

Heat Waves, the New Normal: Summertime Temperature Extremes Will Impact Animals, Ecosystems, and Human Communities

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A consequence of climate change is the increased frequency and severity of extreme heat waves. This is occurring now as most of the warmest summers and most intense heat waves ever recorded have been during the past decade. In this review, I describe the ways in which animals and human populations are likely to respond to increased extreme heat, suggest how to study those responses, and reflect on the importance of those studies for countering the devastating impacts of climate change.

Introduction

Summertime is quickly becoming a deadly season for life on Earth. We may pleasantly recall summer as that time of the year for relaxed enjoyment of the sun's comfortable warmth during long and restful days. However, due to global warming, summer temperatures now, and increasingly into the future, are frequently too hot for comfort. During extreme heat waves, temperatures can reach levels inconsistent with life. Animals in terrestrial and marine ecosystems have experienced increased mortality during heat waves of the early 21st century. Summer heat-wave mortality of animal populations is making summer a season of stress and survival, altering populations and ecosystems. As climate change continues, heat waves are going to intensify and become the strong, although stochastic, impact of climate change on life (14, 136).

Earth's biosphere is changing at an unprecedented pace because of human activities. Organisms have been moved around the planet, habitats have been fragmented, polluted, or entirely lost, and global physical and chemical properties have been shifted. Of immediate importance is the increased frequency and severity of heat waves occurring around the planet, exposing life to elevated, and often physiologically stressful, temperatures now more than ever before during the past 150 years (23, 40). The hottest years on record since the mid-19th century have nearly all occurred within the past decade (38, 77) (FIGURE 1). Thermal stress associated with the heat waves during those warm years has directly, widely, and negatively affected animal life (61, 80), including increased mortality of humans in geographically widespread regions (22, 52, 103). Globally, humans in heat waves have increased occurrence of disease

(23, 56, 116, 129) as well as heat-stroke-related mortality (129), the latter of which was recently observed during 2018 July heat waves in Japan and Canada (10). Hence, climate change-related increases in the frequency and severity of heat waves are a present threat to animal life, including humans, especially considering that urbanization increases the intensity of heat extremes (32), and most humans live in urbanized areas.

Central predictions of climate change are that, in addition to increases in mean temperatures, there will be increases in temperature variation, resulting in the increased probability of extreme warm temperatures (5, 52, 65). This is true for terrestrial habitats across continents (2, 4, 18, 22–24, 33, 38, 39, 51, 67, 72, 77, 135, 140), and oceanic and coastal marine habitats (30, 41, 47, 88, 93). The increased probability of extreme warm temperatures will lead to future heat waves that are longer in duration, have warmer maximal and minimal temperatures, and occur during a wider range of dates spanning from late spring through early fall (5, 65). For example, heat waves during the latter three decades of the 21st century are certain to be at least as long and as warm as the devastating 2003 heat wave of central Europe and may be up to four times longer and much warmer, depending on future carbon emissions (FIGURE 2). In other words, the unusually extreme heat waves of the early 21st century will be the norm during summer thermal maxima of the late 21st century (5, 65). Thus, in the near future, animal life will be coping with heat waves that have increased intensity and last for longer than the most devastating heat waves experienced to date.

Although heat waves may occur for only a short duration relative to an animal's entire life, heat waves need only occur once during the pre-reproductive developmental period to strongly reduce

reproductive success (14, 127). Since reproductive success is a complex interaction of organismal traits and ecological interactions, ecosystems will change as the environment changes, since each member of an ecosystem has its own response to environmental change. To understand the impacts of environmental change on physiological adaptation, we must consider selection for organismal traits in the context of the changes in an organism's habitat (59) as well as changes in the ecosystem they are a part of, especially species interactions such as mutualisms (123), competition (49), predator-prey (111), and host-parasite (85), and the prevalence and penetration of infectious diseases, such as the temperature-sensitive response to the densovirus causing sea star wasting disease outbreaks during marine heatwaves (8, 68, 82).

Studies of animal performance indicate that increased frequency and severity of heat waves will not be beneficial for animals that have adapted their heat tolerance in response to selection to warmer thermal habitats (117, 136), and hence global warming will reduce fitness (62, 63). Populations living at the warm edge or in "hot spots" of the species distribution, can respond in several ways when faced with environmental change that reduces fitness: they can move, adjust, or die (FIGURE 3). Those responses are not mutually exclusive, and species may simultaneously respond to inhospitable climate change in all three ways in a context-dependent fashion (e.g., where in the species' range a population is). Here, I consider aspects of movement, adjustment, and death (or selection) that we are likely to observe in animal

populations in a future characterized by increased frequency and severity of heat waves.

Movement (Migration)

Movement can happen at the level of the individual (i.e., migratory species) or at the level of a population (i.e., shift in a species' distribution). For individuals, migration is the process of moving across a landscape on daily, seasonal, or multi-year timescales to environments that support different aspects of their lives. For example, salmon (20) make multi-year movements between breeding sites and foraging refugia, whereas birds (71) migrate annually between breeding sites and overwintering refugia. Salmon undertake a strenuous journey between foraging sites in the ocean and spawning sites in streams (55), and populations from spawning sites close to and far from the oceans have swimming performance and temperature sensitivity that are physiologically adapted to the migrations they undertake (35). Shifts in river hydrology coupled with heat waves can make the river temperatures high enough so that spawning migrations are negatively impacted due to loss of aerobic scope of fish (36). Migratory species may be required to shift their seasonal and annual migration routes to avoid locations where thermal conditions have become too hot, and may also take advantage of new habitat in locations where thermal conditions were formerly too cool, and, as a result, the species' distributions will shift (71). Migration may also shift population demographics when thermal thresholds for migration vary in sex or age subsets of the population. For example,

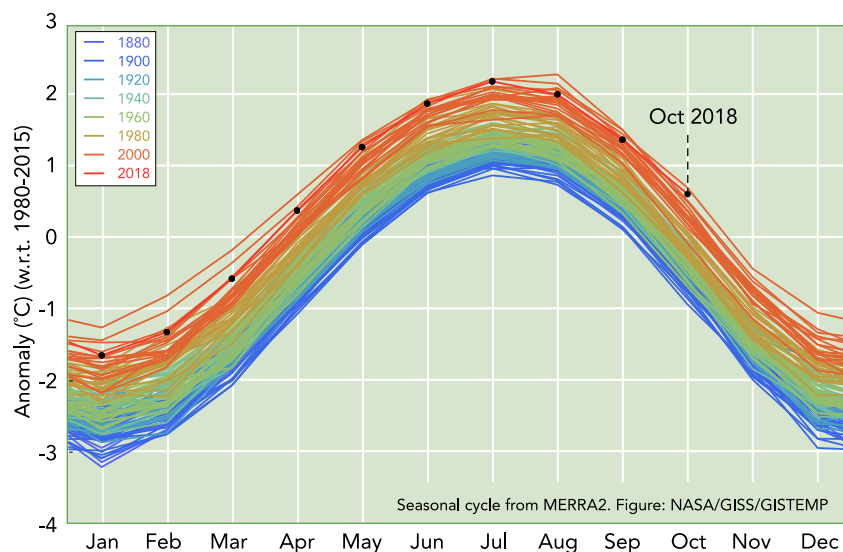


FIGURE 1. Global average surface temperatures are higher in the early 21st century than the prior 120 years

Surface temperature anomalies (with respect to the mean values of 1980–2015) are plotted by month. Colors indicate time period from late 19th century (blue) to mid-20th century (green) and early 21st century (red). Black dots show 2018 data. Figure are from GISTEMP (53, 125) (<https://data.giss.nasa.gov/gistemp/graphs/>) and reproduced with permission from *Reviews of Geophysics* and NASA.

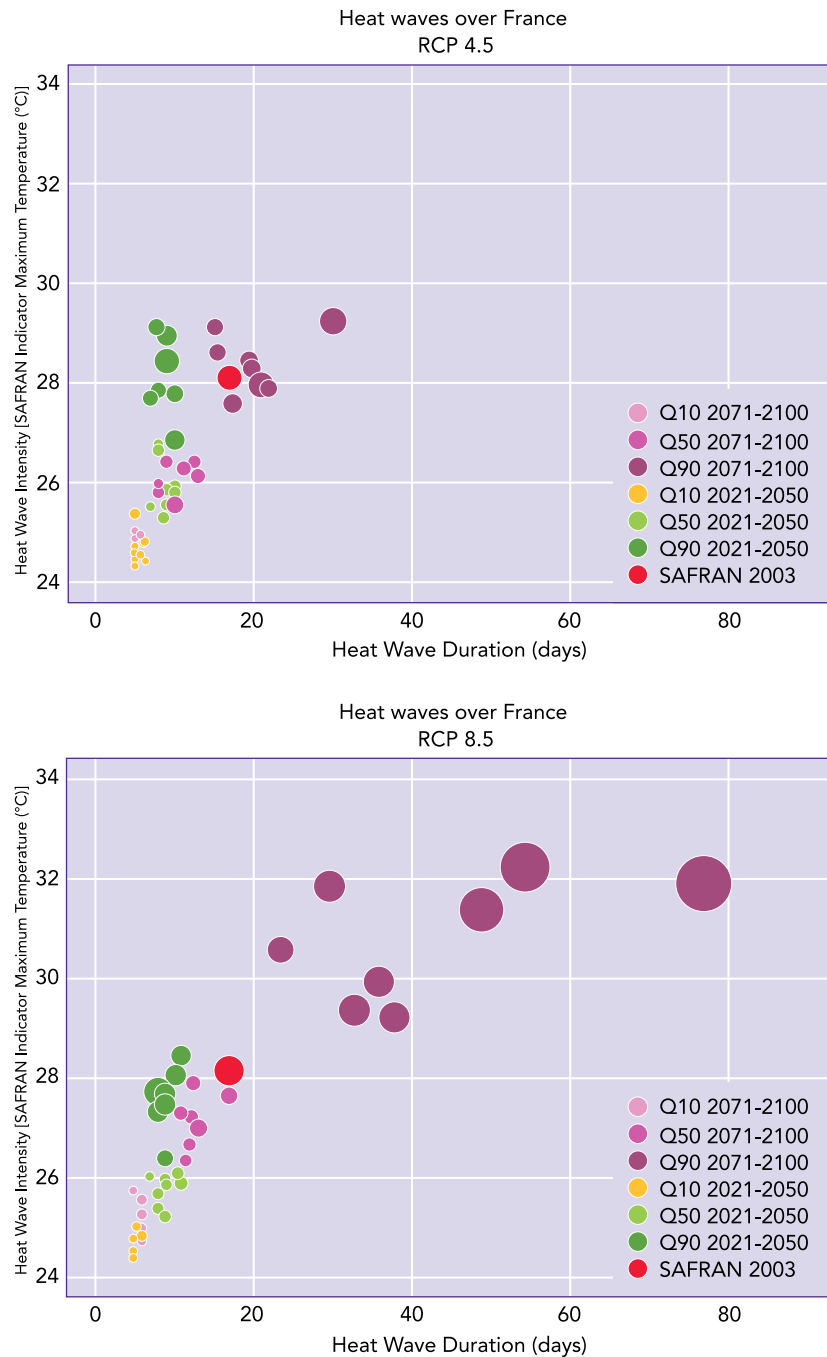


FIGURE 2. Climate models developed to assess the duration and intensity of heat waves during the 21st century

Climate models developed to assess the duration and intensity of heat waves during the 21st century indicate that we are likely to see an increase in heat wave duration and intensity in the future under two carbon emission scenarios from the IPCC AR5 report. *Top: RCP4.5* (peak carbon emissions occur in year 2040 followed by emission reduction). *Bottom: RCP8.5* (continuous increase in carbon emissions through the 21st century, or “business as usual”). This plot (from Fig. 9 in Ref. 90 and reproduced with permission of Creative Commons Attribution 4.0 International) presents the results of model simulations of heat waves in France using EURO-CORDEX simulations. The red dot (SAFRAN 2003) represents the atmospheric conditions during the summer 2003 heat wave over France, the most intense heat wave that had occurred across central Europe for hundreds of years and that killed tens of thousands of people in western Europe. The other dots represent 10th, 50th, and 90th percentiles of modeled heat waves during the near future (years 2021–2050) and far future (years 2071–2100) 21st century. The size of the dots represents the area over which the heat wave impact would be felt (larger = bigger area). Regardless of the carbon-emission scenarios, there is a high probability that several heat waves will occur during the 21st century that are more intense than the 2003 event.

migration behavior of male, but not female, great bustards has been shown to be directly correlated with thermal extremes during the summer reproductive season (3). Increased future heat waves are thus likely to shift the timing and reproductive success of those birds as males spend increasingly less time with females.

Migration of species distribution ranges, in other words, a shift of the species range away from the edge of the range where habitat change negatively impacts fitness, has also been observed as a response to increases in thermal extremes (13, 94, 95). Often this is a poleward migration, which has been observed in many cases associated with warming but also is dependent on habitat type (71, 128). In this case, organisms move to maintain the habitat properties they have physiologically adapted to (e.g., similar thermal conditions). However, the movement may have associated fitness consequences because of shifts in biotic interactions (e.g., species assemblage combinations that reduce reproductive success) because populations and ecosystems may shift with the environmental properties of habitats and ecosystem community composition at different rates and scales (71, 84). Due to natural landscape variation and especially due to human changes to terrestrial landscapes (e.g., deforestation, barriers), many animal populations no longer have appropriate migration corridors in which the population could make a shift to maintain thermal habitat characteristics. In

these cases, human intervention may be required to help animal populations bypass the migration barriers.

Migration can be limited if an organism's physiology requires a specific set of environmental parameters that are not likely to change as warming continues. For example, reef-building corals require the consistent year-round tropical photoperiod supporting their photosymbiosis (92, 130, 137). Those same corals are presently often occurring in locations where extreme habitat temperatures during heat waves are at or exceed coral thermal tolerance, causing massive amounts of coral bleaching (64, 137). This is especially true at the low latitudes of a coral's distribution range (121). Although some poleward movement of corals is possible, poleward migration of corals reefs beyond current high-latitude range edges is unlikely to occur because corals require photoperiod and light-intensity characteristics of the equatorial tropics. Since photoperiod does not change in conjunction with warming, corals will be limited in the extent of their poleward movement. Similarly, marine species require a specific temperature as well as level of dissolved oxygen (30). Although hypoxia and high temperatures often co-occur in aquatic ecosystems, shifts in temperature and dissolved oxygen are not necessarily coupled in all ecosystems. For example, warming and oxygenation of coastal marine habitats are unlikely to shift concomitantly since geographic controls of ocean oxygenation control processes decoupled from

Migratory Species change migration patterns

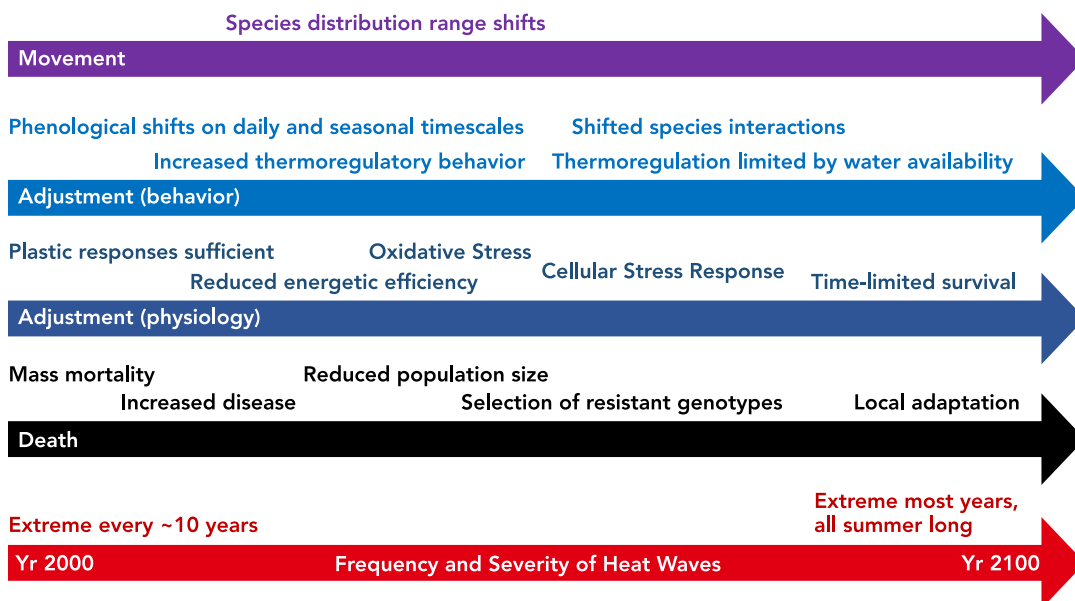


FIGURE 3. Animal populations are likely to respond to increased frequency and severity of heat waves by several different modes

Animal populations are likely to respond to increased frequency and severity of heat waves by several different modes: movement, adjustment, and death (or selection). In this graphic, the types of responses for each of those modes are organized from *left* (low frequency and severity of heat waves characteristic of early 21st century) to *right* of the arrow (high frequency and severity of heat waves expected in the late 21st century per the RCP8.5 carbon scenario).

warming (e.g., upwelling, water circulation in bays). In another example, high-altitude organisms may move higher up the slopes of mountains as the climate warms to seek cooler habitat at higher altitude to maintain the thermocline they prefer (46, 122). However, other environmental factors are unlikely to shift up the mountain with temperature (e.g., soil moisture, plant forage, oxygen), and so those alpine taxa may not find suitable habitat in their preferred temperature range at higher elevation (133). Thus, in a similar fashion as for tropical corals, the species distribution may retract from hotter part of their habitat, but not expand into the cooler part of their habitat, effectively reducing the range size and likely causing population declines.

As global change continues, it is likely that shifts in the environment related to extreme temperature as well as myriad other environmental factors (e.g., drought, flooding, disease, food, and freshwater shortage, as well as political instability) will change the ability of human populations to persist in some locations that historically and currently support large populations (11, 44, 65, 112). Increased global movement of human populations (i.e., refugees) poses infrastructure (e.g., food, shelter, population density) and public health (e.g., global redistri-

bution of infectious diseases) concerns that will be a growing problem for the world to solve, and will require innovative approaches to medicine and health care across the globe (11, 44, 112).

Adjustment (Behavior)

In the most integrated sense, an organism's physiology is evidenced at the behavioral level. Behavioral shifts of organisms are expected if they are energetically challenged in a changed environment, including one characterized by greater occurrence of heat waves (83) (FIGURES 3 AND 4). Thermoregulatory maintenance of physiological homeostasis will require a greater percentage of basal metabolism, and organisms will need to shift behavior one way or another in response to increased intensity of heat waves (83, 89, 122). The behavioral shifts of ectothermic thermoregulating animals induced by increased thermal extremes could include time spent in warm and cool microhabitats within the local range, shifts in daily phenology for foraging or mating, time spent resting, and overall caloric intake per unit of time (16, 42). Behavioral shifts in response to extreme heat in endothermic homeotherms (i.e., birds, mammals) are most likely to increase the time spent evaporatively cooling (e.g., sweating, panting, gular flutter-

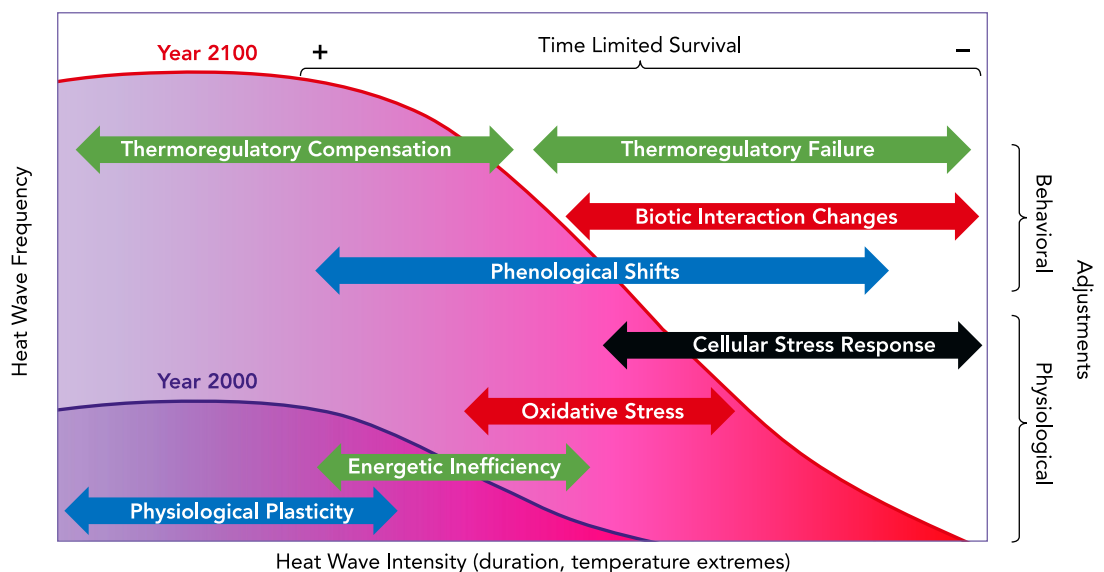


FIGURE 4. Schematic of behavioral and physiological adjustments that animals make to heat waves

In year 2100 (assuming RCP8.5 carbon scenario, see FIGURE 2), heat waves are expected to be more frequent and of greater intensity than in year 2000. Animals will be experiencing temperatures more frequently that will necessitate behavioral and physiological changes. Where behavioral shifts in thermoregulation and physiological plasticity allow organisms to maintain physiological homeostasis, survival will not be impacted even as heat waves become more frequent. However, survival will become time limited during the highest-intensity heat waves, more so in year 2100 than year 2000. Physiological responses to increasingly intense heat waves will cause reduction in energetic efficiency, oxidative stress, and induction of the cellular stress response as a survival mechanism. Behavioral responses to increased heat waves will include shifts in daily and seasonal phenology, which combined with differences in migratory patterns and shifts in species distributions are likely to result in changed biotic interactions. As heat intensity is at its highest, and especially in xeric habitats, thermoregulatory failure will occur, causing mortality, especially in small-bodied animals. Mass mortality can be expected during the most intense heat waves in years close to 2100.

ing, swimming), with a concomitant increase in water demands (41, 126). Thus drought associated with heat waves will be especially difficult for those taxa, since core body temperatures will increase with prolonged dehydration (41), both of which are physiologically stressful and can lead to morbidity and mortality. For example, Arabian ungulates shift their daily activity from diurnal to nocturnal during dry and hot weather, but by doing so increase their interactions with nocturnally active predators (41). Some animals may adopt a more quiescent behavior during the hottest part of the day to reduce thermoregulatory costs and water loss, shifting daily phenology (41). Other animals may adopt a more aggressive foraging or predation behavior to augment energy intake necessary to support the increased basal metabolic demands for physiological homeostasis (16, 34, 50, 81, 126). For animals that spend little of their time foraging and inhabit food-rich areas, increased feeding could be expected to meet increased energetic and water balance demands associated with increased heat waves (70). In contrast, animals that already maximize foraging times in environments where food is scarce cannot further increase energy intake and are more likely to adopt a quiescence strategy. If those animals increase foraging efforts, their greater energy expenditure during foraging may exceed the caloric payoff, resulting in decreased body condition and reproductive output, as has been observed in southern pied babbler birds from hot, arid regions of southern Africa (34). Behavioral thermoregulation will likely vary across similar types of animals, along with species-specific variation in other traits, as has been demonstrated in birds (126).

Quantifying behavioral shifts of animals as a result of increasingly severe heat waves is possible when field-based ethogram surveys have quantified behavior during the time period before the 1980s (i.e., before the period of time when temperature anomalies became as distinct from baseline as they are today) (41). Resurveying behavior in nature using the same ethogram would be a worthwhile endeavor to determine whether warming has induced behavioral changes. Of course, to infer any observed behavioral shifts, data on other aspects of habitat would be required at past and present survey times, including thermal profiles and the presence of forage. Behavioral shifts may also be indicative of changes in distribution of the focal species or other taxa that interact competitively in a non-consumptive fashion. Such shifts could decrease foraging efficiency and increase energetic cost of foraging.

Shifts in the behavior of human societies will also be required in response to increased severity of heat waves, especially in populations that have

not historically experienced daily activity routines during dangerous levels of extreme heat. Just as urban areas in some parts of the U.S. monitor air quality for conditions where levels of pollution are likely to accumulate to dangerous levels and encourage the population to prevent further accumulation of pollutants (e.g., “Spare the Air” days in the San Francisco Bay Area), so too should cities and employers adopt intervention and adaptation measures to prevent excessive exposure to heat during extremely hot days (78). This is especially true for humans living in cities, not only because heat waves are more intense in urban areas (32, 124) but also because work and commute schedules in urban areas are likely to decrease the potential for people to thermoregulate (e.g., lower access to bodies of water). Urbanized areas will likely need to increase large-scale cooling devices (e.g., misters), access to fresh water to prevent dehydration, and curtail activities that would result in heat exposure that could cause morbidity or mortality (78, 124), especially in athletes or other adults engaging in metabolically demanding tasks and in the thermally susceptible young and elderly; all of which will require concerted governmental action to adopt and funding to enact. The extent to which human society will need to adjust is strongly dependent on the amount of warming. At the time of writing, the IPCC has suggested that limiting warming to 1.5°C, compared with 2.0°C of warming, will have large implications in the degree to which human societies will need to shift how, when, and where they invest their energy (<http://www.ipcc.ch/report/sr15/>).

Adjustment (Physiology)

Adjustment of organisms to environmental change can occur by two means: within-generation or among-generations. Within-generation means that animals may adjust to changed environments (most often where the environment changes predictably during development or across seasons) through phenotypic plasticity to shift their environmental sensitivity and maintain homeostasis despite an increase in the intensity of heat waves (FIGURES 4 AND 5). Prior thermal adaptation likely plays a role in the capacity for plastic responses, as has been observed in comparative studies of temperate and tropical ectotherms (31, 117, 132) (FIGURE 5). The cellular and biochemical basis of within-generation plasticity has been eloquently reviewed and summarized in the series of *Biochemical Adaptation* books (58, 113). The most commonly observed cellular mechanisms by which organisms adjust their sensitivity to thermal extremes include shifts in the levels and types of proteins present,

shifts in membrane properties, and shifts in the small molecules that comprise the cytoplasm (58, 113). Increased expression of heat shock proteins (HSPs)—the molecular chaperones that prevent protein misfolding during extreme temperatures—are frequently observed in organisms that have enhanced heat tolerance (or “heat hardening”) (25, 58, 113). Levels of HSPs shift across seasonal shifts in extreme heat in diverse animals, from coastal molluscs (102) to bull testicles (115). Furthermore, HSP upregulation in response to thermal stress can be dependent on developmental stage (54), highlighting the importance of early life-stage studies of responses to thermal extremes (14, 76, 127).

Shifts in proteins that regulate cellular energy balance and temperature-sensitive signal-transduction cascades, such as AMP-activated protein kinases (66) and temperature-sensitive ion channels [i.e., thermo transient receptor potential (thermoTRP) channels], provide another means for shifts in physiological responses in thermal extremes. Across animals with different thermal optima, orthologs of temperature-sensitive thermoTRP channels are thermally “tuned” to a particular range of temperatures (106). Thus variation in the specific TRP proteins expressed can shift the temperature thresholds for gene expression responses (45, 60,

106). Shifts in gene expression may regulate levels of proteins that confer thermoprotection, such as HSPs, or shift the thermal properties of proteins through expression of different protein isoforms. In species with multiple copies of a gene, the loci may evolve differences in primary structure that lead to different thermal properties (i.e., thermally adapted paralogous homologs), and differential expression of those genes can be involved with thermal acclimation, as in the above-mentioned thermoTRPs, and has also been demonstrated in myofibrillar proteins (113). Where multiple loci for a gene are not available, there is potential for allelic variants to be differentially expressed—a phenomenon that has often been characterized as important for thermal adaptation of populations (25, 100) but is not well supported by evidence for plasticity within individuals (113). Some organisms possess enhanced capacity to produce proteins with diverse thermal properties from a single gene by editing the mRNA transcripts from that gene before translation. RNA editing by ADAR proteins, which functionally shift A nucleotides to G in codons, can result in differences in primary structure (depending on the codon) and has been shown to be an important mechanism in producing thermally adapted ion channels of cephalopod mollusks where there was no physiological diversity encoded in the

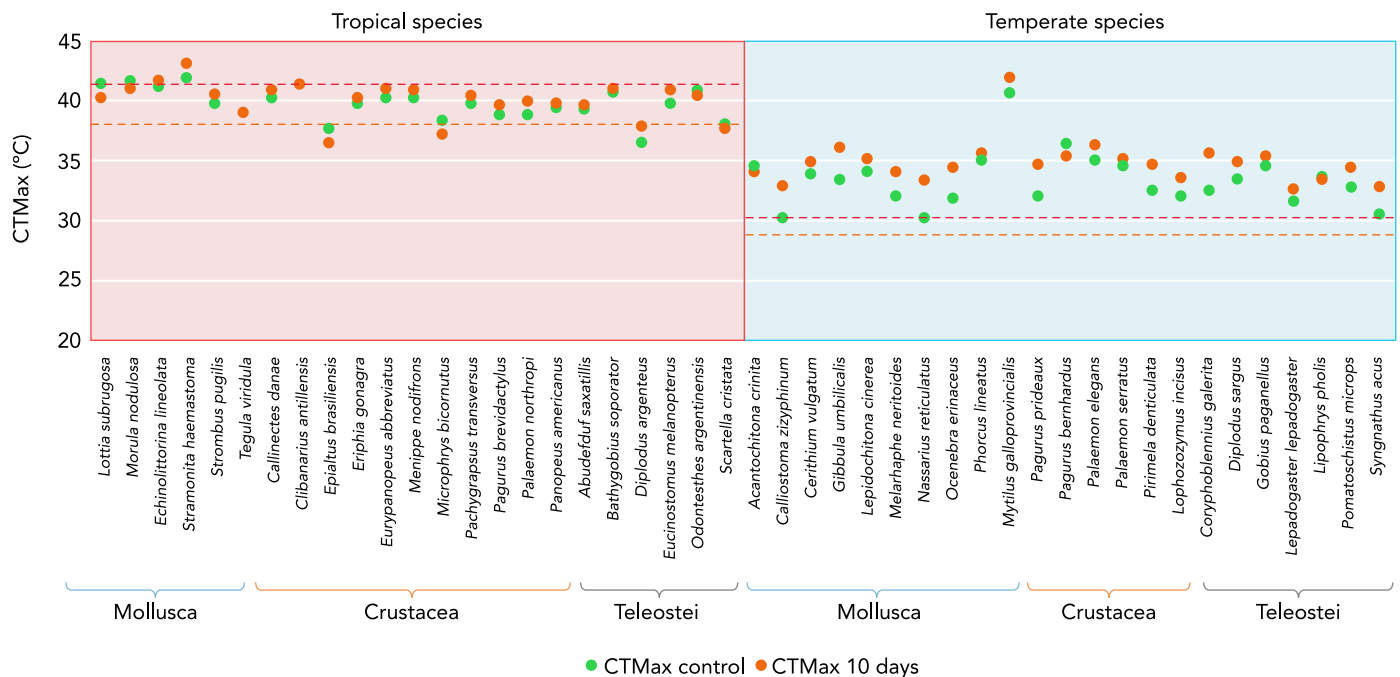


FIGURE 5. Thermal tolerance limits of tropical and temperate tidepool animals in the context of heat wave thermal extremes (Fig. 2 from Ref. 132, reproduced with permission of Creative Commons Attribution 4.0 International; <https://journals.plos.org/plosone/s/licenses-and-copyright>). Critical thermal maximum (CTMax) of the control (CTMax_{control}) is in green dots, and after 10 days at a +3°C temperature (CTMax_{10 days}) is in orange dots for tropical species (red background area) and temperate species (blue background area). The red broken line indicates the highest recorded water temperature in tropical (41.5°C) and temperate (30.6°C) tide pools. The orange broken line indicates the 99.5 percentile of water temperature in tropical (37.9°C) and temperate (29.0°C) tide pools. The data indicate that tropical tidepool organisms are likely to be the most sensitive to increased frequency and severity of heat waves because they have heat tolerances that match current thermal extremes and have negative acclimation response ratios (i.e., *Epiplatys brasiliensis* and *Microphrys bicornutus*). In general, even with plasticity, tropical species are unlikely to tolerate increased intensity of heat waves with climate change. In contrast, temperate species have larger safety margins (heat tolerances above historical maxima) and plasticity, meaning that populations of some species will physiologically tolerate increased intensity of heat waves.

genome (43, 74, 105). RNA editing by ADAR proteins has also been demonstrated as important in stress resistance of arthropods (26, 119). The extent to which plastic responses to thermal extremes could be modified by RNA editing is a topic that largely remains to be examined in most animals (105).

Organisms may also exhibit plasticity in adjusting heat tolerance by repressing genes, either through reduction of synthesis and degradation or through regulatory posttranslational modification. For example, fatty acid desaturase proteins act to increase the number of double bonds in acyl chains of phospholipids and increase fluidity of membranes. When temperatures increase, with concomitant increase in membrane fluidity (113), the repression of desaturases can act to limit further increases in fluidity and membrane disorder (57). Although silencing of fatty acid desaturases as a mechanism for enhancing heat tolerance has primarily been demonstrated in plants (141), this exists as a potential mechanism for plasticity of heat tolerance in animals. Posttranslational modification (e.g., protein phosphorylation of rate-limiting glycolytic and aerobic respiration enzymes) has been demonstrated as an important mechanism to downregulate the activities of enzymes and slow down metabolism as animals enter dormancy (120). Dormancy is an important mechanism for animals to survive when environmental conditions are too extreme to maintain homeostasis while fully active (97).

When the environment changes beyond the level that can be accommodated by plasticity, adjustments to maintain a physiological state that support maximal fitness are no longer possible within a lifetime. In these cases, organisms may be compromised when temperature increases cause malfunction of critical intracellular biochemical systems and will have time-limited survival depending on the degree of compromise (FIGURE 4). Membranes are extremely temperature sensitive, and increased temperature beyond the limits of plasticity can decrease mitochondrial membrane function, increasing proton leak and decreasing the efficiency by which organisms convert the energy stored in reduced electron carriers (e.g., NADH) into energy stored in ATP (73). For organisms in an energy-rich environment where food and foraging behavior are not limited, the reduction in efficiency, essentially the number of ATP generated per food molecule input, may not have severe consequences. For most organisms, the reduction in mitochondrial efficiency will have serious consequences since less ATP per unit time will be available, and, as a result, motor output (i.e., potential for behavior) will be diminished.

In addition to mitochondrial efficiency due to proton leak, increased thermal stress is likely to increase oxidative stress as a result of greater mitochondrial activity (21, 113). Increased reactive oxygen species will cause increased levels of oxidative damage to proteins, lipids, and nucleic acids (113). Those damaged molecules cause additional deleterious effects in organisms (e.g., gene expression shifts, membrane malfunction). In response to increased oxidative stress, organisms induce the expression of anti-oxidants (e.g., catalase, superoxide dismutase, glutathione peroxidases) to scavenge the reactive oxygen species (21, 28, 75, 134). An increased anti-oxidant defense response comes at an energetic cost for organisms, further reducing available ATP beyond the reduction in mitochondrial efficiency from proton leak (28, 87).

Under conditions of thermal stress when mitochondrial function is impaired, or when oxygen delivery is inadequate to fully support ATP demand through mitochondrial respiration, organisms may shift to fermentative, anaerobic metabolism (98). Fermentative metabolism (i.e., substrate-level phosphorylation of ADP to produce ATP) is able to produce ATP rapidly, but at a cost of efficiency, as the number of ATP per energy molecule (i.e., glucose) is ~1/18th of oxidative phosphorylation. Evidence for increased expression of genes supporting fermentative metabolism in response to thermal stress has been observed in fish and aquatic invertebrates at elevated temperatures (6, 27, 109). Similar responses were observed during heat stress in Antarctic fishes, although the threshold temperature for heat stress in these fish is 8°C (28), near their instantaneous lethal limit.

When high temperatures become extreme enough to cause direct damage to proteins by breaking the weak bonds that maintain protein tertiary and quaternary structure, the cellular stress response is induced (69). In this response, additional ATP is diverted to the expression and function of molecular chaperones (e.g., HSPs) that attempt to repair the damage to unfolded or misfolded proteins (19). This additional expenditure of ATP further reduces the stored energy available for behavior and further reduces fitness. Although the temperature extremes associated with induction of the cellular stress response are likely to be transient, they will be induced with greater frequency since future summers will be characterized by increasingly frequent heat waves, with respect to the environmental temperatures in which physiological systems evolved (FIGURES 2 AND 4). Thus cellular stress and heat shock responses may be more frequent in the future, causing an energetic shift away from use of ATP for behavior and reproduction that is likely to result in reduced overall fitness.

The ability to determine whether organisms are increasingly experiencing temperatures high enough to compromise mitochondrial function, leading to increases in oxidative damage, levels of antioxidants, and induction of the cellular stress response, requires a substantial amount of baseline data under non-stressful conditions. Ample research has pointed to molecular markers (e.g., transcripts, proteins) associated with shifts in antioxidant response and cellular stress response induced by increases in habitat temperatures. Although most of those studies have been conducted under laboratory conditions, some have sampled animals in nature (118). Although it is unlikely that a large volume of high-resolution biochemical data from before 1980 exists for most taxa, there are likely to be some data that would be adequate to set a baseline for the relative energy an organism spends on restoring cellular homeostasis under conditions that induce oxidative or other cellular stress. Temporally—and spatially—explicit studies of cell physiology of populations in nature are not easy to perform, but they have the ability to assess just how much organisms in nature are “feeling the heat,” so to speak. Laboratory studies have produced a wealth of information about cellular responses to environmental change, but just as the “forced dive response” of seals does not reflect their diving physiology for the vast majority of the time in nature, cellular stress responses characterized under laboratory conditions may not occur the same way in nature. So, just as in diving mammals, we must study organisms experiencing warming in the natural habitat to infer how they respond to warming. Unfortunately, it is not easy to conduct such studies. They require time, frequent sampling, and processing of many samples to demonstrate that the physiological state of free-living animals is characterized by a greater level of physiological stress due to climate change. In some cases, historical records of the environment as well as “time capsules” of earlier life do exist. In one such example, “resurrected” resting eggs of ancient *Daphnia pulex* populations collected from sediments when ponds were cooler were used to compare to modern populations when the ponds were warmer (139). Modern *D. pulex* were more heat tolerant and expressed more hsp70 than the ancient population (139). Commonly, a “time for space” convention is used, by which populations that occur in regions that locally differ in climate (e.g., at edge and center of species distributions) are used as a proxy for how one population would respond plastically to change over time. This has been demonstrated in coastal invertebrates whose distributions overlap

considerable spatial variation in ocean pH conditions (37, 96). This convention is especially useful when population genetic analyses are also performed so that researchers are able to correctly characterize population differences that are plastic (no genetic differentiation) or potentially adaptive (if populations are genetically distinct). For example, in natural populations of *Drosophila* collected from temperate and tropical regions, the key population differences for success in future expected temperature conditions was adult thermal tolerance (91).

Among-generation plasticity is likely to be extremely important in population responses to increased thermal extremes, although the specific mechanisms driving this type of plasticity is less well understood than within-generation (14). Here, maternal effects (e.g., the provisioning of eggs with specific proteins and RNAs, or with energy resources) or epigenetic effects (e.g., genome methylation or histone modification) can transduce a physiological response to experienced (or expected) increased temperature to the offspring, changing the physiological performance of the offspring from that of the parents (6, 114). For example, in insects (107) and fish (104), the thermal environment during oogenesis influences maternal provisioning of TRP proteins and regulatory RNAs that direct the developing embryo to either enter or bypass an embryonic diapause. Such plasticity, which potentially can persist for multiple generations, is difficult to predict, especially since specific epigenetic effects are not well understood outside of a few model organisms and since the roles of regulatory RNAs (e.g., micro-RNAs) are not yet well characterized in most taxa. Although it is relatively straightforward to identify non-coding RNAs, their functions in non-model organisms largely remain to be determined (101). Interestingly, expression of RNA-editing ADAR proteins have been observed in stress-resistant post-diapause embryos of *Artemia* (26), suggesting that embryonic physiological diversity may be greater than would be predicted based on the genomic complement of potential RNA molecules, further highlighting the need to study plasticity across development to develop a holistic understanding of responses to climate change (14).

Importantly, animals that have adapted to the warmest environments typically have the least plasticity in their heat tolerance (61, 117) (FIGURE 5), a phenomenon that may be strongly dependent on the manner in which organisms maintain aerobic metabolic scope under temperature extremes (20, 86, 98, 99, 131). Across taxa, animals are generally limited in the degree to which plasticity in thermal tolerance can keep pace with increases in the intensity of heat waves, suggesting that plasticity will largely be inadequate for

long-term persistence of populations in future increases of extreme heat (48, 50). That inadequate plasticity means that it is unlikely that most animals will remain in their present habitat without shifting their physiological energetics and ecological interactions. That is to say, acclimatization is not likely to be adequate to allow organisms to maintain homeostasis under future projected increases in extreme heat events. Either animals will have to move or populations will experience significant mortality as the intensity and duration of heat waves continues to increase.

Death (and Selection)

Mortality has been observed in populations of organisms who are unable to escape or adjust to heat

waves. For example, mass mortality of arid habitat birds has been observed during heat waves in which birds are unable to adequately cool evaporatively to maintain their core body temperature (1, 80). Dehydration during evaporative cooling is especially challenging for small birds and mammals since evaporative water loss rates exponentially increase as body size decreases and ambient temperature increases (80, 81). During heat waves, these birds may have survival times of just a few hours (1) (FIGURE 6), making escape impossible, and widespread mortality events have occurred in populations of small bodied birds and mammals living in desert environments. Climate change is predicted to increase exposure to temperatures that cause time-limited survival by increasing the number of days each summer that extreme tem-

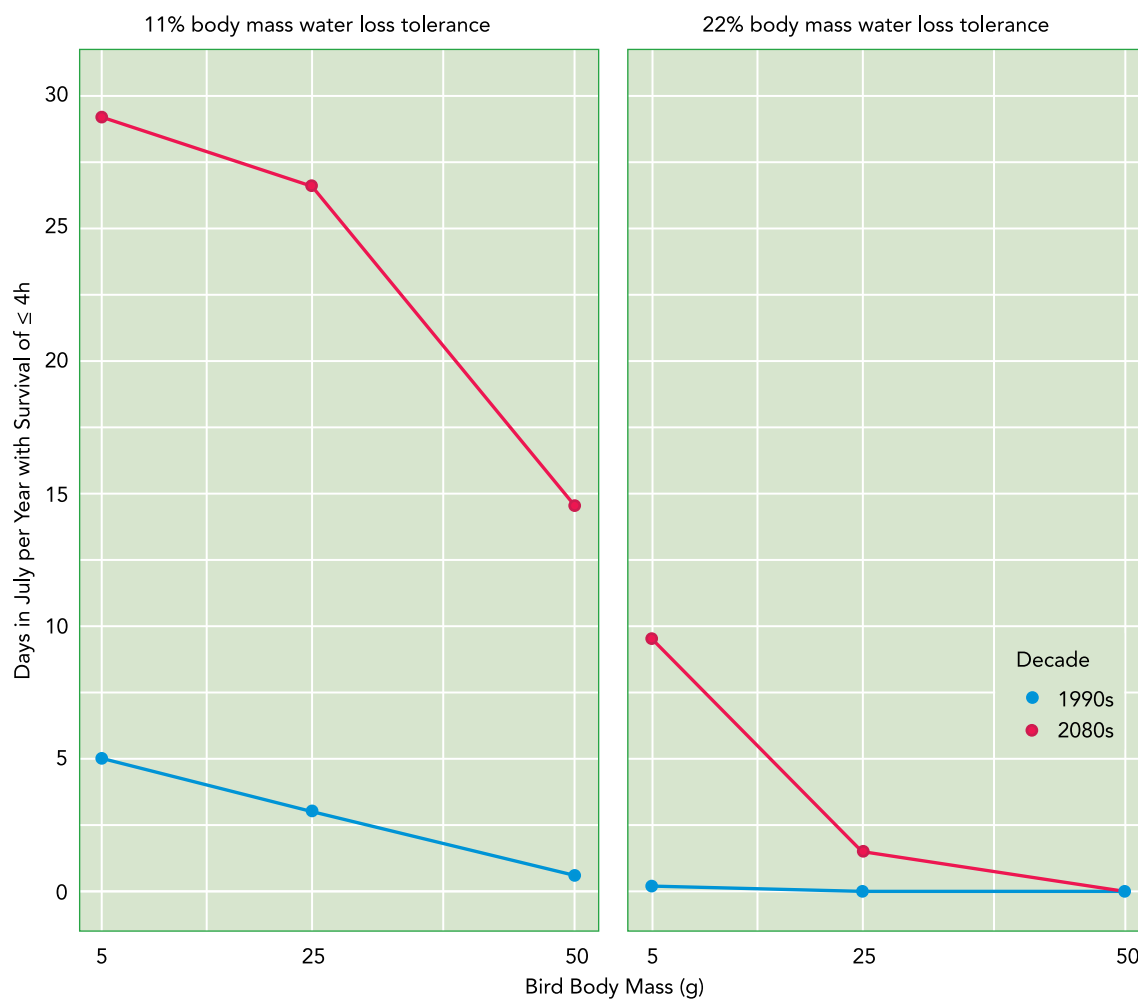


FIGURE 6. Survival times of desert birds during heat waves

Survival times of desert birds during heat waves will be shorter in the future, in a size- and desiccation-dependent fashion. Data extracted from Fig. 2 in Ref. 80 and replotted. Small birds (5- to 50-g body mass) at Yuma AZ, will be exposed to heat that results in survival times of 4 h or less much more frequently during mid-summer heat waves in the decade of the 2080s (red points and lines) compared with the decade of the 1990s (blue points and lines). The number of days with survival of ≤ 4 h is strongly dependent on dehydration tolerances (via evaporative cooling), with far fewer time-limited survival days at a water loss tolerance of 22% of body mass (*right*) relative to a tolerance of 11% of body mass (*left*). For the smallest birds with low dehydration tolerance, nearly every day during July at the end of the 21st century is likely to have high potential for lethal consequences. In contrast, birds of 50 g with high desiccation tolerance are unlikely to experience lethal thermal conditions as a consequence of climate change. For details, see Ref. 80.

peratures occur (FIGURE 6), as well as the extent across a species' range in which they occur (1). Certainly, not all birds have the same sensitivity to dehydration due to differences in body size and evaporative cooling capacity (126), but generally heat waves by the end of the 21st century are likely to cause increased mortality rates over a greater percentage of a species range than presently experienced.

Animals that have thermal limits adapted to extreme habitat temperatures such as the intertidal zone or exposed rock pools are likely to incur greater mortality as heat waves become more common in the future due to accumulated effects of heat exposure (110, 132). Additionally, pathogen load and severity of response are strong interactors with thermal stress responses. For example, mass mortality and extirpation of sea stars due to pathogenic viral infections has been associated with anomalously warm water temperatures (15, 108). Mass mortality events are increasing as global climate change increases the frequency and severity of heat waves, drought, and other extremes that challenge the physiological limits of organisms. A predictive understanding of mass mortality due to thermal stress requires detailed knowledge of individual-level organism-environment interactions (29).

One example of how mass mortality-driven genetic bottlenecks may be revealing physiological adaptation is in bleaching and mortality of corals across large areas of the Great Barrier Reef during the increase in water temperatures of the past few years (64). Most, but not all, of the corals within the more equatorial regions of the Great Barrier Reef were severely impacted (64). Although the loss of most of the corals on the reef is devastating for the coral reef ecosystem (121), the surviving corals, few and far between, may possess physiological adaptations that make them more tolerant to warmer oceans. The conservation of corals and the biodiverse ecosystems they build and support is of immediate importance because coral reefs are becoming increasingly degraded as water temperatures and other anthropogenic impacts increase (137). Those survivors offer hope for selection of genotypes able to help coral reefs persist in a warmer future. Scientists plan to protect, clonally propagate, and study the surviving corals to ascertain whether they are the "supercorals" of the future (130). Local adaptation of corals to high temperature has been characterized in several species, including reef-building corals distributed across consistent gradients in environmental temperature (7, 92). Whether corals adapted to high temperatures are differentially able to respond to increased thermal extremes associated with climate change may depend on the rate at which

climate change occurs (79), where adaptation is only possible with rates of warming lower than the present climate change predictions (9). Additionally, scientists are selecting coral individuals generated by sexual reproduction (i.e., novel genetic recombination) to identify genotypes that are more tolerant of future ocean conditions (130). Sadly, we tragically lost a most-beloved leading coral biologist actively engaged in these types of investigations, Dr. Ruth Gates, who passed away during the final revision of this manuscript. Ruth was a champion for coral reefs and an inspirational leader of students and colleagues who carry forward Ruth's positivity for the potential for science to discover ways to protect and save the coral reefs of the world (138).

How Physiology Informs Climate Change Research

An increasingly important role for environmental physiologists is to connect the dots between global climate change and shifts in species distribution and abundance. Although many factors can contribute to the connection between these two large-scale phenomena, the performance of individuals and the nature of individuals within populations are at the center of the connections. Climate change shifts the habitat in which organisms live, which in turn affects how particular organisms live, as well as the lives of the other organisms with which they interact (i.e., the ecosystem). Although oversimplified, it follows that the transduction of climate change to ecosystem change requires an understanding of the physiological state of animals that experience the climatic stressor. Physiologists can provide the mechanistic details that describe how an organism's physiological state changes as the environment warms, make predictive statements about how those mechanisms will shift the performance of organisms in nature, and demonstrate the shifts in performance as the environment continues to warm and become more extreme with climate change. Although physiologists know a great deal about how diverse arrays of animals perform as environments change, most of the studies are conducted in controlled laboratory or semi-controlled field conditions, and often the most mechanistic studies are performed on a small subset of animals that serve as model organisms. What we need, increasingly, is for physiologists to focus on characterizing shifts in performance in animals from uncontrolled wild populations. With experimental designs that emphasize field physiology and include laboratory experiments as appropriate, researchers can generate the data that demonstrate whether and how animal life has been altered due to climate change. Those data are

of great importance for policymakers who use evidence-based approaches in their decision-making. Essentially, physiologists generate the “smoking gun” needed to make the case that there are direct impacts of climate change on organisms whose physiology and behavior ultimately influence the health and welfare of entire ecosystems, including human constituents.

Is More Evidence Necessary to Combat Climate Change and Sustain Ecosystems?

This article makes the case for the contribution of physiologists to the deliberations of decision and policy makers, providing the “smoking gun” that links climate change to ecosystem shifts. A remaining question is whether a higher-resolution or more powerful “smoking gun” is even needed to establish that climate change is, today, affecting animal populations across most of the biosphere, with concomitant effects on ecosystem function and human well-being. The world’s climate is undeniably changing. Weather patterns are bringing more intense storms, heat waves, floods, fires, and other such natural disasters than ever before. Species are disappearing off the face of the earth at an accelerating pace from over-exploitation, disease, habitat loss, and other factors. People understand inherently that natural resources are finite and that species struggle to survive when their habitat is damaged (e.g., by pollution) or lost (e.g., to urbanization), because we experience those challenges in our own lives. This was spelled out clearly in Rachel Carson’s groundbreaking book *Silent Spring* (17) that spawned the 1960s environmentalist movement and resulted in the creation of the U.S. Environmental Protection Agency, whose mission is to protect nature so that nature could support ecosystems, including those that humanity depends on. Yet, recent dismantling of components of the EPA is compromising the structure of ecosystems within which animals and humans live. Humanity has a poor track record of employing evidence-based decision-making when it comes to environmental issues that occur over the long term, especially when balanced with economic issues that run counter to environmental issues in the short term. Climate change is one such issue. If physiologists continue to generate increasingly detailed data sets to demonstrate how climate change influences animals and ecosystems, will decision and policy makers ever use that information? The argument can be made that, when it comes to developing evidence-based policies related to climate change, we (environmental physiologists) may already have the sufficient smoking gun to guide decisions regarding local and global man-

agement of natural resources in the face of an every-growing human population, producing increasing levels of carbon emissions, and living in a rapidly changing climate (12). Today’s cohort of ecological, evolutionary, and environmental physiologists, along with the next generation of scientists being mentored by them, have crucial roles to play in producing, communicating, and translating the science-based evidence that responsible policy makers require to address the effects of short- and long-term consequence of climate change on animals, including humans. ■

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