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Glossary

Critical thermal limits (CTL): CTLs are a suite of commonly used measures of the maximum and minimum temperatures at which organisms can viably function. Individuals are exposed to either static stressful temperatures or gradually ramping temperatures and observed for physiological failure; e.g., uncoordinated movement, heat coma, or death [1]. Typically, either the duration of exposure or the temperature at which loss of viability is observed is recorded as the thermal limit.

Fecundity: The total number of offspring an individual can produce across a set interval or lifetime.

Fertility: The ability of an organism to produce viable offspring. Fertility can be measured in a number of ways but always reaches its lower limit when conditions prevent an individual from producing any offspring (i.e. sterility).

Hardening: Increased thermal tolerance shown by organisms after a short period of exposure to a stressful but non-lethal temperature within the same life stage. Hardening tests are one component of a species plastic response when exposed to stressful temperatures [2].

Sterility: Describes an individual that cannot produce any offspring over a defined period, and thus is synonymous with complete infertility.

Thermal fertility limits (TFL): Outlined here for the first time, TFLs refer to a level and duration of thermal stress that renders individuals unable to reproduce. For populations and species this can be defined as the temperature at which a given proportion of individuals are qualitatively sterile and it includes both higher (TF_{MAX}) and lower (TF_{MIN}) thermal stress limits. For example, the upper TF_{MAX} of male *Drosophila buzzatii* – measured as sterility of 80% of individuals after 6 hours – is 36°C [3].

Abstract

Rising global temperatures are threatening biodiversity. Studies on the impact of temperature on natural populations usually use lethal or viability thresholds, termed the 'critical thermal limit'. However, this overlooks important sub-lethal impacts of temperature that could affect species' persistence. Here, we discuss a critical but overlooked trait, fertility, which can deteriorate at temperatures less severe than an organism's lethal limit. We argue that studies examining the ecological and evolutionary impacts of climate change should consider the 'Thermal Fertility Limit' (TFL) of species; we propose that a framework for designing TFL studies across taxa be developed. Given the importance of fertility for population persistence, understanding how climate change affects TFLs is vital for assessing future biodiversity impacts.

1. Biodiversity Under Climate Change

Climate change will continue to have an increasingly dramatic effect on the global thermal environment [4], including increases in average local temperatures and the frequency of heat waves [5, 6]. These shifts present a major threat to biodiversity and are starting to have severe impacts on the distribution and abundance of natural populations and species [7, 8]. The capacity of species to respond ecologically and evolutionarily to the challenges of global thermal change will affect future biodiversity. Determining key thermally-sensitive traits across species, and quantifying the ability of species to buffer the effects of thermal stress on these traits, is therefore a critical research priority [9].

Understanding the long-term impacts of climate change on populations requires robust predictive models that can project responses to both current global temperatures and future climate change scenarios. Currently, many such models are based on empirically derived 'critical thermal limit' (CTL, see Glossary) estimates, which describe the upper and lower temperature bounds beyond which critical biological functions (e.g. movement or respiration) fail [8, 10]. Comparative studies have shown that measures of such viability limits more robustly predict the current distributions of many species than measures derived from changes in mean fitness traits under thermal stress [11]. For this reason, CTLs have also been used to infer species' sensitivity to climate change [8, 12-14]. However, using only thermal limits to viability may be misleading because different measures of CTLs do not always correlate within a single species or population, leading to inconsistent estimates of population persistence [15]. It has been suggested that a multi-trait approach to thermal tolerance may be give more robust estimates of species responses to climate change [15]. In particular, the focus of thermal limits needs to move away from the incapacitating and lethal effects of thermal stress, to investigate how sub-lethal temperatures impact fitness-related traits such as reproduction, which are critical for population stability and persistence.

2. Sensitivity of Fertility to Temperature

Fertility is a major component of individual fitness and is a central determinant of population growth and persistence. Evidence from a wide variety of taxa suggest that the germ line and associated reproductive physiology is sensitive to thermal stress, particularly high temperatures [16-20]. Evidence, mostly from pollen development, suggests that meiosis is a more thermally sensitive process than mitosis [reviewed in 21, 22]. In mammals, the descended testicle has evolved to ensure that spermatogenesis occurs at cooler-than-body temperatures [23 and references therein]. Indeed, temperature induced infertility imposes major economic costs in tropical climates (Pena 2008). However, although a number of studies have examined how temperature impacts reproductive traits (Table 1), these often use vastly different methodologies and measure different aspects of reproductive biology. This collection of disparate studies makes quantitative comparisons of the impact of high temperature on reproduction very difficult. Possibly for this reason, thermal limits to fertility have not been systematically incorporated into predictions of species responses to climate change.

Here, we argue that the effect of temperature on fertility requires a broad analogue of CTL, termed the 'Thermal Fertility Limit' (TFL). This term would capture both the upper (TF_{MAX}) and lower (TF_{MIN}) temperature boundaries at which a species loses fertility. This new term will facilitate researchers in bringing together related work on how environmental stress impacts this broadly important component of biology, and will highlight the important biological and ecological distinction between fertility and survival when assessing species' response to climate change. We suggest that a framework be developed that will allow researchers to design and conduct thermal fertility studies in a way that generates comparable datasets across taxa. A large database of TFL measures across multiple species and populations relevant to thermal stress levels encountered in nature would provide the power to answer important evolutionary and ecological questions regarding the impact of climate change on natural populations at risk (Box 1 and Figure 1). We do not propose that TFL measures would replace CTLs. Rather, we suggest that the combination of these measures, the geographic distribution of these two limits, and the extent to which they correlate within and among species, will give valuable insight into species' ability to persist and adapt to global thermal change. To do this, we need to consider how temperature is likely to affect fertility at a mechanistic level, and how researchers can design and conduct studies of TFLs in a standardised and broadly comparable way.

3. Towards a Methodological Framework for the Study of TFLs

The adoption of standardised measures for CTLs [11, 24], typically either a direct or proxy measure of viability, has facilitated large-scale comparative studies of species' responses to climate change [8]. A challenge for the study of TFLs will be to develop a similarly standardised measure for fertility. This is a non-trivial task given the inherent complexity and potential species-specificity of reproductive components that contribute to fertility (Figure 2). This complexity is highlighted by the diverse methodologies and metrics of fertility employed in the existing literature on the effect of temperature on fertility (Table 1). For maximum utility, TFL studies should be carefully designed to either produce a quantitative point estimate of temperature limits for fertility for comparative species distribution modelling, or to generate effect size estimates for fertility loss at a given thermal stress level for future meta-analyses between groups.

Factors in Designing TFL Studies

Despite the diverse elements of fertility described in Figure 2, we argue that the most ecologically precise limit to fertility is the point at which the qualitative ability of an organism to produce viable adult offspring under controlled conditions is lost. This limit yields a precise metric that can be applied to quantitative comparisons among taxa.

However, for many species, measuring offspring production directly may be impractical, for instance if generation times are extremely slow. In such instances, proxy measurements that can be empirically correlated with fertility may also serve to capture the effect of temperature. For example, in some *Drosophila*, qualitative sperm motility has been used to quantify male fertility following heat stress, as this correlates strongly with reproductive output [reviewed in 29]. In plants, the percentage of pollen grains that germinate *in vitro* correlates with fruit productivity and has been employed as a measure of TFLs [21, 30]. It would be unrealistic to attempt to identify a trait that captures the effect of temperature on fertility across all of biology, but taxa-specific proxies like these may be sufficient to enable meaningful comparative studies.

Whichever measurement is used, assessing fertility over a range of static temperatures will allow us to generate a fertility reaction norm. From these reaction norms we can determine the temperature at which fertility drops by a given percentage compared to benign controls; a measure analogous to a ‘Lethal Dosage’ in toxicology and one already used for some measures of CTLs [31]. The exact proportion of fertility loss that is ecologically relevant for population stability and thus represents a true thermal fertility limit, is likely to vary from species to species. With enough data on the reproductive and population biology of a given organism, these thresholds could be explicitly modelled. Or, if reaction norms are established across a broad enough range of temperatures then it should be possible to determine any threshold and to assess if these are correlated across species.

Further, unlike viability limits, fertility is not necessarily an irreversible binary trait. Evidence suggests that complete sterility at extreme temperatures is preceded by quantitative fertility loss at intermediate conditions [25, 26]. Furthermore, recovery of fertility can occur in some heat-sterilised animals if they are returned to benign conditions [27, 28], although under severe thermal stress sterility can be permanent [3, pers. obs., 19]. Researchers should carefully consider the time frame over which qualitative fertility is assessed following heat stress, and potentially account for the recovery of fertility over time; a two-day knock-down in fertility may be inconsequential for long-lived species but catastrophic for organisms that exist as adults for only days. This highlights an important consideration when comparing the utility of CTLs and TFLs, reinforcing that TFLs have a much more complicated relationship with time than CTLs.

A second important practical consideration arises when selecting an ecologically relevant temperature treatment. Researchers have shown that the response of organisms to thermal stress is affected by both the intensity of the temperature chosen and also the duration of exposure [24]. This is further complicated when one considers the effect that hardening treatments [1], ramping [13], and the observed differences between static and cyclic temperature treatments [32, and references therein] have on thermal performance in many organisms. Unlike CTLs, where the effect of temperature is often immediately visible, loss of fertility requires subsequent assays following exposure to heat, and so ramping assays are unlikely to be useful. Instead, researchers must choose regimes of static or fluctuating temperature stress that reflect current or future thermal extremes for natural populations. The need to finely balance high-throughput, standardised repeatable assays with ecological realism will be a major challenge for TFL research.

To summarise, if researchers think about the exact trait they are going to measure, the thermal regime under which it will be measured, and consider that fertility may recover over time, then they will be well on their way to having a robust framework for studying

TFLs (Box 2). Investigating this in model species, and testing whether it predicts species distributions better than current methods, will be a key step in determining how important TFLs are in nature.

4. Can Species Maintain Fertility in the Face of Thermal Change?

Many species are predicted to have populations pushed beyond their critical thermal maxima (CT_{MAX}) by climate change [14]. As thermal fertility maxima (TF_{MAX}) are expected to often be lower than CT_{MAX}, rapid climate change is likely to push many populations and species beyond their TF_{MAX}. Developing standardised measures of TFLs will provide tools to investigate how species might physiologically acclimate and adapt to these changing thermal environments.

Are Thermal Fertility Limits Plastic?

Organisms could show phenotypic plasticity in TFLs within their own lifetime or through intergenerational carry-over effects. Sub-optimal temperatures experienced at early life-history stages can affect traits such as adult size [33]. Experiencing some level of thermal stress can increase the fitness of individuals for a similar stress later in life, a process known as acclimation. For CTLs there is significant, but very limited, scope for coping with rising temperatures through plasticity [34]. For instance, the degree of plasticity in upper thermal tolerance appears weakly associated with species distribution ranges [13]. However, it is not known if similar plasticity exists for TFLs, and whether plasticity in TFLs is greater than that for CTLs. Exposing organisms to acclimation treatments followed by TFL measurement, or investigating inter-generation carry-over effects for TFLs, may shed new light on the ability of organisms to buffer the effects on fitness of ecological change.

There is mixed evidence for the impact of acclimation on temperature-induced sterility. Male *Drosophila buzzatti* regain fertility faster following a heat stress if they had previous experienced a heat-shock [3]. However, both *Drosophila subobscura* and *Tribolium castaneum* have been shown to exhibit more extreme fertility loss when exposed to multiple rather than single periods of heat stress, which does not indicate an acclimation response [17]. Where plasticity in thermal fertility traits does exist, the underlying mechanisms remain largely unknown. However, individuals are likely to cope with stress in part by using heat-shock proteins, which are important in mediating upper thermal limits in insect species [35]. Many, including Hsp70, are up-regulated during hardening treatments, helping individuals to offset the negative fitness consequences of thermal stress [36]. Heat shock proteins are a ubiquitous component in living systems: importantly, they are found in gametes, including human spermatozoa [37]. Exploring the scope for heat-shock protein expression to buffer the deleterious effect of high temperature on fertility, and the variation in this within closely related species might explain patterns of variation in TFLs.

Can Thermal Fertility Limits Evolve?

Over long periods of environmental change, selection should favour more thermally-tolerant genotypes and a rise in both CTLs and TFLs. Including the evolvability of thermally sensitive traits into models of species’ response to climate change generates vastly different predictions than equivalent models parameterised with only current measure of thermal sensitivity [8]. However, current evidence suggests there is very little standing genetic variation and evolvability for high temperature CTLs [8], although this is debated [reviewed in 24]. Whether TFLs can evolve rapidly is unknown. Limited evidence in *Drosophila* has shown male sterility under heat stress can be variable within species and may be under selection to be locally adapted across populations originating from different thermal regimes [17, 19, 27, 39], suggesting that TFLs may be evolvable. Quantifying standing variation in TFLs across genotypes and populations of multiple species would be a good first approach for testing this.

Species with CTLs that are low and evolutionarily constrained are predicted to be at particular risk from climate change [12]. For instance, tropical species have been shown to often lack genetic variation that would enable rapid evolution to cope with changing climatic variables such as temperature and desiccation [14, 40]. Establishing how these species' TFLs respond to increasing temperatures may be critical for predicting how they will be impacted by climate change. If TFLs are substantially lower than CTLs, then these species may be more vulnerable than currently predicted. However, if TFLs are more evolvable than CTLs, this may compensate for their initially low TFLs, making CTLs more important predictors of distributions in a warming world. Until both CTLs and TFLs are examined across a variety of taxa, and the evolvability of TFLs determined, confidence in predictions about which taxa are going to be particularly vulnerable will be low (Box 1).

Whether populations or species can respond to thermally-induced loss of fertility, either through short-term plasticity or long-term adaptive change, is unclear. This is partly because of knowledge gaps regarding the impact of extreme temperature on fertility in animals and plants. A fundamental understanding of how extreme increases and decreases in temperature influence reproduction with negative effects on fertility is required before the ecological relevance and potential evolution of TFLs can be determined. However, it is precisely these answers that are ultimately among the most important to know, as they will improve predictions on how climate change may affect species abundance and distribution, and thereby change biodiversity across the globe.

Concluding Remarks

Here, we have introduced and discussed the idea that measuring the thermal limit of fertility across multiple species and a broad range of taxa could be critical when assessing the impacts of global thermal change on biodiversity. While the use of critical thermal limits has proven to be informative for modelling current and future distributions of species [8, 13, 14], CTLs may overestimate species' ability to cope with stressful temperatures**.** Research exploring TFLs (see Outstanding Questions) is needed to ascertain the extent to which they correlate with CTLs**.** To this end, we propose a general framework for TFL studies to promote large-scale cross-taxa assessments of this important but largely neglected trait**.** Focusing on TFLs with broadly standardised methodologies may improve our knowledge of how climate change will affect species' abundance, distribution, and persistence. However, the current literature on how thermal stress impacts fertility is fragmented. Stronger and more unified thermal fertility research might radically improve our predictions about the impacts of global thermal change.

Box 1: Groups at Risk

Figure 1 Examples of organisms that may be particularly at risk to losing fertility due to high temperatures. Clockwise from top left: broadcast spawning fish such as carp, small ectothermic insects including pollinating bees, endemic animals with limited latitudinal or elevation ranges such as the flightless cormorant, disease vectors including mosquitos, coral species that are important to highly diverse reefs, and endemic plant species including the Scottish primrose. All photos in this figure are licensed under CC BY 2.0, Credits: Joaquim Alves Gaspar, Charles Sharp, Toby Hudson & David Glass).

Certain groups of organisms are likely to be most vulnerable to temperature-driven fertility loss. These groups may provide important case studies and primary avenues of research (Fig 1).

Ectothermic Species

Most plant species cannot regulate the temperature of their tissues (excluding a number of species of flower [41]), forcing them to withstand ambient temperatures. Likewise, ectothermic animals may also be vulnerable [5], as they rely on behavioural rather than physiological thermoregulation to avoid stressful microenvironments. Smaller ectothermic animals are even more at risk, as they will reach ambient temperatures faster.

Endemic Species and Species with Small Ranges

Rare or endemic species with small latitudinal ranges are likely to be particularly at risk to losing fertility as ambient temperatures increase because i) they are likely to lack the genetic variation and gene flow required to adapt to novel stressors [7], and ii) in many cases they may be unable to shift their distribution range to track changing climates. This will be particularly true for island endemics and species that live within specialised elevational niches in mountains.

Aquatic Species

Aquatic species, particularly broadcast spawners, are likely to be at risk because the specific heat capacity of water will result in rapid changes in tissue temperatures. Further, gametes in the water from spawning organisms will exposed directly to stressful temperatures, so will need to evolve robust physiological responses to high temperatures to retain form and function. This is likely to be a greater issue for freshwater and shallow water organisms, as these environments experience greater fluctuations in temperatures, exposing these organisms to acute stress events.

Sessile Species and Life Stages

Sessile organisms, such as plants, corals and juvenile stages (e.g. pupal stages in holometabolous insects), in which movement to cooler areas during temperature spikes is not possible, may be particularly vulnerable. Similarly, due to their limited dispersal ability, belowground communities may be especially vulnerable to fertility loss under climate change [42].

Box 2 Considerations When Designing TFL Experiments

1. **Trait selection:** We suggest that wherever possible researchers measure both qualitative and quantitative offspring production in order to capture the ecological impact of high temperature on fertility. Where this is impossible, careful selection of

proxy measures of fertility that can be empirically correlated with an individual's ability to produce offspring could be considered. Holistic measures such as these are most likely to generate broadly comparable data sets across taxa.

2. **Life-history stage:** Whilst reproduction occurs almost invariably during adult life-history stages, reproductive development and maturation can begin much earlier. Researchers should therefore consider which life stage(s) of their organism to expose to stress. For instance, do heat-treated juveniles mature into sterile adults whilst heated adults remain fertile?

3. **Ecologically valid thermal environment:** Careful attention should be given to selecting temperature regimes that reflect the current or future extremes that organisms are likely to face. For instance, are temperature spikes over a matter of a few hours more likely to impact a species' fertility than a rise in mean daytime temperature? A large body of work on CTLs has demonstrated that measures of thermal performance can be highly sensitive to the duration of stress [24], rates of temperature ramping [13] and the intensity and frequency of any temperature fluctuations [43]. The latter point in particular may be key for thermal fertility, as some animals can recover fertility during periods of benign temperatures including night time [44]. Once researchers have selected a regime of temperature delivery they should strive, where possible, to measure thermal fertility over a range of temperature values. This will help capture the thermal fertility reaction norm of their organism.

4. **Implications for population stability:** To estimate the population-level effects of high temperature on fertility, researchers should consider what percentage loss of fertility represents a meaningful threat to population stability. Factors such as the effective population size of the organism in a nature, the potential fecundity of individuals and their generation time could be used to estimate a specie's sensitivity to fertility loss. Researchers can then determine the degree of thermal stress required to push their study organism beyond this threshold.

5. **Critical thermal and fertility limits:** The power of TFLs to predict species' response to climate change will be related to the extent to which fertility and viability limits correlate with each other and across species. Low correlation would suggest that one metric cannot be substituted for the other. Which species have high and which species have low correlation and what impacts this relationship? Thus, researchers should determine both fertility and viability limits of their organism under relevant thermal regimes.

Table 1: Examples of Thermal Impacts on Fertility

Taxonomic group	Organism	Species	Impact of temperature on fertility	Measure	Refs
Cnidarian	Coral	*Acropora digitifera*	Increase of 2°C reduced the number of sperm bundles by almost 50%, and reduced egg size	Gamete number	[45]
Insect	Bed bug	*Cimex lectularius*	Egg production and hatching success can fall to almost zero as a result of thermal stress	Fecundity	[26]
	Red mason bee	*Osmia bicornis*	Changed odour profile, altering female mating preference	Mating preference	[46]
	Beetle	*Callosobruchus maculatus*	Males reared at extreme high temperatures produce smaller sperm than benign controls	Sperm form and function	[47]
	Beetle	*Tribolium castaneum*	Stressed males reduce sperm viability, competitiveness. Inseminated sperm within female storage organs less viable when female stressed. Transgenerational impact reducing longevity of offspring sired by stressed males	Sperm form and function, offspring production	[48]
	Dragonfly	*Micrathyria spp.*	Species within the genus that struggle to maintain optimal body temperatures are less efficient at defending perches at high temperatures, and lose out on breeding sites to larger species	Courtship behaviour	[49]
	Fruit fly	*Bactrocera tryoni*	Reduced mating latency at cold temperatures, reduced mating frequency at cold temperatures	Mating latency, mating frequency,	[50]
	Fruit fly	Family: Drosophilidae	Reduced mating success. Impairment of sperm elongation, resulting in loss of sperm motility and thus lower fertility	Offspring production, mating success, sperm motility	[17, 25, 27, 29, 51-53]
	Oriental fruit moth	*Grapholita molesta*	A 2h heat stress during pupation reduced fecundity but increased other adult fitness traits such as survival	Fecundity, gamete viability	[54]
	Wasp	*Aphidius avenae*	Low mating success rate due to reduced courtship behaviour. Reduced sperm count after developmental stress, with males at high stress fully sterile. Reduced fertilisation results in fewer females, secondarily altering sex ratios. Stressed females produce fewer eggs	Courtship behaviour, gamete number, fertilisation success and offspring production	[28, 55]

Poales	Barley	*Hordeum vulgare*	Developing anther cells are compromised during thermal stress, while developing ovule cells are not	Gamete viability	[56]
	Rice	*Oryza sativa*	High temperature during flowering increased pollen sterility, with greater sterility if CO_2 levels were high	Gamete viability	[57]
Polemoniales	Tomato	*Solanum lycopersicum*	Under thermal stress pollen viability was reduced and anthers developed abnormalities. Thermally tolerant genotypes showed resistance	Gamete viability	[58]
Vertebrate	Chicken	*Gallus gallus domesticus*	An 8 week thermal stress results in increased sperm death and associated drop in fertility	Sperm concentration	[18]
	Cow	*Bos taurus*	Ovulation failure and abortion rate is higher in cows inseminated during warm seasons	Fertilization	[59]
	Guppy fish	*Poecilia reticulata*	Males raised at stressful temperatures have shorter, slower sperm than individuals raised at benign temperatures	Sperm form and function	[60]
	Mouse	*Mus musculus*	Reduced sperm count for over 60 days after 30 minute heat shock	Gamete number	[16]
	Pig	*Sus sp.*	Sperm DNA damage higher and sperm concentration lower during warm wet season.	Sperm form and function	[61]
	Sea lion	*Otaria flavescens*	Stressed males desert females to thermoregulate, foregoing mating opportunities	Courtship and mating behaviour	[62]
	Zebra finch	*Taeniopygia guttata*	Daily heat waves reduced the proportion of sperm exhibiting normal morphology	Sperm form and function	[63]

Figure 2: A Generalized and Simplified Schematic of the Stages in Sexual Reproduction and Examples of Organisms for which the Effect of Temperature has been Measured on these Stages (see Table 1)

Fertility is the emergent product of multiple physiological, developmental and behavioural processes. Not all steps are relevant to all organisms, indeed the diversity and complexity of this cascade across sexual organisms is not fully captured here. However, in all cases the ‘success’ of fertility begins by generating gametes and ends with the production of viable offspring. High temperature may perturbate single or multiple steps in this process but early meiotic stages can be particularly thermally sensitive [21]. High temperature may affect several of these traits simultaneously within an individual, for example by both arresting gametogenesis and reducing investment in copulation behaviours. On the other hand, the effect of high temperature on a single trait, say testis development, may subsequently have cascading effects on downstream elements of reproduction such as sperm counts and motility. Photo credits: A (barley) = Raul Dupagne, B (guppy) = Baskua, C (*Drosophila* mating) = D. Chai, D (coral reef) = Toby Hudson, E (rooster) = Pete Linforth. All photos licensed under CC BY 2.0.

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