change and rising aridity through evolution, Hoffmann points out that *Drosophila* hit a ceiling in their ability to cope with higher temperatures due to their low heritability/evolvability in response to high temperatures. However, other *Drosophila* species seem better able to evolve in response to survival in cooling environments. Hoffmann is optimistic that tropical species of *Drosophila* will be no more threatened by rising temperatures than temperate species, because their upper thermal thresholds are well above the high temperature extremes that they may experience in the wild.

Moving to the marine domain, Hans-Otto Pörtner discusses the effects of climate change on aquatic ectotherms (p. 881). Describing the relationship between tissue oxygen supply and aerobic fitness and the effect that it has on an organism's ability to function within in an ecosystem, Pörtner discusses the effects of thermal stress coupled with changing CO_2 and O_2 levels on water breathing animals. Explaining that aquatic animals, like other organisms, of necessity survive within specific thermal windows, Pörtner adds that this leaves species vulnerable to the effects of climate change, which may bring with it temperatures outside of an organism's thermal window. This trend will be exacerbated under hypoxia or elevated CO_2 levels, both of which can narrow an organism's thermal window of performance. He emphasizes that we must better understand the relationship between energy turnover, activity capacities and the thermal window to understand how aquatic species specialise within a specific niche and appreciate their vulnerability to climate change. Pörtner emphasises the importance of laboratory studies in establishing the mechanisms that underlie climate change effects on species and provide a link between physiology and ecology to give us a greater understanding of ecosystems at a physiological level.

One of the most fascinating marine ecosystems is the coral reef. Boasting enormous species diversity and underpinning the economic activities of many human populations, these fragile ecosystems are some of the most vulnerable on the planet, already exhibiting significant damage due to environmental degradation. Coral bleaching, ocean acidification and increased storm frequency are all factors in


Shaun Wilson

the loss of coral reefs. Focusing on the fish communities that depend upon and populate coral reefs, Shaun Wilson, from the Department of Environment and Conservation, Australia, and a consortium of 32 collaborators have drawn up a list of 53 crucial questions which they feel must be addressed to 'advance our understanding of how climate change will affect reef fishes and improve the capacity of managers to mitigate such impacts,' says Wilson (p. 894). Almost half of the questions address the issues of habitat associations and community dynamics, while the remainder focus on expanding our understanding of fish physiology, behaviour and management. The consortium hopes that the questions will guide future research, ultimately resulting in better conservation strategies.

While some populations of marine species are relatively restricted to a few small ecosystems, loggerhead turtles are true nomads of the sea. However, as large ectotherms, several of the loggerhead's life stages are significantly influenced by environmental factors, placing them at risk from climate change. Annette Broderick and colleagues from the University of Exeter, Bangor University and the North Carolina Wildlife Resources Commission, outline the threats posed by increased temperatures to loggerhead sex ratios, which are determined by the temperature of the egg during incubation (p. 901). Concerns about the feminisation of the population due to increased nest temperatures led Broderick and her colleagues to call for a better understanding of the influence of temperature on loggerhead sex determination, the identification of nesting sites at risk from high temperatures and the development of intervention strategies for the most vulnerable locations. But it isn't all bad news for the loggerhead. Broderick acknowledges that temperature changes could extend the loggerheads' range north and adds that their broad diet reduces their vulnerability to shifts in prey populations.

Continuing the theme of climate change on terrestrial and marine populations, George Somero from the Hopkins Marine Station, California, tackles the question of how an organism's ability to acclimatise and adapt genetically will determine whether it becomes one of the winners or losers in the race to survive (p. 912). Focusing on intertidal species, which routinely experience extreme thermal stress in their rocky environment, Somero outlines four sets of questions that address: species' responses to climate change; the physiological mechanisms that determine an organism's ability to adapt to a new thermal environment; the issue of whether protein evolution can 'keep pace' with climate change; and how an organism's ability to adapt is affected by the regulatory machinery encoded in its genome. Having identified that warm-adapted intertidal species are most at risk from rising temperatures as they are already close to their thermal limits, Somero suggests that survival could be limited by cardiac failure at high temperatures in some species. He adds that although the simple substitution of a single amino acid can improve the thermal stability of many proteins, the loss of entire regions of genome essential for survival at high temperatures places Antarctic marine stenotherms at risk should temperatures in their thermally stable domain begin to rise. Somero concludes by saying that 'extreme stenotherms, along with warm-adapted eurytherms living near their thermal limits, may be the major "losers" from climate change'.

Having discussed the specific effects of climate change on a range of species, Tyrone Hayes addresses one of the most shocking ecological disasters that we currently face: the catastrophic loss of amphibian species, which has been referred to by some as the 'Earth's sixth mass extinction'. Cataloguing the unprecedented decline in amphibian species (p. 921), Hayes outlines the main factors that he explains underpin this phenomenal reduction in biodiversity. Citing climate (atmospheric) change, environmental pollutants, habitat loss, invasive species and pathogens as the most likely causes of the global amphibian decline, Hayes summarises how many of these factors interact to reduce amphibian breeding success rates and increase mortality rates. Focusing on the function of pollutants as endocrine disruptors that impact reproduction and act as immunosuppressants, Hayes warns that 'increased attention to recruitment [reproduction] and ultimate factors [such as environmental change] that interact with pathogens are important in addressing this global crisis'.

DISEASE AND ZOONOSIS IN RESPONSE TO CLIMATE CHANGE

Malcolm Gordon, from the University of California Los Angeles, has been intrigued by the effects of disease on animal ecology for more than half a century. Gordon remembers debating the issue with one of the founders of island biogeography, Bob MacArthur, while he was a graduate student at Yale 50 years ago. 'We used to discuss the role of disease in terms of animal ecology and to what extent diseases were important factors in determining where animals occur, how many are there and what the densities are,' remembers Gordon. Recognising the effect of disease at this time of unprecedented environmental change, Gordon invited Laura Mydlarz and her colleagues Elizabeth McGinty and Drew Harvell to review the condition of coral reefs and their responses to climate warming and disease.

Reviewing the disastrous impact of rising temperatures and emerging diseases on coral populations (p. 934), Mydlarz and her colleagues state that 'the crux of both coral susceptibility and resilience to warming lies in holobiont and symbiont physiological responses to temperature, UV and pathogens'. Defences, such as fluorescent proteins that protect coral animals and their algal lodgers from radiation, heat shock responses and cellular immunity to disease, offer some protection. Mydlarz also points out that despite some catastrophic bleaching events, corals have been able to switch to heterotrophic food intake after losing their algal symbionts and have even been able to repopulate their lost algal community with more thermally robust species. Equipped with innate immune systems, some corals have also been able to withstand diseases that plague other species. 'Researchers are finding indications of resistance and resilience, and in some instances recovery, growth, acclimation and possible adaptation,' say Mydlarz and her colleagues. However, the trio also point out that 33% of coral species currently face possible extinction and suspect that 'it is unlikely that even the compensatory factors outlined here will allow for the survival of intact coral reef systems during upcoming rapid climate changes'.

Climate change is also predicted to impact vector-borne diseases and their episystems in equally dramatic ways. According to Walter Tabachnick, from the University of Florida Medical Entomology Laboratory, vector-borne diseases are extremely sensitive to climate change and he says that 'vector-borne diseases can serve as the "canary in the mine" as a first alert of changes due to climate,' (p. 946). However, predicting changes in disease distributions and epidemic outbreaks is going to raise a significant challenge. Outlining the close relationships between vector-borne diseases and their environment, Tabachnick discusses the effects that climate can have at various levels in vector-borne disease systems. Focusing on two key examples, Bluetongue virus and West Nile virus, Tabachnick emphasizes the complexity of vector-borne disease episystems. He points out that there are many possible causes for the emergence of either disease in their new locations, and the role of climate is uncertain. However, since climate is an important component of these systems, in order to predict future events, it is essential that we better understand the 'mechanisms controlling and influencing specific components of the complex vector–pathogen–host cycle,' says Tabachnick.

Environmental change is not restricted to the effects of climate. Human encroachment on pristine territories also results in significant ecosystem damage through deforestation and land degradation. The direct impact of deforestation on avian populations is well established; however, the indirect effect of landscape change on bird populations through disease is less well understood. Ravinder Sehgal from San Francisco State University explains that birds harbour and spread several diseases that can affect human populations. Discussing the effects of various pathogens on avian populations, Sehgal explains that the effects of deforestation are currently unclear (p. 955). Presenting evidence for the impact of landscape change on various diseases including avian influenza and malaria, Sehgal says that 'the impacts of deforestation on avian infectious diseases will be diverse, and in many cases go undetected,' but goes on to point out what we could learn about the effects of deforestation by looking at the effects of landscape on the diseases of avian populations.

Concluding the section on the interaction between environmental change and disease, Pieter Johnson from the University of Colorado, USA, and David Thieltges from the University of Otago, New Zealand, discuss how the loss of biodiversity can promote increases in disease within communities (p. 961). According to Johnson, species-rich communities can potentially snuff out transmission of pathogens, such as parasites, by 'wasted' transmissions to hosts who are unable to pass the parasite on to the next life stage. Listing diseases that thrive in communities with low biodiversity, ranging from malformation in frogs to schistosomiasis in humans, Johnson outlines the mechanisms that reduce disease transmission in species-rich communities and lists factors that must be considered when assessing the likelihood that a community will exhibit such a 'disease dilution' effect. Johnson concludes by saying that 'we are only beginning to understand the importance of diversity in complex disease systems,' but adds that 'the rapid decline of many populations and species coupled with an increase in species invasions can be expected to have ramifications for disease dynamics'.

Pieter Johnson

ANIMAL RESILIENCE, ADAPTATION AND PREDICTIONS FOR COPING WITH CHANGE

While resilience, the ability to respond to change, is a well understood ecological concept, Brian Barnes from The University of Alaska Fairbanks explains his own interest is in the physiological responses that underpin resilience. 'Resilience isn't stasis,' he explains, 'but where you can end up in a place where you can still maintain homeostatic relationships and functional systems but they may be different.' Given the changes that many species are already encountering, resilience will be a key factor that will allow them to adapt to rapidly changing environmental conditions.

Ectothermic species that survive in the intertidal zone experience some of the most extreme diurnal body temperature ranges on the planet. Lars Tomanek from California Polytechnic State University, USA, explains that intertidal species can experience and survive daily rises in body temperature of 20°C: 4 times the most extreme human fever. Many of these thermally tolerant species owe their survival to a system known as the heat shock response, which protects proteins and cells from damage at high temperatures. However, many animals in regions that have been thermally stable for thousands of years, such as the polar oceans, appear to have lost these heat shock responses and would seem to be more vulnerable to climate change than their intertidal relatives. Curious to find out which marine invertebrates will be most vulnerable to rising global temperatures, Tomanek reviews the literature (p. 971) and finds that even though intertidal species have a well established heat shock response they are as vulnerable to climate change as polar species, because intertidal populations live close to their thermal limit and are unable to mount a heat shock response to temperatures higher than their current maximal body temperatures. In contrast, subtidal species that survive in more moderate thermal environments are able to produce a heat shock response when exposed to higher temperatures and so are less vulnerable to climate change.

Moving from marine invertebrates to insects, Jeff Bale from The University of Birmingham, UK, explains that while it is convenient to classify overwintering insects as either freeze tolerant or freeze avoiding, in reality the great majority of insects are killed by cold not freezing. So how will overwintering insects be affected as winter temperatures rise? Bale predicts that temperature rises between 1 and 5°C will lead to increased insect survival (p. 980); however, he adds that this effect is 'unlikely to be universal'. Explaining that polar insects are currently protected from lethally low temperatures by snow cover, Bale predicts that these species could become more vulnerable as temperatures rise and snow cover is lost. Higher temperatures could also impact insect developmental rates, causing the progression of critical life stages to become unsynchronised from the day length signal that usually triggers the transition to a subsequent life stage. Bale adds that some regions will become too hot for insects to survive and concludes that while a rise in global temperatures will be unharmful, or even beneficial, for the majority of insect species, the impact of higher temperatures may be profound for polar and tropical species.

Having discussed how species may respond to alterations in the climate, it is also essential that scientists make accurate predictions of areas that may be under the most extreme threat from climate change. Brian Helmuth from the University of South Carolina explains that the factors, such as body temperature, that directly affect an organism's physiological response, may bare little relation to the environmental air temperature. Returning to the intertidal zone, Helmuth and colleagues explain that the body temperature of a mussel is dependent on a wide range of local factors, such as the mollusc's orientation to the sun, the extent of cloud cover and wind speed. Focusing on the 'climatology' of body temperatures, Helmuth describes how he has collected body temperature data on the organismal scale with 'robomussel' data loggers in Pacific Grove, California, every 10 min since 2000 (p. 995). Describing how dramatically the robomussel's 'body' temperature differs from the environmental (e.g. air) temperature, Helmuth says, 'these results strongly suggest that estimates of stress in the field need to be derived from niche-level measurements or models relevant to physiological performance such as temperature'. Helmuth concludes by saying that 'forecasting the location, magnitude and timing of the impacts of climate change on ecosystems is a critically important task,' and is optimistic that his approach to measuring the climatology of body temperatures could improve our prediction of catastrophic events.

SURVIVAL IN A CHANGING WORLD: THE FUTURE

With the failure of the Copenhagen summit to draft a legally binding agreement on the reduction of global CO_2 emission rates, it seems almost certain that we will see further rapid changes in the global climate. But, as far as Malcolm Gordon is concerned, 'the argument about whether the change in climate is the result of human activity or some other natural changes is of little relevance as far as the subject of this special issue is concerned. The changes are happening and they are affecting everything – plants, animals, entire ecosystems – and the changes will also affect the climate of the atmosphere and the oceanic climate and current distributions'. Gordon goes on to point out that environmental physiologists have never been better poised to influence global conservation policy. Documenting the consequences of environmental change and the mechanisms that will allow some species to adapt, while leaving others vulnerable to extinction, it is clear that environmental physiologists will have a pivotal role in guiding the global response to climate change. Ultimately, Gordon and Barnes are optimistic that this collection of reviews will help inspire the next generation of environmental physiologists to address these challenges, raise awareness and begin influencing global environmental policy.

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