

COMMENTARY

Do endotherms have thermal performance curves?

Danielle L. Levesque^{1,*} and Katie E. Marshall²**ABSTRACT**

Temperature is an important environmental factor governing the ability of organisms to grow, survive and reproduce. Thermal performance curves (TPCs), with some caveats, are useful for charting the relationship between body temperature and some measure of performance in ectotherms, and provide a standardized set of characteristics for interspecific comparisons. Endotherms, however, have a more complicated relationship with environmental temperature, as endothermy leads to a decoupling of body temperature from external temperature through use of metabolic heat production, large changes in insulation and variable rates of evaporative heat loss. This has impeded our ability to model endothermic performance in relation to environmental temperature as well as to readily compare performance between species. In this Commentary, we compare the strengths and weaknesses of potential TPC analogues (including other useful proxies for linking performance to temperature) in endotherms and suggest several ways forward in the comparative ecophysiology of endotherms. Our goal is to provide a common language with which ecologists and physiologists can evaluate the effects of temperature on performance. Key directions for improving our understanding of endotherm thermoregulatory physiology include a comparative approach to the study of the level and precision of body temperature, measuring performance directly over a range of body temperatures and building comprehensive mechanistic models of endotherm responses to environmental temperatures. We believe the answer to the question posed in the title could be ‘yes’, but only if ‘performance’ is well defined and understood in relation to body temperature variation, and the costs and benefits of endothermy are specifically modelled.

KEY WORDS: Temperature, Heterothermy, Thermal profiles, Scholander–Irving model, Critical limits, Thermal tolerance

Introduction

Over the last few decades, there has been a concerted effort to increase both our understanding of the physiological mechanisms that drive species range distributions (e.g. Kearney and Porter, 2009; Buckley et al., 2010; Kearney et al., 2010; Maino et al., 2016; Mathewson et al., 2017; Buckley et al., 2018) and our knowledge of the ability of species to feed, grow and reproduce in response to warming environmental temperatures (e.g. Creel et al., 2016; Attias et al., 2018; Cooper et al., 2019; van de Ven et al., 2019). At the moment, many of these models are species or taxa specific and there is, as of yet, no unifying model for assessing endotherm performance in the face of changing global climates. Developing a full mechanistic understanding of the effects of temperature on a species’ performance, and ultimately fitness, is labour intensive;

therefore, shortcuts, models and/or proxies are common (Huey et al., 2012; Sinclair et al., 2016).

One commonly used conceptual model in thermal physiology is the ‘thermal performance curve’ (TPC; Fig. 1). Predominantly applied in studies of ectothermic organisms, these curves are the result of assessing some form of performance (e.g. running speed, growth rate, heart rate) in relation to body temperature (T_b), which in ectotherms is often closely related to environmental temperature (Fig. 1; Huey and Slatkin, 1976; Angilletta, 2009; Schulte, 2015; Sinclair et al., 2016). TPCs usually follow a characteristic shape: performance increases as T_b increases, peaks at a certain temperature (the optimal temperature, T_{opt} ; Fig. 1), and then decreases sharply as temperatures continue to rise (Huey and Stevenson, 1979). The temperatures bookending the TPC (CT_{min} and CT_{max}) are the threshold temperatures beyond which the index of performance equals zero (Huey and Slatkin, 1976; Somero et al., 2016). The shared characteristics of TPCs – CT_{min} , CT_{max} and T_{opt} – allow for direct comparisons with both current and past environmental temperatures, as well as among species and populations (Dowd et al., 2015; Sinclair et al., 2016). Further, comparing the characteristics and limits of TPCs among species allows for relatively straightforward assessment of the limits on performance and distribution of species in relation to environmental temperature (Sunday et al., 2012, 2014). Understanding these relationships has proven useful in both understanding physiological adaptation to local climates and predicting responses to changing temperatures (Deutsch et al., 2008; Huey et al., 2009, 2012; Sheldon and Tewksbury, 2014; Sinclair et al., 2016).

In ectotherms, there has been significant interest in modelling performance as a function of environmental temperature for predicting the effects of climate change on range boundaries and population growth (e.g. Deutsch et al., 2008; Levy et al., 2015; Dillon et al., 2016; Sunday et al., 2014). Although this may seem relatively straightforward, there are a number of assumptions about the relationships that must be made (Fig. 2). As a result, several commentators have pointed out a host of conceptual and practical difficulties due to the broad array of assumptions that must be made about the relationships among performance, T_b and environment (Stevenson et al., 1985; Sinclair et al., 2016; Khelifa et al., 2019). For example, even small ectotherms are able to behaviourally thermoregulate (Fig. 2; Kearney et al., 2009), decoupling the relationship between body and environmental temperatures. Similarly, seasonal acclimation and local adaptation may significantly change the shape of the TPC, altering the relationship between T_b and performance (Fig. 2; Khelifa et al., 2019). Yet, both the shape and the standard parameters of TPCs (T_{opt} , CT_{max} and CT_{min}) continue to be used by numerous researchers (Sinclair et al., 2016). Our goal in this Commentary, however, is not to focus on ectotherms, as TPCs in this group have been thoroughly dissected by the above commentators, and we direct our readers to these reviews.

The question we posed in the title is not easy to answer, and the issues involved in measuring and applying ectotherm TPCs extend equally to endotherms. Fundamentally, thermal performance in endotherms can be considered in two ways. The first – performance

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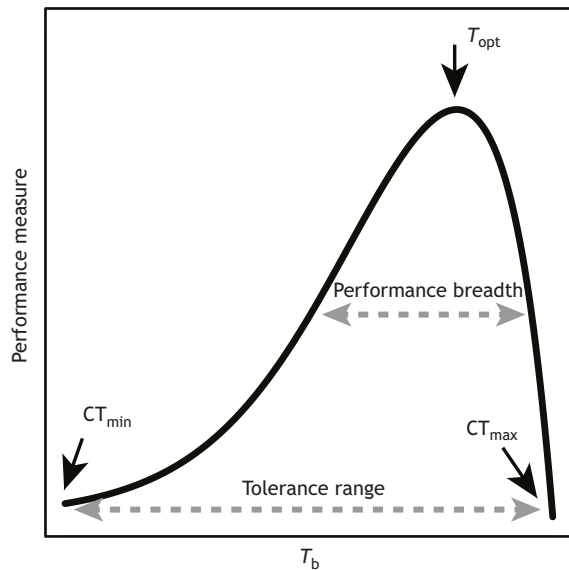


Fig. 1. Thermal performance curves in ectotherms. A hypothetical thermal performance curve (TPC) for an ectotherm (adapted from Huey and Stevenson, 1979), showing an increase in performance (often metabolic rate, and generally assumed to be correlated with fitness, but see discussion in Sinclair et al., 2016) as body temperature (T_b) increases until the optimal temperature (T_{opt}) is reached. Performance is reduced completely at temperatures below the critical minimum (CT_{min}) and above the critical maximum (CT_{max}). In most ectotherms, T_b closely follows ambient temperature (T_a); therefore, the x-axis for TPCs is often equivalent to T_a (but see Sinclair et al., 2016, and Fig. 2 for caveats).

in relation to T_b – is predominantly of interest to evolutionary biologists and physiologists (Angilletta, 2009; Angilletta et al., 2010; Lovegrove, 2012a). The second – the relationship between performance and environmental temperatures – is of greater interest for determining fitness and predicting vulnerability to changes in climate (Huey et al., 2012; Urban et al., 2016). Here, we will briefly highlight the first, but focus on the second interpretation of thermal performance in the hopes of bridging the gap between ecologists and physiologists with the goal of better modelling endotherm fitness in a rapidly changing world.

Endotherms employ not only behavioural but also a wide variety of physiological mechanisms to regulate body temperature and, compared with ectotherms, they have significantly more variable energetic and water costs. Thus, connecting temperature and performance in endotherms is no simple task (Fig. 2C; Angilletta et al., 2010; Boyles et al., 2013; McCain and King, 2014; Levesque et al., 2016; Withers et al., 2016). At present, there is no model describing the relationships among environmental temperature, T_b and fitness in endotherms that is as standardisable or as useful as TPCs have been for ectotherms (Clarke and Rothery, 2008; Angilletta et al., 2010; Huey et al., 2012). Our objective for this Commentary is therefore to discuss potential TPC analogues or proxies – a way to predict performance from environmental temperature – for endotherms to break down the conceptual links between air temperature and fitness as (outlined in Fig. 2), and to provide a potential framework for future comparative studies of endotherms.

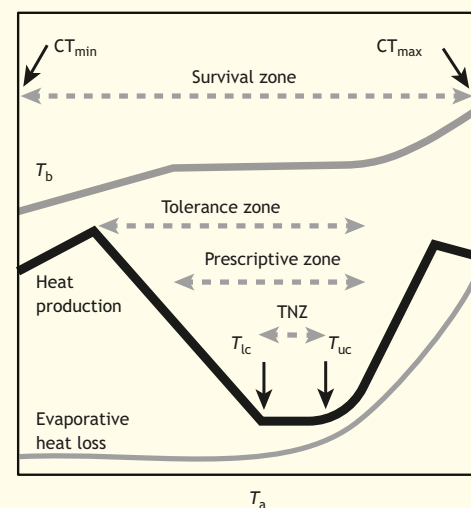
Linking air temperature to body temperature

Many comparative analyses in thermal biology aim to understand the pressures that the thermal environment places on an organism (Fig. 2A; ‘Goal of TPC approach’). The boundaries of TPCs (CT_{min}

Box 1. Scholander–Irving curves are not thermal performance curves

Using the Scholander–Irving model as an analogue for a thermal performance curve (TPC) is substantially flawed (reviewed in Mitchell et al., 2018; Boyles et al., 2019). In endotherms, the capacity to vary heat production and loss leads to a different relationship to ambient temperature compared with that of ectotherms, and species with more energy-efficient means of evaporative water loss or higher flexibility in body temperature (T_b) have different responses to high ambient temperature (T_a), which can complicate inter-specific comparisons (McKechnie et al., 2016; Smit et al., 2018; Gerson et al., 2019; McKechnie and Wolf, 2019). When attempting to draw a direct equivalent to ectotherm TPCs, some of the terms describing the thermoneutral zone (TNZ), in particular the use of ‘critical’ for lower and upper critical limit (T_{lc} and T_{uc} , respectively) are deeply misleading (see figure; Mitchell et al., 2018). The ‘critical’ limits of the TNZ refer to threshold temperatures at which metabolism, or evaporative water loss, starts to increase compared with basal rates, rather than the absolute bounds to thermal tolerance or to performance. The vast majority of small birds and mammals spend most of their lives at temperatures below their T_{lc} (Porter and Kearney, 2009; Humphries and Careau, 2011; Swanson et al., 2017), and will preferentially choose a T_a below their T_{lc} when active (Refinetti, 1998; Gordon, 2012). A large mammal, particularly one that can store large amounts of water, can survive at temperatures above their TNZ for extended periods of time, especially if they have access to water (Schmidt-Nielsen et al., 1957; Hetem et al., 2016; Boyers et al., 2019). In contrast, few ectothermic species can survive more than short bouts at T_a below their CT_{min} or above their CT_{max} . Therefore, the TNZ cannot be considered a tolerance breadth in the same way as ectothermic T_b between CT_{min} and CT_{max} (see box figure below; reviewed in Mitchell et al., 2018), yet large databases and macroanalyses continue to treat it as such (Araújo et al., 2016; Khaliq et al., 2017; Bennett et al., 2018; Sunday et al., 2019).

Perhaps most importantly, Scholander–Irving curves cannot be considered analogous to TPCs because they do not measure fitness, or even performance, nor were they ever intended to. Constrained by the techniques used to measure them, the curves apply only to a very narrow range of circumstances: that of a resting, non-reproductive, non-digesting animal under stable thermal conditions (Porter and Kearney, 2009; Rezende and Bacigalupe, 2015). An individual that persists in such a state will very likely have zero fitness. At present, there are, unfortunately, few consistent comparable measurements of the limits of thermal tolerance in endotherms. In addition to lethal temperatures, some other good measurements exist, such as temperatures at which wild dogs (*Lycaon pictus*) hunt less on warmer days (Rabaiotti and Woodroffe, 2019), or temperatures above which desert birds can no longer gain weight while foraging (du Plessis et al., 2012; Cunningham et al., 2013; Conradie et al., 2019). As the collection of these ecologically relevant values becomes more common, we encourage their inclusion in large comparative datasets rather than the relatively useless boundaries of the TNZ.



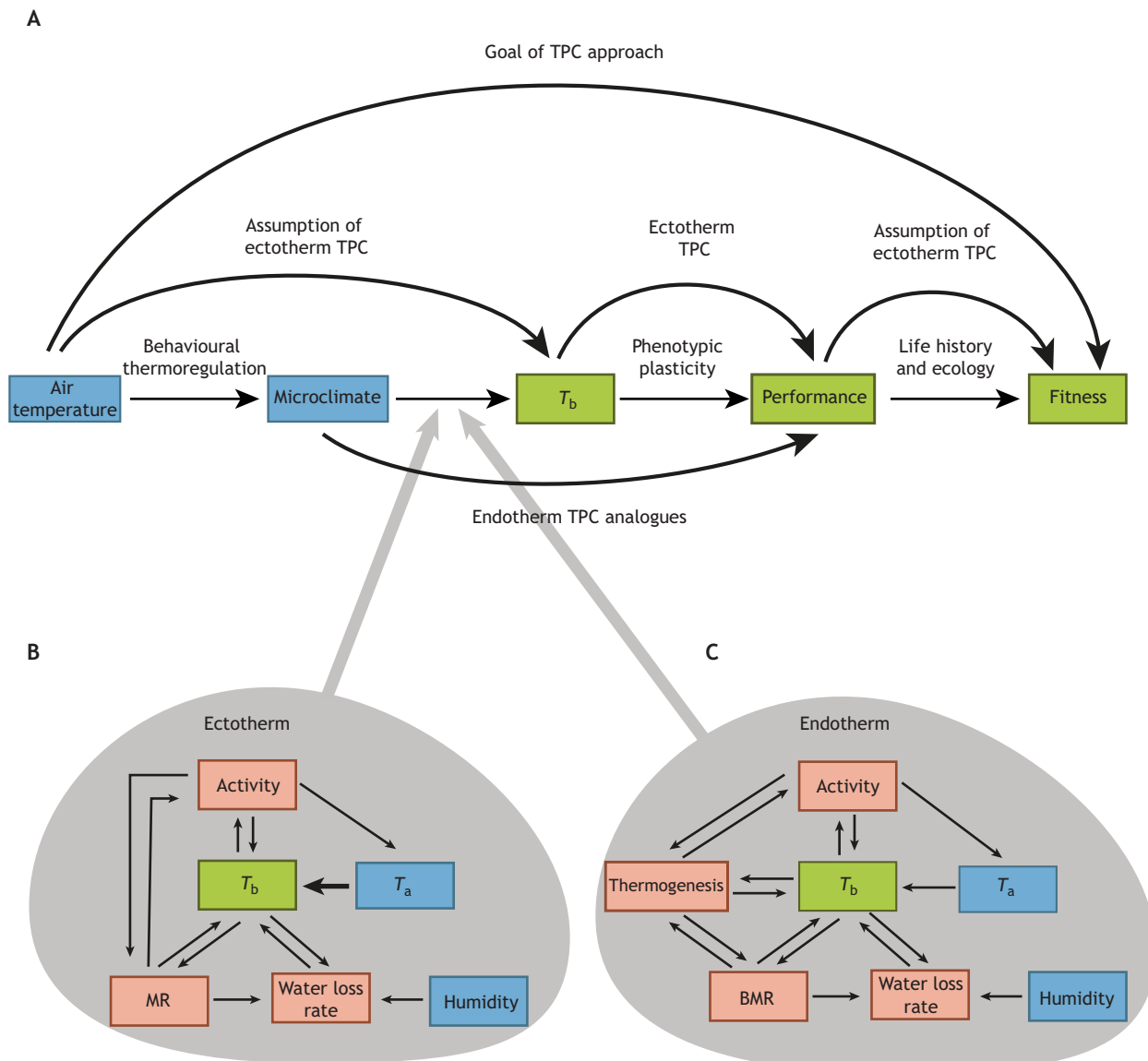


Fig. 2. Assumptions embedded in using thermal performance curves to predict fitness. (A) Comparative and predictive studies of thermal biology rely on, through a series of logical steps, relating air temperature to fitness impacts in animals. Here, we outline some of the relationships modelled by various approaches (e.g. relating air temperature to T_b), and some of the modulators of these relationships (e.g. behavioural thermoregulation). Examples are given in the text. The relationship between T_a and T_b is particularly complex, and we have briefly outlined the various feedback loops for ectotherms (B) and endotherms (C). In both ectotherms and endotherms, the relative strengths of each feedback relationship vary in a species-specific way. We have represented internal processes in red and environmental processes in blue. In general, ectotherms (B) have a relatively low rate of basal metabolism (MR, metabolic rate) which, combined with poor insulation and generally small body sizes, and therefore a low capacity to retain heat, means that they rely predominantly on behavioural means of thermoregulation with some capacity to use evaporative cooling. In contrast, endotherms (C) have relatively high basal metabolic rates (BMR), which are the result of leaky mitochondrial membranes that produce heat as a by-product. Outside of the thermoneutral zone, heat produced by BMR is supplemented by either activity or thermogenesis, the rates of which are determined by ambient temperatures. Additionally, as T_a approaches or surpasses the upper limits of thermoneutrality, either T_b increases via heat loading or it remains cool via an increase in the rate of evaporative water loss (reviewed in McKechnie and Wolf, 2019). Evaporation is, in turn, impacted by humidity, and high levels of ambient heat and activity can lead to heat stress.

and CT_{max}) are one of the most commonly used proxies for thermal tolerance in macroanalyses (Deutsch et al., 2008; Sunday et al., 2011). In its purest form, a TPC has T_b on the x -axis, yet (for the reasons mentioned above) this is of limited use in predicting effects of environmental temperature on performance. Linking air temperature (which is the most readily available environmental data) to T_b is therefore the first conceptual link that must be made when considering the effects of environmental temperature on fitness. In both ectotherms and endotherms, the relationship between air temperature (which refers specifically to temperature measured in

the shade at 2 m from the ground) and the thermal environment actually experienced by the animal (including radiation, wind speed and humidity; reviewed in Mitchell et al., 2018) must be described. In practice, this link usually comes with the assumption that behavioural thermoregulation has minimal effect in terms of both microclimate selection and the effect of the animal on microclimate temperatures. However, as the impact of behavioural thermoregulation is well appreciated in both ectotherms and endotherms (see reviews in Kearney et al., 2009; McCain and King, 2014; Abram et al., 2017; Mitchell et al., 2018), we will not belabour this point here.

The next link that must be made is the relationship between microclimate temperature and T_b . In ectotherms, this is often presumed to be completely predictable, but practically there are several feedback loops in this relationship (Fig. 2B; reviewed by Seebacher, 2009; Andrade et al., 2015), including the effects of humidity and air movement (IUPS Thermal Commission, 2003). By contrast, endotherms have a more flexible relationship between external temperatures and fitness because of their ability to manipulate internal temperatures, if there is sufficient energy intake, using varying rates of both heat production and heat loss (Fig. 2C; reviewed in Mitchell et al., 2018; McKechnie and Wolf, 2019), potentially complicating comparative approaches. As a result, complex mechanistic physiological or biophysical models such as Dynamic Energy Budget and NicheMapper have been developed to estimate the relationships between environmental temperature and performance (as outlined in Fig. 2). These models incorporate both biological and physical energy flows to model the energy and water budgets of animals under varying environmental conditions. However, there are few species for which sufficient data exists to deploy them (Fig. 2C; Kearney and Porter, 2009; Kooijman and Kooijman, 2010).

Almost all endotherms are thermal specialists (*sensu* Huey and Slatkin, 1976) as they are, for the most part, only capable of activity over a very narrow range of T_b compared with ectotherms (Angilletta et al., 2010; Boyles and Warne, 2013; Clarke, 2017; Seebacher and Little, 2017). However, it is likely, at least in mammals, that endothermy evolved via heterothermy (Crompton et al., 1978; Grigg et al., 2004; Lovegrove, 2017), and that a degree of variability in both the level and precision of T_b regulation is the norm rather than the exception in mammals. Thus, mammals may have greater thermal breadth than was first thought (Lovegrove, 2012a; Boyles et al., 2013). Whether a higher level of variability in active T_b leads to a similar drop in performance to that seen in generalist ectotherms (see Huey and Hertz, 1984) is presently unknown (Angilletta et al., 2010; Boyles and Warne, 2013). Differing degrees of T_b variability in endotherms have yet to be directly examined using the ‘generalist’ versus ‘specialist’ dichotomy that predominates the ectotherm literature, providing an interesting and promising avenue for research.

Some knowledge of both the level and precision of T_b regulation is essential for understanding the interactions between air and body temperature, as low and loose regulation comes at a much lower metabolic cost than strict homeothermy (Grigg et al., 2004; Levesque et al., 2014). As most existing T_b datasets focus on single values (generally the mean T_b) rather than the full range of T_b exhibited by an animal (Boyles et al., 2013; Clarke and O’Connor, 2014), this is an area of research that could benefit from more data collected from free-ranging endotherms across a wide range of phylogeny and zoogeography. If we know the lability of a species’ body temperature and how this lability affects performance, then these variables can be taken into account in predictive models (reviewed in Levesque et al., 2016). Such models are unlikely to look anything like a simple performance curve but may look something like the thermoregulatory polygons proposed by Rezende and Bacigalupe (2015; Fig. 3C).

Defining performance and linking it to body temperature

The notion of a ‘thermal performance curve’ requires that the y -axis presents ‘performance’. In ectotherms, this usually means a whole-animal measure such as developmental rate, running speed, reproductive output or some other measure that is readily relatable to fitness (but see Sinclair et al., 2016). The idea of a TPC for endotherms is particularly captivating because it suggests that we can build bottom-up models predicting endotherm performance from a

few physiological parameters measured in the laboratory (*sensu* Buckley et al., 2010). Yet, examples of direct measures of T_b versus performance in endotherms (with the exception of humans, e.g. Bergh and Ekblom, 1979; Sawka et al., 2012) are rare, largely because of the difficulties in manipulating T_b in a standardisable way. A handful of studies, mostly in small mammals, have been able to measure whole-body performance (in the form of righting time, running speed or the ability to pull a weight) at higher T_b with mixed results, with some showing an increase in performance at higher T_b (Seymour et al., 1998; Rojas et al., 2012; Stawski et al., 2017; Treat et al., 2018), whereas others found no difference (Wooden and Walsberg, 2004). Studies that directly measure muscle performance in relation to muscle temperature in endotherms (with the exception of studies on humans) are equally rare and have found differences according to which muscle (core versus periphery) is measured, the temperatures under which the muscles developed, as well as the species (Angilletta et al., 2010; James et al., 2015; Little and Seebacher, 2016; Rummel et al., 2018). As the data are taxonomically sparse, we currently lack large comparative studies; however, higher T_b in mammals generally correlates with faster running speed (Lovegrove, 2012b), higher basal metabolic rate (Clarke et al., 2010) and greater thermogenesis, which supports the hypothesis that muscle power scales with temperature (Clarke and Pörtner, 2010; James, 2013).

The metabolic theory of ecology (MTE) hypothesises that individual metabolic rates drive life history and ecological processes; therefore, a TPC with metabolic rate on the y -axis could link T_b and fitness (Brown et al., 2004; Clarke, 2006). However, this hypothesis has been significantly criticised in ectotherms (Price et al., 2012; Sinclair et al., 2016), and the variable control of T_b in endotherms only exacerbates the issues. In a similar vein, the search for a readily available analogue for thermal performance in endotherms that could be used in biogeographical or macroecological analyses has led to the use of parameters from species’ Scholander–Irving curves (Scholander et al., 1950b; but see Box 1) as a means to relate air temperature to performance and thermal tolerance (Araújo et al., 2013; Riek and Geiser, 2013; Khaliq et al., 2014; Fristoe et al., 2015; Buckley and Huey, 2016; Bennett et al., 2018).

Scholander–Irving curves are estimated using resting metabolic rate (RMR) measured in inactive endotherms in the lab over a range of air temperatures. The lowest RMR is equal to the basal metabolic rate (BMR) when the animal is adult, post-absorptive, awake, resting, non-torpid, drug-free and non-reproductive. The thermoneutral zone (TNZ) is defined as the temperature range where RMR is lowest, and RMR increases outside of the TNZ. RMR increases at temperatures below the lower critical limit (T_{lc}) as a result of thermogenesis (metabolic heat production). Upper critical limits (T_{uc}) are more contentious and have been variably defined as either the temperature at which evaporation increases (IUPS Thermal Commission, 2003; Withers et al., 2016) or the rate at which metabolism increases (King, 1964; Riek and Geiser, 2013; Khaliq et al., 2014). It is worth noting, however, that not all species demonstrate an increase in metabolic rate at high temperatures and only a limited number of studies measure evaporative water loss; therefore, the values for T_{uc} in most comparative datasets are, in fact, not comparable (reviewed in Wolf et al., 2017; McKechnie and Wolf, 2019; Thonis et al., 2020). Energetically neutral changes in thermal conductance (the rate at which heat is lost from the body) such as changes in posture or blood flow allow for BMR to remain stable over a range of ambient temperature (T_a) within the TNZ (Scholander et al., 1950a). All of these changes result in the emergence of a common ‘L- or U-shaped’ relationship between air temperature and metabolic rate that can be compared among species (but see Box 1).

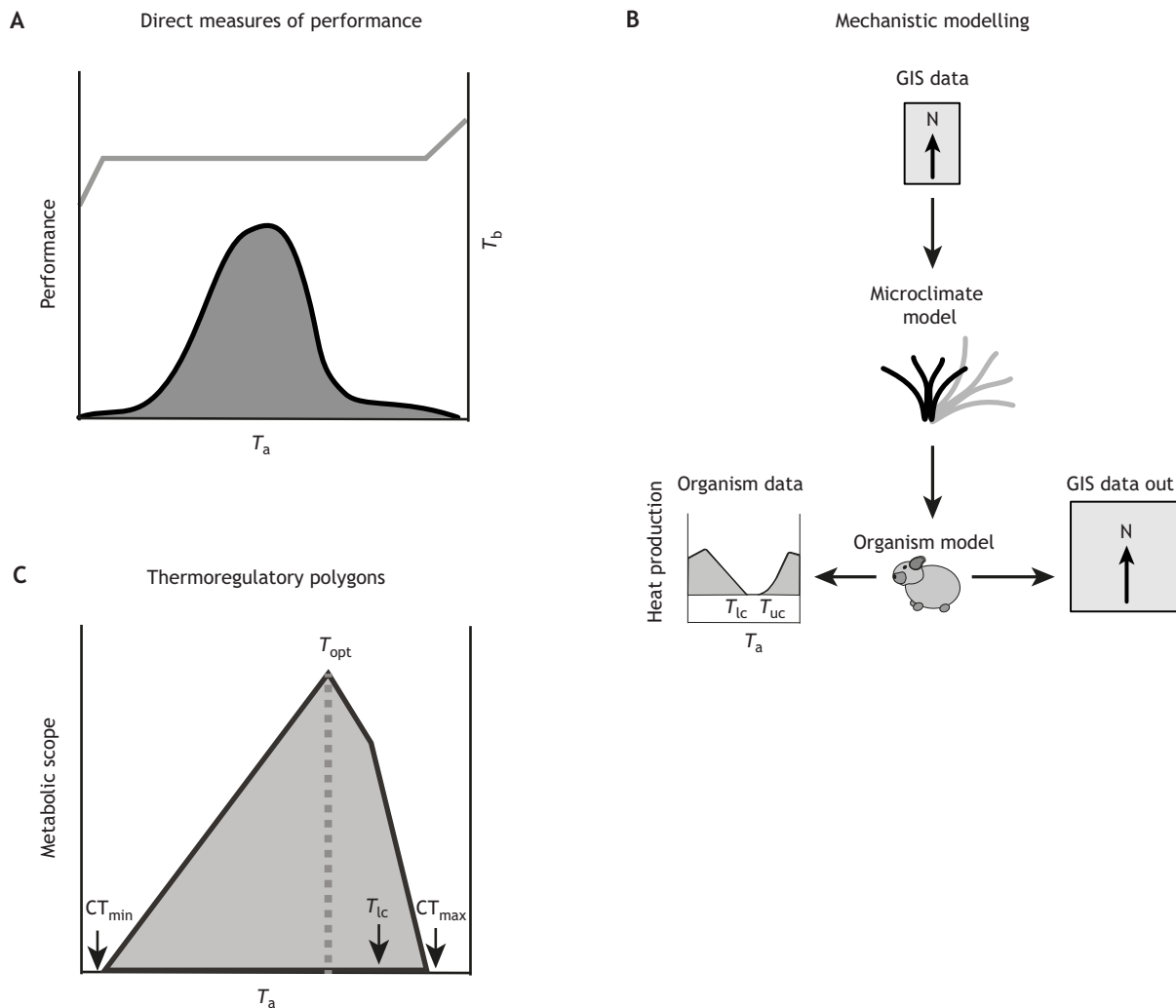


Fig. 3. Potential TPC analogues for endotherms. A few proxies for thermal performance in endotherms have been proposed. (A) Direct measures of performance: ideally, an understanding of the relationships between performance and T_a in endotherms would be obtained by directly observing performance in relation to temperature. However, as endotherms control their internal temperatures, there must always be a choice between measuring performance (e.g. strength, running speed, fitness) in relation to T_b versus performance in relation to T_a . The ability of endotherms to selectively vary the former can make 'performance' in the latter difficult to compare between species. Performance at different muscle temperatures is very difficult to assess, as it involves multiple physiological parameters and a choice between evaluating performance in relation to T_a or T_b . There has been more success in measuring performance in relation to T_a (e.g. Creel et al., 2016; Attias et al., 2018; Cooper et al., 2019; van de Ven et al., 2019), but the physiological and behavioural responses involved are often species specific. These have not been used in any comparative studies to date. (B) Mechanistic niche modelling (Kearney and Porter, 2009): niche modelling aims to incorporate mechanistic physiological traits into species distribution models which classically relied on using current geographical distributions to determine the suite of environmental variables that limit species ranges. As applied to endotherms, it includes incorporating biophysical ecology (interactions between the animal and its environment) as well as the effects of body shape and size on the fundamental niche (Porter and Kearney, 2009). These are the most useful models for predicting range shifts and responses to climate change, and they can be comparable between species. Two primary examples of niche modelling are the NicheMapper model (e.g. Kearney et al., 2010) and Dynamic Energy Budget modelling (Kooijman and Kooijman, 2010). However, these models require a large amount of physiological data and are time consuming to construct. GIS, geographic information system T_{lc} , lower critical limit; T_{uc} , upper critical limit. (C) Thermoregulatory polygons (Rezende and Bacigalupe, 2015): these expand the Scholander–Irving model to include environmental temperatures and increases in heat production due to activity. Their utility and drawbacks are similar to those of Scholander–Irving curves (see Box 1) in that they assume that T_b remains constant and that heat exchange clearly follows Newton's Laws of Cooling. They also have air temperature as the x-axis, which is potentially problematic for the reasons outlined in Fig. 2. Not used in any comparative studies to date, as data only exist for a handful of species.

If Scholander–Irving curves describe the relationship between heat production and heat loss in an endotherm at rest, can they be extrapolated to active animals? The ready answer is 'maybe', but whether the number of caveats involved allows for comparable metrics between species is debatable. The first major hurdle is that Scholander–Irving curves are mostly measured during the rest phase where, in most endotherms, metabolism and T_b are reduced significantly compared with the active phase (Aschoff, 1983; Schleucher and Prinzinger, 2006; Tattersall, 2012; van der Vinne

et al., 2015). Furthermore, important characteristics, such as the slope of thermal sensitivity of metabolic rate below the lower critical limit and the breadth of the TNZ, are largely shaped by thermal conductance, which, in turn, is determined by posture and the degree of vasoconstriction or vasodilatation, both of which change significantly with activity (Aschoff, 1981; Lovegrove et al., 1991; Rezende and Bacigalupe, 2015; van der Vinne et al., 2015). Similarly, excess heat produced during activity leads to a decrease in the temperature at which thermogenesis (at the lower limit) and

evaporative cooling (at the upper limit) occur. The limitations of using the TNZ as a proxy for thermal tolerance have recently been reviewed by Mitchell et al. (2018). They suggest expanding the classical TNZ model to include a 'prescriptive zone', a wider range of temperatures that encompasses all temperatures where a species can operate normally (forage, grow, reproduce, etc.), a 'tolerance zone', where they can survive but perhaps not for long or where they cannot reproduce, and finally a 'survival zone' bounded by the upper and lower lethal temperatures (Box 1). At present, the data needed to delineate all of these zones are largely unknown for most endotherms and, as we outline below, future efforts should focus on collecting the data needed to characterize these, as well as determining how they are linked (or not, as the case may be) to the TNZ.

Relating air temperature to fitness in endotherms

'Overall, an evaluation of vulnerability proxies for endotherms requires further investigation. Perhaps the first step is developing a full mechanistic understanding of factors that increase endotherm vulnerability to warming...'
Huey et al. (2012)

A number of potential metrics have been proposed that could serve a similar function to TPCs linking performance to air temperature (reviewed in Fig. 3). One clear example of this approach is found in the extensive literature on the effects of temperature on milk production in dairy cattle (Johnson, 1965; Fuquay, 1981; Baumgard and Rhoads, 2013). All of these metrics have their utility, as well as their drawbacks; however, we lack much of the data necessary for a comprehensive synthesis. A combination of mechanistic niche modelling (to determine performance in relation to air temperature; Fig. 3B) and direct measures of performance in relation to environmental temperatures (Fig. 3A) would be the closest direct equivalent to TPCs. The number of species from which both are available is, at present, limited to a small handful. The increased use of biologging may help to increase this number, with accelerometers providing a direct measure of activity (Chmura et al., 2018) and heart rate providing a proxy for aerobic performance (Halsey et al., 2019), as well as concurrent measures of T_b to correlate with activity levels (Menziez et al., 2020; Thompson et al., 2020). At present, there are no laboratory experiments that can serve as equally good proxies for relating environmental temperature to performance.

One alternative is to avoid the use of mechanistic models at all. For instance, top-down approaches can successfully predict lethal heat events in widely distributed endotherms such as humans. For example, using machine-learning methods, Mora et al. (2017) found that the occurrence of 'lethal heat days' (that is, days that cause significant human mortality) are related to both mean daily air temperature and mean daily relative humidity. In endotherms, it is clear that the ability to dissipate heat is key for survival at high temperatures, a process which is impaired in high-humidity conditions (Gerson et al., 2014; Withers and Cooper, 2014) and can be highly species specific (Fig. 2; reviewed in McKechnie and Wolf, 2019). A better understanding of how differing means of evaporative cooling can impact responses to high temperature is needed before predictions can be widely generalised across species.

Conclusions and the way forward

If we were to directly answer the question posed in the title, our answer would be, yes, endotherms do have TPCs, but they differ dramatically depending on what you want to use them for. Performance in relation to air temperature will be vastly different to performance in relation to T_b , and there is often no clear link between

the two. In addition to metabolic control, the central thermoregulatory system in endotherms is also closely linked to systems controlling other homeostatic functions, such as osmoregulation, biological rhythm generation (i.e. ultradian, circadian and seasonal rhythms), respiration, appetite and sleep, all which have been shown to vary considerably at both the intraspecific and interspecific level (Aschoff, 1963; Romanovsky, 2007; Williams et al., 2014; Maloney et al., 2019). However, with the notable exception of our own species, the central mechanisms underlying these functional relationships are poorly understood. Are there particular characteristics of endotherms that we can use to predict their performance in the face of changing temperatures? Does having a generalist-type T_b response curve lead to a similar generalist-type response to environmental temperatures, or are they decoupled? What, if anything, is the relationship between T_b and performance in endotherms and how dependent is it on both ecology and phylogeny? Answers to these questions could greatly improve our understanding of endothermy and our ability both to understand the past evolutionary history of endotherms and to better predict their future in a changing world.

We currently have some, but not all, of the data needed to answer these questions, and a concerted effort is needed to collect comparable data from species across a wide phylogenetic and geographical range. At what air temperatures is foraging impeded and how does microclimate availability or humidity affect this? To what degree does a greater ability to pant or sweat affect performance? Does acclimation to high temperature impede the ability to respond to cold temperatures and vice versa? These questions have been answered in individual species, but as of yet there are no easy ways to generalise the answers. Fundamentally, the way forward depends on: (1) precise definitions of 'performance' in studies (i.e. do we mean direct muscle performance or fitness?), (2) recognition and further comparative study of heterothermy in endotherms and its relationship to performance metrics, and (3) integration of the costs and benefits of T_b regulation into ecological studies of endotherms. Our ability to synthesise and draw generalities grows with the number of species for which detailed mechanistic physiological models or in-depth field studies are available. With more data, there is hope for better classifications of phenotype (e.g. activity patterns, level of heterothermy, capacity to heat or cool) that will allow for more accurate generalisations. These generalisations will then aid in refining our ability to access and predict the vulnerability of species to climate change as well as broaden our understanding of endotherm physiology in relation to environmental temperature.

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Competing interests

The authors declare no competing or financial interests.

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