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A series of unfortunate events: characterizing the contingent nature of physiological extremes using long-term environmental records

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Accelerating shifts in global climate have focused the attention of ecologists and physiologists on extreme environmental events. However, the dynamic process of physiological acclimatization complicates study of these events' consequences. Depending on the range of plasticity and the amplitude and speed of environmental variation, physiology can be either in tune with the surroundings or dangerously out of synch. We implement a modified quantitative approach to identifying extreme events in environmental records, proposing that organisms are stressed by deviations of the environment from the current level of acclimatization, rather than by the environment's absolute state. This approach facilitates an unambiguous null model for the consequences of environmental variation, identifying a unique subset of events as 'extremes'. Specifically, it allows one to examine how both the temporal extent (the acclimatization window) and type of an environmental signal affect the magnitude and timing of extreme environmental events. For example, if physiology responds to the moving average of past conditions, a longer acclimatization window generally results in greater imposed stress. If instead physiology responds to historical maxima, longer acclimatization windows reduce imposed stress, albeit perhaps at greater constitutive cost. This approach should be further informed and tested with empirical experiments addressing the history-dependent nature of acclimatization.

1. Introduction

In the light of ongoing dramatic shifts in global climate, extreme environmental events have become a focus for ecologists and environmental physiologists [1–9]. However, the study of the biological consequences of these events is hampered by complexities inherent in the dynamic interaction between organism and environment. These complexities include physiological acclimatization, the process by which organisms adjust their physiology to maintain function under prevailing environmental conditions. This acclimatization takes time (e.g. [10])—in a temporally variable world, physiology is often chasing the environment. Depending on the range of an organism's physiological plasticity (which can be small or large), the environmental signal(s) to which an organism responds (which could incorporate many aspects of temporal variation), and the amplitude and speed of environmental fluctuations (which vary drastically among habitats), an organism's physiology can be well adjusted to potential stressors or dangerously out of synch. Thus, our ability to predict extreme events and their consequences hinges not only on our ability to predict changes in the physical environment but also on our understanding of the complex temporal mechanics of acclimatization [6,8].

At present, this understanding is woefully incomplete. For example, experimental studies of acclimation (the laboratory analogue of acclimatization)

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typically measure an organism's physiological response to a step change to a new constant environment, such as the change in thermal tolerance caused by moving from a constant low temperature to a constant higher temperature [11,12]. Although such experiments provide useful demonstrations of the degree of physiological plasticity, it is difficult to translate their results to nature, where environments vary continuously. A next step towards disentangling the interactions between environment and physiology might be to obtain paired time series of a pertinent environmental factor and simultaneous physiological capacity (e.g. a year-long record of water temperature and the co-occurring thermal limits of an aquatic organism). From these paired records, time-series analysis [13] could identify pertinent aspects of thermal history that affect the acclimatization of thermal tolerance. For instance, an organism's current level of acclimatization might be correlated with the average daily maximum temperature encountered in the preceding 3 days. One could then predict how a shift in environmental variability would affect the likelihood of the organism exceeding its thermal limits. Furthermore, this knowledge would allow one to more efficiently address the physiological mechanisms underlying acclimatization (e.g. production of heat-shock proteins, shifts in membrane fluidity) [14] by focusing the design of future experiments. However, to our knowledge, there are few, if any, available time series pairing high-frequency measurements of physiological limits with environmental records. Existing physiological time series are typically restricted to either short durations or infrequent (approximately monthly) sampling [15,16]. The reasons for this are largely logistical. For instance, measuring a species's thermal limits requires killing many organisms; a lengthy time series of such measurements in any single population would be impractical, if not unethical.

The current paucity of physiological time series does not preclude theoretical exploration of how acclimatization could affect the magnitude and likelihood of stressful events. To that end, in this exploration we:

1. Identify several potential environmental signals to which physiology might acclimatize.
2. Use environmental time-series from representative habitats to analyse how the temporal extent of each environmental signal affects the magnitude and frequency of stressful events.
3. Discuss physiological studies that are needed to further clarify the relationship between environmental variation and physiological acclimatization.

We couch our discussion in the context of elevated body temperature and its relationship with organismal physiology, a choice driven by three considerations. (1) Concerns over global change give issues of temperature variation unusual and immediate importance. (2) Unlike other environmental factors (e.g. salinity, pH, oxygen concentration), the biological effects of temperature change are nearly universal [17]; thus, any conclusions likely apply across taxa. (3) Long-term temperature records are readily available.

We make a simplifying assumption regarding the physiological consequences of environmental variation: that the stress placed on an organism scales, perhaps nonlinearly, with the difference between the current state of acclimatization (that is, what the organism's physiology 'expects') and what the environment imposes. This deviation-based index of environmental stress is both easily quantified and intuitive. For example, if, based on recent experience or endogenous rhythms, an organism has acclimatized to a winter temperature of 10°C, sudden imposition of 25°C (a 15°C deviation) could be stressful. For the same organism acclimatized in summer to 20°C, imposition of 25°C (a mere 5°C deviation) would probably be benign.

We acknowledge that this simple, deviation-based characterization of stress does not consider all potential aspects of the complex physiology involved in organism/environment interactions. For example, instead of (or in addition to) the magnitude of deviation, the acute rate of environmental change during a stressful event might be important [18,19]. It is also possible that the same magnitude of deviation might have different consequences in different seasons. These aspects could be integrated in the future, but here we concentrate solely on the magnitude of deviation.

This idea of extremes as local 'anomalies' or 'pulses' against a background that is itself dynamic has recently received attention [3,20,21]. However, this approach is far from universal, and studies often do not account for acclimatization. For example, even recent studies of extreme temperatures address only the highest values within one season (e.g. [9]). We suggest that the deviation-based method represents an improved, unambiguous null model for the degree of physiological stress experienced by organisms inhabiting realistically dynamic environments.

(a) Environmental signals for acclimatization

Our first task is to identify aspects of the environment (signals) to which physiology might respond to maintain organismal performance. Here, we evaluate four of many possible indices that plausibly could serve as environmental signals in the context of thermal physiology:

1. The *average temperature*, the moving, weighted average of all temperatures encountered over some recent time interval: the *acclimatization window.*
2. The *average daily maximum (or minimum) temperature*, the moving, weighted average of daily maxima (or minima) over the window.
3. The *absolute maximum (or minimum) temperature*, the single highest (or lowest) value encountered over the window.
4. The *historical periodic temperature*, the temperature 'expected' by an organism's physiology for predictable, periodic fluctuations based on information from previous experience or inherited from prior generations. For example, if endogenous rhythms tell an organism that air temperature fluctuates sinusoidally with a 365-day period, it can prepare its physiology accordingly. (Note that this mechanism provides a means to remove the lag between environmental change and acclimatization intrinsic to the first three indices.)

It is possible that different traits respond to different environmental signals [22], or that other indices (and combinations of indices) could inform physiology, but these four provide a broad set of heuristic examples.

Here, we model the adjustment of physiology to prevailing environmental conditions via acclimatization as a continuous process; we assume that physiology is constantly updated

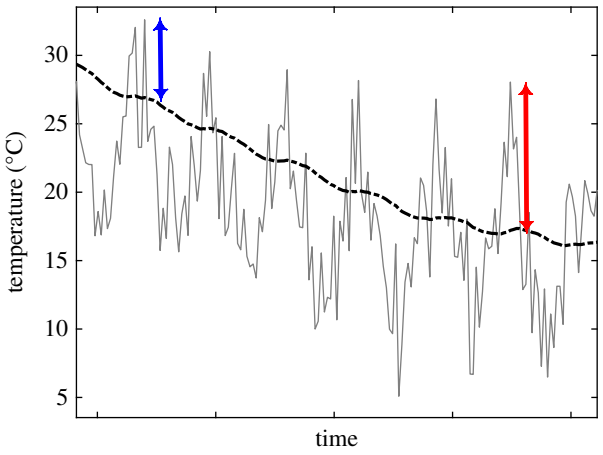

Figure 1. A modified approach to delineating stressful events in environmental records. Here, a hypothetical organism experiences a series of body temperatures (grey line; 1 week is depicted). Expected values at each time were generated using a retrospective LOWESS smoothing function on hourly data (average-temperature index in the text) with an acclimatization window of 7 days (dashed black line). Extremes can be defined as the largest deviations between the 'observed' and 'expected' conditions. Using this approach, the absolute warmest temperatures are not always extreme. For example, compare the length of the arrow to the upper left (small deviation at high temperature) to that of the arrow to the right (large deviation at low temperature). (Online version in colour.)

based on the most recent index value. For example, if the signal is the average temperature in a 7-day acclimatization window, we assume that, at any given time, the organism is as adjusted as its physiology allows to the previous 7 days. Note that this assumption does not imply that physiology is necessarily adjusted to the current temperature. For instance, during a period of continuous temperature increase, physiology will be acclimatized to a temperature cooler than that the organism currently experiences.

To calculate the average-temperature index, we use a moving, locally weighted smoothing algorithm (a modified LOWESS regression) [23] (figure 1). Given a time-series of environmental temperature data (e.g. hourly air temperature), a weighted linear regression is fitted to the data within an acclimatization window of n temperatures preceding and including the current time point. (By contrast, the standard LOWESS approach uses a window extending in both directions from the current point.) The weight given to each temperature in the window declines for temperatures farther in the past, thus implementing an implicit assumption that physiology is most influenced by the most recent conditions (we return to this assumption in the Discussion). The value of the weighted regression at the current time is then taken as the expected (acclimatized) temperature. This retrospective calculation can be repeated for all points in the time-series except for the initial $n-1$ points.

Indices 2 and 3 are then estimated for the same acclimatization window. To calculate the average daily maximum temperature index, we reapply the locally weighted algorithm using only the daily maxima in the acclimatization window preceding, but not including, the present day (today's maximum is not yet known). For the absolute-maximum temperature index, we simply record the highest temperature in the acclimatization window preceding, but not including, the present.

To estimate the historical periodic temperature index, we average temperatures at each given time in a year across all years of the environmental time series. For example, for a 20-year time series, we average all 20 measurements of the temperature at 8.40 on 23 March to generate the index for that date and time in any year. This procedure captures both circadian and annual temperature fluctuations, but it smooths over tidal fluctuations, whose lunar period aligns with neither the solar calendar nor the 24 h clock.

The acclimatization window—which incorporates both the interval over which the environment is monitored and the time allowed for physiological adjustment—could vary from extremely short cycles (e.g. tidal cycles [24,25]) to diel oscillations [26] to annual cycles or perhaps even longer periods [27]. Our analyses address this potential diversity by repeating the calculations above using acclimatization windows from 4 h to 1 year. To calculate temperature deviations for a given signal index and acclimatization window, we subtract the time series of expected/acclimatized temperatures from the corresponding time series of measured values. These results allow us to dissect the effect of acclimatization-window duration on the resulting distribution of temperature deviations, and thereby on the proposed degree of physiological stress. The acclimatization window acts as a low-pass filter; the longer the window, the less sensitive a signal is to high-frequency thermal variation and the rate of temperature change. As a result, the magnitude of deviations depends on both acclimatization-window length (the strength of the low-pass filter) and frequency-dependent variation in the thermal environment.

(b) Definitions: 'extreme' versus 'threshold-exceeding'

Given a time series of thermal deviations, our next task is to identify the subset of deviations that are potentially of physiological, ecological and evolutionary interest. However, we must first deal with a semantic issue. Typically, these events are referred to as 'extreme', and we have used this term informally above. However, dictionary definitions of 'extreme' encapsulate two distinct ideas:

1. *An event is extreme if it is both rare and far from the average.* This statistical definition refers to the low-probability events in a distribution's tails. For example, one might reasonably propose that, to be extreme, a high-temperature event must fall within the highest $x\%$ of all measurements, where x is small (e.g. [9]).
2. *Alternatively, an event is extreme if it exceeds prescribed bounds.* In a biological context, this refers to events that exceed some functional threshold (e.g. the critical thermal maximum) and, therefore, have deleterious consequences. For example, Gutschick & BassiriRad [4] defined extremes as events that exceed an organism's acclimatory capacity.

The same concepts apply to values in the lower tail of a distribution or values that fall below some lower critical threshold (e.g. temperatures below the freezing point). Biologists have struggled to reconcile these two components—statistical rarity and biological consequences—into utilitarian definitions of an extreme event [1,4,28–30].

To avoid confusion, henceforth we refer to events that satisfy definition 1 as *extreme*, and those that exceed a functional threshold—and, therefore, satisfy definition 2—as

threshold-exceeding. The distinction is useful because a given event need not satisfy both definitions: events that are rare may not have functional consequences, while events that exceed a given threshold might not be rare. For example, limited plasticity of upper thermal-tolerance thresholds, observed in many ectotherms [12], implies absolute constraints on physiological limits. Consequently, the warmest temperatures in a particularly warm spell of a warm year could exceed thermal tolerance thresholds without falling in the uppermost percentiles of deviations from expected. The distinct terms threshold-exceeding and extreme allow clear discussion of such circumstances.

In the analyses below, we focus on the delineation of extreme and threshold-exceeding events from environmental datasets. Using definition 1, we (arbitrarily) define extreme events as those lying in the top 5% of a distribution, whether that distribution is the raw distribution of temperatures (raw extremes) or the distribution of deviations (deviation extremes); the electronic supplementary material includes results for other percentiles. In some scenarios, physiologists have identified seasonal or otherwise appropriate absolute-temperature thresholds (e.g. [10,31]), but we are unaware of comparable deviation-based biological threshold estimates. To identify threshold-exceeding deviations from acclimatized temperature using definition 2, we explore the consequences of setting a range of threshold values. We systematically examine patterns of extreme and threshold-exceeding events when the percentile/threshold, the environmental signal and the length of the acclimatization window change.

(c) Temperature datasets

To illustrate the resulting patterns, we employ three representative time series, with a focus on environments for which it is reasonable to assume that operative body temperatures of ectothermic organisms follow recorded environmental patterns (for details of each record, see electronic supplementary material, table S1):

1. A 29-year record of air temperature at an arctic field site, recorded hourly [32].
2. An 18-year record of mid-latitude desert soil temperature, recorded hourly at a depth of 20 cm [33].
3. A 7-year record of nearshore tropical-ocean temperature, recorded every half-hour [34].

With few exceptions (e.g. some corals [35]), aquatic ectotherms' body temperatures reliably mirror the temperature of the surrounding liquid medium [36]. Similarly, body temperatures of small, soil-dwelling organisms probably equal their habitat is temperature. By contrast, above-ground terrestrial ectotherms' body temperatures can be heavily influenced by other biophysical factors (e.g. solar irradiance, evaporation), physiological processes (e.g. heat generation), body size [37], and/or behavioural thermoregulation [12,38], leading to large differences between body and air temperatures [36]. Therefore, our record of arctic air temperature approximates that of a hypothetical small ectotherm in a shaded habitat.

The distributions of raw habitat temperatures vary in shape across these datasets (figure 2, insets); none is normally distributed as is often modelled [39]. The tropical sea distribution is left-skewed, the arctic air distribution is relatively flat topped, and the desert soil distribution is bimodal.

2. Results

(a) Expectations matter: The magnitude of extremes and frequency of threshold-exceeding events depend on the environmental signal and length of the acclimatization window

The average magnitude of extreme deviations is sensitive to acclimatization-window length, but the pattern of sensitivity differs dramatically depending on the acclimatization signal. For the average temperature and average daily maximum temperature signals, longer acclimatization windows generate smoother, less variable time-series of physiological expectations. Consequently, the magnitude of deviations tends to increase as the window lengthens, particularly in the desert-soil and arctic-air datasets (figure 3*a* for top 5% of deviations; electronic supplementary material, figure S1A,B,F,G for a range of percentiles). In other words, if organisms in these habitats adjust in response to a moving average, longer acclimatization windows result in greater imposed stress. Physiological lags, most likely acting in concert with excessive energetic costs, prohibit near-instantaneous acclimatization [40]. Nonetheless, if organisms in these habitats respond to some moving average of environmental conditions, they should minimize the length of the acclimatization window; otherwise, they risk being physiologically under-prepared for the next extreme elevated temperature. This pattern is, however, not universal. In the tropical seawater dataset, the mean magnitude of extreme deviations is maximal at an intermediate acclimatization window and is much less sensitive overall to changes in the acclimatization window (figure 3*a*; electronic supplementary material, figure S1 K,L).

In contrast to moving-average signals, if the organism adjusts its physiology in response to the absolute-maximum temperature signal, longer acclimatization windows result in extremes with *decreasing* mean deviations for all three datasets (figure 3*b* for top 5% of deviations; electronic supplementary material, figure S1D,I,N for a range of percentiles). The longer the acclimatization window, the greater the likelihood that one of the few highest values in the overall distribution will be encountered. Consequently, for long acclimatization windows nearly all experienced temperatures are lower than the temperature to which the organism is acclimatized, and the average of extreme deviations becomes increasingly negative (figure 3*b*). Thus, organisms that acclimatize to long-term absolute-maximum temperatures are physiologically adjusted to higher temperatures than they are likely to soon encounter. This conservative strategy might backfire if costs of thermal defences are high [41], and over-preparation could influence life-history trade-offs or related biological phenomena [42]. However, it is not uncommon to find organisms with median thermal tolerances above mean annual maximum temperatures (e.g. [41,43]), perhaps suggesting that costs of thermal defences are not always substantial.

Endogenous programming of responses to periodic temperature changes does not necessarily decrease the magnitude of extreme deviations. For short acclimatization windows (less than approx. 25–30 days), in the desert-soil and artic-air datasets mean extreme deviations from the historical periodic signal (dashed lines in figure 3*a*) are *larger* than those from the average-temperature signal.

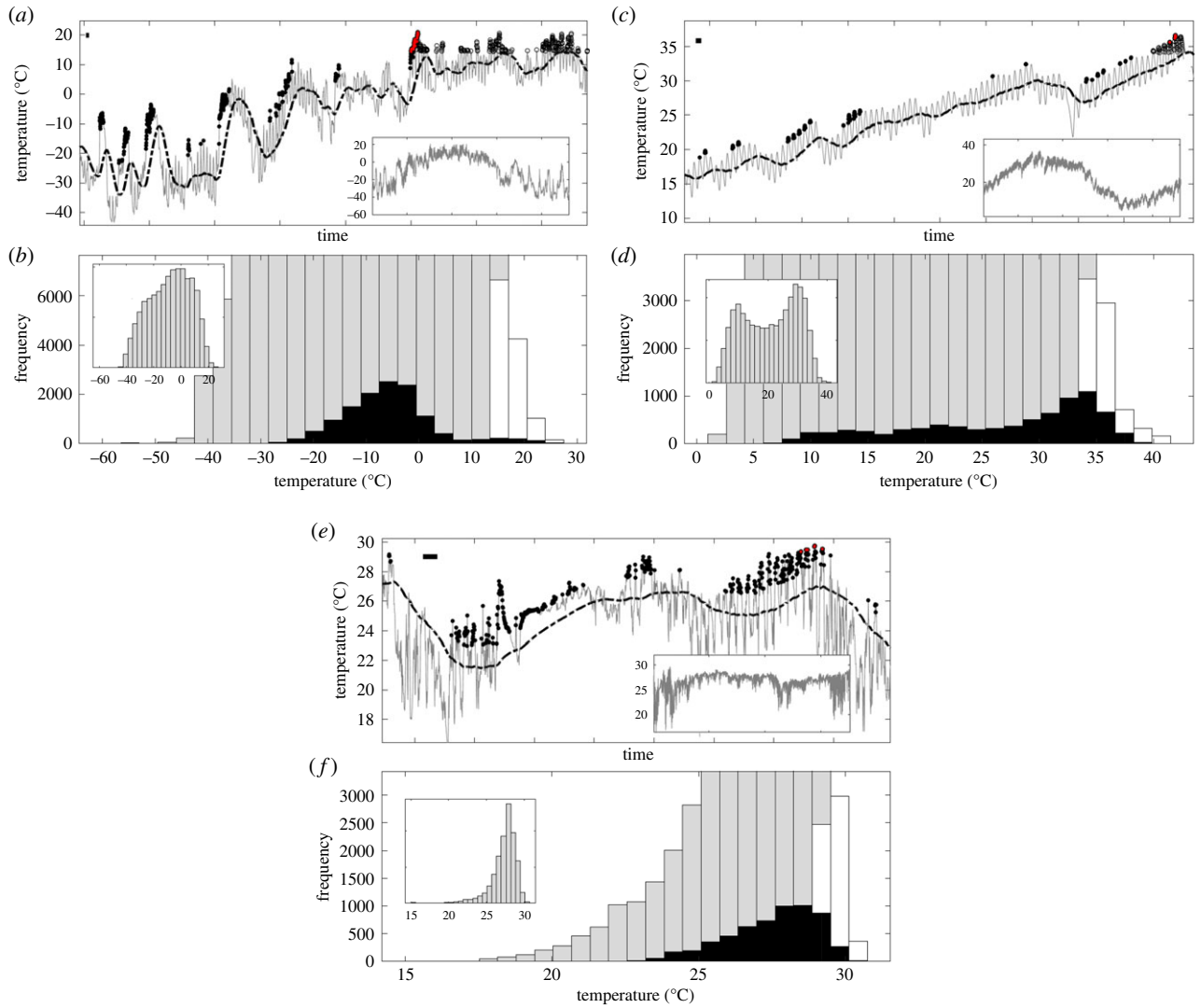

Figure 2. The distribution of extreme deviations from expected/acclimatized temperature varies across habitat types, and deviations identified as extreme represent a surprisingly broad range of absolute temperatures. (*a*) Temperature extremes for the arctic air dataset, recorded at 1 h intervals (thin grey line). Expected values for each time were generated using the average-temperature index (dashed black line) with an acclimatization window of 7 d. Black circles, deviation extremes (largest 5% of deviations from expected); open circles, raw extremes (largest 5% of raw values); red circles (in online version), extreme according to both criteria. The small, black scale bar in the upper left indicates 1 day. The inset shows 1 year of data from this location. (*b*) Histograms illustrating the overall shape of the air temperature distribution (light grey background and inset) as well as the distributions of different varieties of extremes. White bars indicate raw extremes. Superimposed black bars indicate deviation extremes. Panels (*c,d*) same as (*a,b*) but for mid-latitude desert soil at 1 h intervals. Panels (*e,f*) same as (*a,b*) but for 0.5 h intervals in the tropical seawater dataset. (Online version in colour.)

However, this pattern reverses at longer acclimatization windows. In other words, historical knowledge would reduce the intensity of extremes encountered in these two habitats only if the only other option were to respond to a relatively long-term moving average. Over time scales of a few weeks, historical knowledge of periodicity is—somewhat counterintuitively—not beneficial. The picture is again different for tropical ocean temperatures, for which deviations from moving average signals are always less than those from the historical periodic signal. This is likely due to variation in this dataset being driven more by episodic upwelling of cold water and by tidal rhythms than by diel or annual oscillations (electronic supplementary material, figure S2). In sum, the utility of knowledge of environmental periodicity depends on the predictability with which the environment fluctuates.

In order to integrate temporal acclimatization with definition 2 for threshold-exceeding events, we selected a range of deviation magnitudes that might serve as a biological threshold in each dataset. For a given threshold deviation and window length, acclimatizing to the average daily maximum temperature always results in fewer threshold-exceeding events than acclimatizing to the average temperature index (figure 4*a*; electronic supplementary material, figure S3A,B,E,F,I,J). While the frequency of threshold-exceeding events rises monotonically in the arctic air and desert soil datasets for these two indices, as before the tropical seawater dataset is unique. It exhibits local maxima in the frequency of threshold-exceeding events at an intermediate window length (electronic supplementary material, figure S3I,J). Using the absolute-maximum temperature index, the longer the acclimatization window the fewer events cross a given threshold deviation (figure 4*b*; electronic supplementary material, figures S3C,G,K and S4C,G,K). Knowledge of historical periodic temperature reduces the number of threshold-exceeding events per year relative to the moving average indices for the arctic air and desert soil datasets, but only for long acclimatization windows

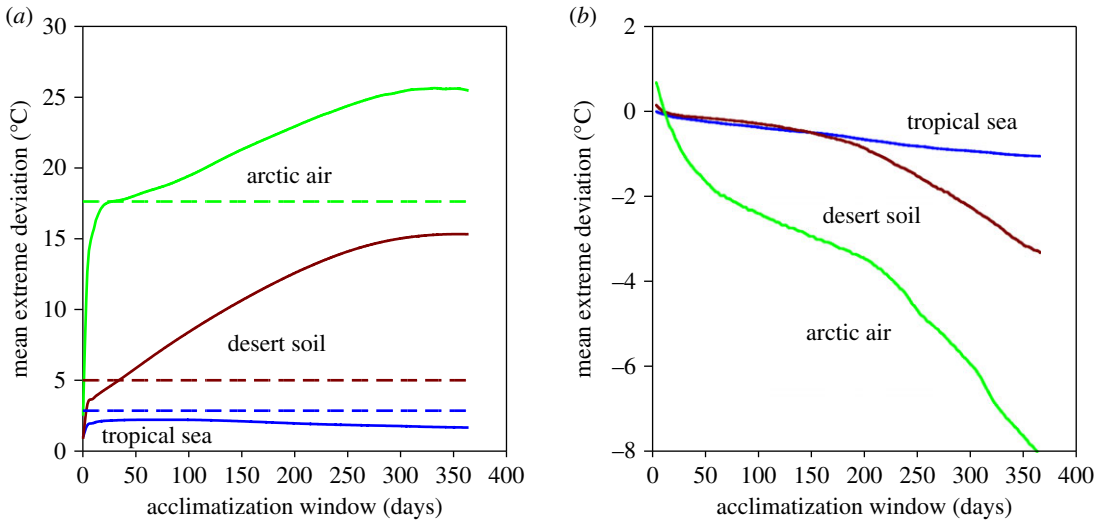

Figure 3. The magnitude of high-temperature deviation extremes varies among habitat types, and it is sensitive to the choice of acclimatization signal. (*a*) The mean of the top 5% of deviations from expected values generated using the average temperature index for the three datasets. Deviations were calculated for acclimatization windows from 4 h to 1 yr. Horizontal, dashed lines indicate the mean extreme deviations using the historical periodic temperature index. (*b*) The mean of deviation extremes generated using the absolute-maximum temperature index, for acclimatization windows of 4 h to 1 yr. Note the difference in *y*-axis scales. Mean deviation extremes for other acclimatization signals and percentiles that could be used to define an extreme are found in electronic supplementary material, figure S1. (Online version in colour.)

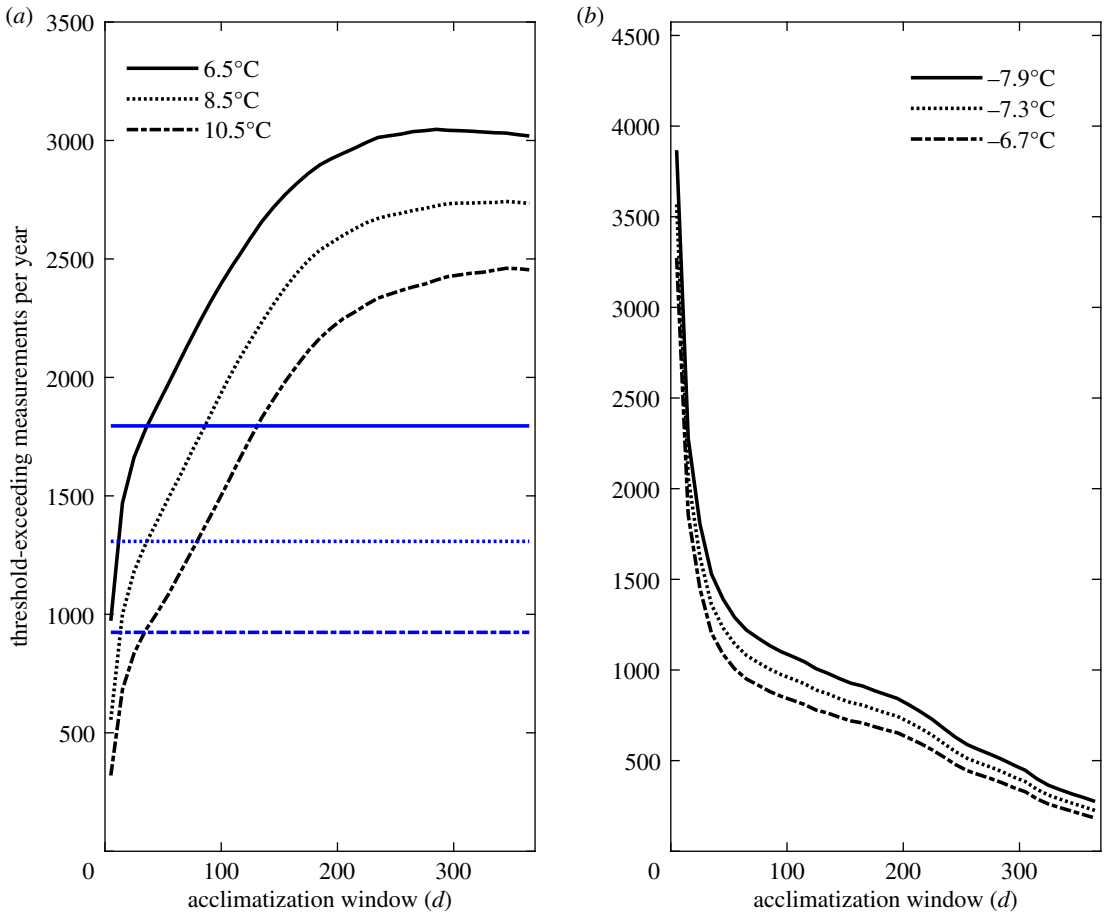

Figure 4. The number of threshold-exceeding events per year in the arctic air dataset varies among acclimatization signals and as the acclimatization window increases in length. (*a*) Events crossing a deviation-based threshold of 6.5, 8.5 or 10.5°C for the average temperature index (black curves) or the historical periodic temperature index (horizontal lines; blue in online version; independent of acclimatization window length). (*b*) Events crossing a different set of thresholds for the absolute-maximum temperature index (most deviations are negative for this index). Analogous plots for the desert soil and tropical seawater datasets are found in electronic supplementary material, figures S3 and S4. (Online version in colour.)

(figure 4*a*; electronic supplementary material, figure S3); such historical knowledge is never advantageous relative to any length window for tropical-sea temperatures (electronic supplementary material, figure S3L). As above for the magnitude of deviation extremes, the historical periodic temperature acclimatization strategy is advantageous in some habitats only if organisms are otherwise restricted to lengthy acclimatization windows.

(b) The temperatures of threshold-exceeding events and extremes need not fall in the tails of a raw distribution

Many temperatures that would be considered mundane in the distribution of raw values nonetheless represent substantial deviations from what an organism expects based on its thermal history (figure 2*b*,*d*,*f*). For example, only temperatures above 14.3°C fall in the top 5% of the raw temperature distribution for the arctic-air dataset, whereas a temperature as low as −33.3°C (only the 6th percentile of the raw data) qualifies as a warm deviation extreme with a 7 d acclimatization window. This context-dependency of an extreme represents perhaps the greatest advantage of defining such events based on deviations from the expected, while also presenting a formidable challenge in identifying the appropriate length of acclimatization window for any given organism (see below).

There is negligible overlap between measurements identified as deviation extremes and those that would be considered raw extremes (see red points in online version of figure 2). This degree of overlap increases as the acclimatization window increases in length, but it rarely exceeds 50% even with windows of up to 1 year (electronic supplementary material, figure S5). At the limit, with exceedingly long windows, deviation extremes will converge on raw extremes. However, such long acclimatization windows are likely to be rare in nature; many organisms live less than a year, and a litany of studies across many taxa have documented short-term plasticity of thermal physiology (reviewed elsewhere, e.g. [12,39]).

3. Discussion

(a) Challenges for the context-dependent approach

One advantage of this context-dependent, quantitative approach is that it makes concrete, testable predictions. Some of these are counterintuitive. For example, it will now be incumbent upon physiologists who study overwintering to ascertain whether sudden deviation to a warmer temperature, still well below the freezing point, can induce the same sorts of cellular perturbations (e.g. of membrane or enzyme structure) that accompany 'canonical' heat stress [14].

There are at least three challenges that must be overcome to take full advantage of this context-dependent approach to extreme and threshold-exceeding events. First, further empirical work is needed to delineate the signals organisms use to set environmental expectations. Progress in this respect has been hampered by physiologists' experimental designs, which only rarely have included realistic temporal patterns of environmental variation (e.g. [44,45]). The optimal signal likely varies considerably among habitats (in our analyses tropical seawater consistently exhibits unique patterns) and among organisms, depending at least in part on the relative contributions of physiology (acclimatization capacity) and behavior (ability to modulate environmental exposure) [12]. Although beyond the scope of this contribution, a synthetic analysis of the time scales of acclimatization in organisms from a variety of habitats exhibiting different spectral qualities of temperature variation would be very informative. In such an analysis, the suite of possible signals identified here could function as null models, yielding testable predictions regarding the magnitude and frequency of stressful events under alternative acclimatization strategies.

A second potential challenge involves the length and sampling frequency of the environmental time series itself. If stressful events occur randomly in time, as they often do [7], the longer the time over which the distribution of events is measured, the more extreme are the raw values encountered (a fundamental conclusion of extreme value theory [46]). Thus, even in the absence of climate warming, the highest temperatures encountered in a year typically are lower than the highest temperatures encountered in a decade. This issue poses a potential problem to the statistical delineation of extremes—the distribution of raw extreme values varies with the length of the environmental time series. However, preliminary assessment of artificially shortened versions of the datasets analysed here indicates that the mean and standard deviation of the magnitude of deviation extremes are relatively insensitive to the length of the time series (electronic supplementary material, figure S6). This observation warrants further attention to examine its generality. In addition, sampling frequency must be sufficiently high [47] to capture the rate of acute change during individual extreme events requires at least hourly sampling.

A third challenge involves the under-explored role of carryover effects between repeated events that are separated by intervals of varying lengths. While much discussion in the biological literature on climate change focuses on changes in the frequency and intensity of extreme events in a warmer and more variable world (e.g. [2]), these events are often treated as discrete, isolated incidents. However, as noted by Gutschik & BassiriRad [4], when environmental conditions exceed biological thresholds they impart a 'legacy' to an organism, modifying (at least temporarily) the manner in which it interacts with its environment. The duration of this legacy varies, and the underlying mechanisms might vary with duration [48]. At one end of the spectrum, hardening has effects that appear to dissipate after one or a few days (e.g. [49,50]). Developmental plasticity, in which early experience irreversibly alters adult traits [51,52], often takes considerably longer. Furthermore, while we may be tempted to conclude that what matters most for an organism is its experience during its lifetime, evolutionary processes, transgenerational effects of environmental experience, and possibly other mechanisms link organisms and environments across considerably longer time spans [14,53,54]. The simple approach we have taken here does not incorporate these carryover effects. For example, we implicitly—but unrealistically—assume that the physiological effect of a given magnitude of thermal deviation is the same before and after another threshold-exceeding or extreme event. Furthermore, for some organisms, the rate of acclimatization as temperatures rise is different from that as temperatures fall [11,55]. These complexities demand greater empirical attention.

Given the likelihood of carryover effects [8], studies of threshold-exceeding and extreme environmental conditions must consider their temporal relationship to each other. In this regard, it is imperative not only to quantify (or forecast) the magnitude of extreme or threshold-exceeding events, but also to quantify distributions of the intensity of extremes (duration × magnitude) and inter-event intervals. These metrics are perhaps the most relevant to forecasting the biological consequences of climate change [2,56]. For example, warm extreme and threshold-exceeding events

tend to occur in clusters (heat waves). Heat waves already show signs of increasing frequency, which may have profound biological effects [21,57–59].

Along with a focus on the temporal distribution of extreme events must come experimental designs that mimic patterns that currently—or soon will—occur in nature and repeated measurements of the state of biological systems experiencing those patterns [6,60]. We believe that physiologists must redouble their efforts to understand the contingent nature of thresholds [61], including their relationship with developmental or life-history transitions. In each of these experimental scenarios, physiologists will need to quantify shifts in critical thresholds, metabolic or developmental rates, and other indicators of functional impairment. A greater emphasis on sublethal thresholds should also provide valuable insight (e.g. [62]). Finally, nonlinearities in physiological (or ecological) rate functions could have profound impacts on the likelihood of exceeding functional thresholds [63], particularly in the likely event that those thresholds vary through time and/or among individuals. Much difficult work remains to be done in reconciling the concepts of extreme and threshold-exceeding in the context of thermal biology in nature.

4. Conclusion

When discussing the biological consequences of environmental fluctuations, and particularly when expounding on likely impacts of global change, biologists often assume that the intensity and frequency of extreme events will increase in the future. A modified approach to delineating extreme and/or threshold-exceeding events from environmental records reveals that incorporating the dynamic process of acclimatization can fundamentally change the subset of environmental conditions that should be the focus of environmental physiologists and ecologists. This approach recognizes and attempts to incorporate the potentially complex, context-dependent interactions between organisms and their variable environments. It also offers unambiguous, testable predictions of the magnitude and frequency of stressful events from long-term environmental records. We hope and expect that, ultimately, a more comprehensive, mechanistic synthesis will emerge from empirical study of biological systems facing these extraordinary circumstances.

Data accessibility. See electronic supplementary material, table S1 for links to publicly available data records. Matlab code is available at https://github.com/wwdowd/Dowd_Denny_thermal_deviations.

Authors' contributions. W.W.D. and M.W.D. developed ideas, analysed datasets, drafted the manuscript and approved its publication.

Competing interests. We declare we have no competing interests.

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