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REVIEW

Lizard thermal trait variation at multiple scales: a review

Susana Clusella-Trullas · Steven L. Chown

Abstract Thermal trait variation is of fundamental importance to forecasting the impacts of environmental change on lizard diversity. Here, we review the literature for patterns of variation in traits of upper and lower sublethal temperature limits, temperature preference and active body temperature in the field, in relation to space, time and phylogeny. Through time, we focus on the direction and magnitude of trait change within days, among seasons and as a consequence of acclimation. Across space, we examine altitudinal and latitudinal patterns, incorporating inter-specific analyses at regional and global scales. This synthesis highlights the consistency or lack thereof, of thermal trait responses, the relative magnitude of change among traits and several knowledge gaps identified in the relationships examined. We suggest that physiological information is becoming essential for forecasting environmental change sensitivity of lizards by providing estimates of plasticity and evolutionary scope.

Keywords Critical thermal limits · Climate change · Diel cycles · Extremes · Macrophysiology · Phenotypic plasticity · Preferred body temperature · Rate of change

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Introduction

Reptiles are among the world's most diverse vertebrates. With *c.* 9,500 known species, the group compares well with c. 10,000 species of birds, *c.* 6,300 amphibians and *c.* 5,700 mammals (Wilson and Reeder 2005; Clements 2007; Vitt and Caldwell 2009). Most of the reptiles are lizards and snakes, which show considerable morphological diversity. For example, in body size alone the group spans some five orders of magnitude, from the dwarf chameleons (smallest *c.* 0.22 g, Meiri 2010; Glaw et al. 2012) to the Komodo Dragon (23.5 kg) (Jessop et al. 2007) (see also Meiri 2008, 2010). The majority of this species-level diversity is located in the tropics and sub-tropics (Jetz and Fine 2012). Herein lies a considerable crisis for this diverse group, which already has some 10 % of its species red listed by the IUCN (www.iucnredlist.org).

Not only are the tropics and subtropics subject to significant anthropogenic habitat change, which has major negative effects on biodiversity (Sala et al. 2000), but recent analyses have also demonstrated that climate change impacts on ectotherms are already and will continue to be profound in this region. The latter have been demonstrated by repeat population censuses and models of population responses (Pounds et al. 1999; Whitfield et al. 2007; Kearney et al. 2009; Sinervo et al. 2010) and by estimation and forecasts from macrophysiological studies (Deutsch et al. 2008; Huey et al. 2009; Dillon et al. 2010; Clusella-Trullas et al. 2011). The macrophysiological assessments have focussed on the characteristic features of thermal performance curves, which in ectotherms usually have an asymmetric, left-skewed form (Kingsolver and Huey 1998; Angilletta et al. 2006; Chown et al. 2010a). The typically linear relationship between temperature and log metabolic rate to the left of the thermal optimum, in conjunction with

assessments of temperature increases over the last 50 years, has formed the basis for the conclusion that the metabolic costs of living have increased dramatically for tropical species (Dillon et al. 2010). In the tropics and sub-tropics, small deviations between habitat temperature and either optimum temperature (i.e. the thermal safety margin) or critical thermal maximum (i.e. warming tolerance) likewise suggest that populations are close to or have exceeded conditions under which fitness is highest (Deutsch et al. 2008; Huey et al. 2009). In other words, for tropical and subtropical populations, both optima and maxima of performance are at temperatures close to those currently characteristic of several habitats, and in several areas habitat temperatures have likely exceeded these values. These impacts are not restricted to reptiles, but are being estimated or documented in other groups of both terrestrial and marine organisms, though with differences in the spatial location of likely maximum impact, especially among the terrestrial and marine species (Hoffmann 2010; Duarte et al. 2012; Nguyen et al. 2011; Richard et al. 2012; Thomas et al. 2012; Hoffmann et al. 2013; Araùjo et al. 2013).

Because the decline in performance (measured either as a physiological trait such as running speed, or a fitness-based trait, such as intrinsic rate of increase—r_{max}) to the right of the optimum is so rapid, chronic and acute increases in average and maximum temperatures, both of which are characteristic of large regions of the planet (e.g. Meehl and Tebaldi 2004; Hansen et al. 2012), are likely to have considerable impacts on lizard populations. How significant these impacts will be depends on several factors. First, impacts will likely depend on the features of the traits themselves, such as basal tolerance, phenotypic plasticity and the evolutionary potential of both (Chevin et al. 2010; Hoffmann 2010; Hoffmann and Sgrò 2011; Terblanche et al. 2011). Second, the extent to which temperature variation can be buffered by lizards via behavioural thermo-regulation (Sinervo et al. 2010; Clusella-Trullas and Chown 2011). Third, how lizards may have responded to environmental variation in the past, so giving rise to their current characteristics (e.g. little variation as a consequence either of phylogenetic inertia or similar environmental circumstances—see Labra et al. 2009; Grigg and Buckley 2013; also Cooper et al. 2011; Kellermann et al. 2012). Fourth, the ways in which other aspects of the environment, such as the extent of cloud cover, water availability and shade might influence thermal responses (Kearney et al. 2009; Clusella-Trullas et al. 2011; Kearney et al. 2013).

The four mechanisms listed above constitute the range of sensitivity of the traits and indicate the extent to which adaptation might be capable of reducing this sensitivity (Dawson et al. 2011). While exposure to changing environments, the velocity of the change and the conservation capacity of landscapes are significant determinants of the likely impacts of climate change (Loarie et al. 2009; Gillson et al. 2013), the sensitivity of populations, and how that might change over time and through space, is a key aspect of vulnerability (Dawson et al. 2011; Bellard et al. 2012). In consequence, understanding the way such sensitivity varies through space (e.g. among populations, assemblages or species—see Gaston et al. 2008; Chown et al. 2010b) and over time, as a consequence of phenotypic plasticity and evolutionary change in both tolerance and optimal performance, is essential for forecasting the future of lizard diversity. Indeed, given the likely extent of no analogue environments in the future, i.e. environments that include combinations of abiotic variables not currently found (Williams and Jackson 2007), mechanistic assessments, based on such traits, are becoming increasingly important tools for conservation decision-making (Bellard et al. 2012; Chown 2012; Higgins et al. 2012; Cooke et al. 2013; Kearney et al. 2013). Their utility derives from the fact that correlational studies, such as those underlying species distribution models, are both theoretically and empirically inappropriate outside the range and combination of variables used in correlational approaches (Araùjo et al. 2013).

Here, we, therefore, provide a review of spatial and temporal variation in the traits typically associated with thermal performance curves—notably critical thermal minimum (CT_{min}) and maximum (CT_{max}) and preferred body temperature (T_p), which is typically correlated with, but often slightly lower than, the thermal optimum (T_{opt}) for physiological performance (Angilletta et al. 2006; Martin and Huey 2008). We also include field active body temperatures because they form such a key component of recent mechanistic models (Kearney et al. 2013) and indicate how well individuals succeed at achieving T_{opt} and T_p given environmental opportunities (thermal accuracy, Hertz et al. 1993; Lutterschmidt and Reinert 2012). Our review takes both a quantitative and synthetic form. Moreover, rather than restricting our assessments to spatial and temporal variation that is typically the subject of such work (e.g. among species or among acclimation treatments), we also investigate daily and seasonal variation in traits because such variation is a key component of organismal responses to the environment (Gilchrist 1995; Angilletta et al. 2002a; Clusella-Trullas and Chown 2011). The goal here is not to be comprehensive. Indeed many thorough reviews of reptile thermal biology and its evolution exist (e.g. Angilletta 2009; Vitt and Caldwell 2009), as do a variety of general reviews of the nature of spatial and temporal physiological variation and its ecological implications (e.g. Spicer and Gaston 1999; McNab 2002; Chown and Terblanche 2007). Rather we draw on our

assessment of variation in these traits of the thermal performance curve to address two main questions. First, what is the extent of phenotypic plasticity typically seen at daily, seasonal and intermediate time scales, and is there any spatial, life history or phylogenetic pattern to this variation? Second, what is the scope of spatial variation among species in these traits? Based upon our current understanding and knowledge of reptilian physiology, how much trait diversity has been produced, insofar as physiological assessments have been made of it, and how is this diversity distributed at large spatial scales? Answers to both questions go to the heart of climate change sensitivity in lizards and its potential to be modified (i.e. adaptability in the broadest sense). For example, if there is much scope for phenotypic plasticity and/or evolutionary change in the critical thermal maximum, then vulnerability might be overestimated currently, especially if evolutionary rates are fastest in the tropics (Chown and Gaston 2000; Cornell 2013). Similarly, if particular traits are influenced not only by the habitat thermal environment, but also by other environmental characteristics, such as shading or precipitation, or by variation among the hemispheres, or as a consequence of behavioural regulation (Huey 1991), then vulnerability may be less straightforward to estimate than based solely on assessments of temperature change (Chown et al. 2004; Clusella-Trullas et al. 2011).

Variation through time

Field body temperatures

Temperature and photoperiod modulate the activity of most lizards, with activity peaks that overlap with periods in which environmental temperatures are favourable for optimal performance (e.g. Grant and Dunham 1988). Thus, activity patterns among species generally reflect unimodal or bimodal distributions depending on the region (tropics vs temperate), habitat type (dense forest vs open field) and season (summer vs winter) (Adolph and Porter 1993). Although most species thermoregulate behaviourally and physiologically to maintain optimal levels, body temperature (T_b) does follow daily rhythms and day-to-day variation of environmental temperature to an extent depending on the amount of temporal and spatial heterogeneity in temperature and resources (territories, mates, prey) and the species life-style and ecology (e.g. diurnal vs nocturnal; terrestrial vs arboreal; sit-and-wait vs wide forager; thermoregulator vs thermoconformer) (Ruibal 1961; Heatwole 1970; Cogger 1974; Clark and Kroll 1974; Huey and Pianka 1977; Huey et al. 1989; Firth and Belan 1998; Rock and Cree 2008). The strong coupling of T_b and environmental conditions indicates that T_b will also change with

the seasons. Despite compensatory mechanisms such as changes in activity times, shuttling behaviour, postural modifications and microsite selection which can buffer climate variations to some degree (e.g. Bogert 1949; Vrcibradic and Rocha 1998; Díaz and Cabezas-Díaz 2004), differences in T_b across seasons are well documented (e.g. Huey and Pianka 1977; Christian et al. 1983; Hertz 1992; Andrews 2008). In general, year-round active species tend to maintain lower T_b in winter/dry than summer/wet months in seasonal temperate and tropical zones (e.g. McGinnis 1966; Van Damme et al. 1987; Hertz 1992; Christian and Bedford 1995, 1996; Christian and Weavers 1996; Navarro-García et al. 2008). In semi-arid and desert areas, these patterns are also maintained with higher T_b during the driest and hottest periods of the year (e.g. Pianka 1971; Cogger 1974; Huey and Pianka 1977; Wilms et al. 2011). Out of 46 species for which active T_b has been monitored between winter/dry and summer/wet seasons (compiled from 30 published studies), only three species had no significant differences in active T_b between seasons. The lack of significant differences in T_b between seasons can originate from activity patterns that compensate for temperature variation between seasons or atypical climate regimes in the region or habitat investigated. These are very different alternative explanations in the context of understanding environmental responses and require further investigation, especially the extent to which microclimate selection plays a role in active T_b variation in environments that vary in different ways between the seasons (e.g. in the extent of precipitation). In species with seasonal differences, the magnitude of the seasonal effect (between summer/wet and winter/dry seasons) on active T_b averaged 3.4 ± 1.9 °C ($n = 37$ species, Fig. 1), and 3.7 ± 2.3, 3.6 ± 1.5 and 2.8 ± 2.1 °C for temperate ($n = 9$), arid (including tropical dry forests; $n = 18$) and tropical ($n = 10$) species, respectively. In consequence, behavioural adjustments cannot overcome seasonal variation in differences in operative environmental temperatures.

Over longer time scales, long-term or intergenerational monitoring of T_b in the field is rare, with the exception of comparisons made between juvenile and adult T_b (e.g. Middendorf and Simon 1988). This gap is likely due to logistical and time constraints when gathering these data. Monitoring T_b in the long term requires a dedicated and intensive programme with extended periods in the field, a year-to-year monitoring scheme and expensive radio-telemetry and/or tagging techniques. Most intergenerational and among-year studies obtain data on environmental parameters and lizard life-history variables such as reproductive output/performance, mating systems and body size (e.g. Tinkle et al. 1993; Marquis et al. 2008; Zani 2008; Olsson et al. 2011). However, prediction of the impacts of environmental change on lizard populations will
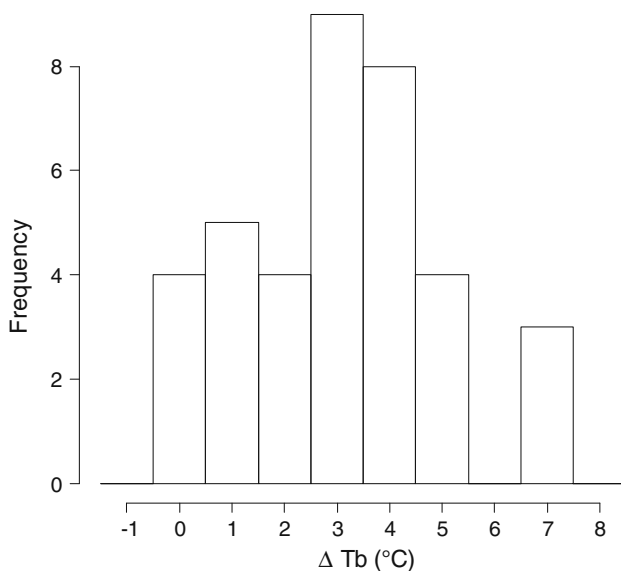
Fig. 1 Frequency distribution of differences in active body temperature (ΔT_b) between summer/wet and winter/dry seasons. $N = 37$ lizard species as not all publications provide T_b data to calculate seasonal differences

likely rely on the assessment of lizards' ability to buffer T_b with thermoregulation and of potential shifts of the thermal performance curve via plastic and evolutionary processes. It is likely that the latter can only be achieved by utilising much longer-term frameworks than those currently used.

To distinguish whether daily or seasonal differences in T_b originate from environmental variability (i.e. thermal constraints) or from shifts in thermal behaviour or physiology, such as plasticity of preferred or optimal body temperature, is not straightforward. The complexity of these relationships was recognised early on (Heath 1964; Huey and Pianka 1977). A detailed protocol used to define the accuracy and effectiveness of thermoregulation was proposed by Hertz et al. (1993) and widely used since the 1990s (e.g. Bauwens et al. 1996; Christian and Weavers 1996; Clusella-Trullas et al. 2009). The protocol includes the measurement of (1) operative temperatures (i.e. temperature of an inanimate object of zero heat capacity that matches the body size, shape and skin reflectance of the animal studied; Bakken 1992) available in the habitat which allow mapping of thermal opportunities, (2) T_b in the field and (3) preferred T_b (referred to as T_p) selected in a laboratory temperature gradient devoid of physical and biotic factors such as predation or competition (see Angilletta 2009 for a review). T_p is generally correlated with the optimal temperature of physiological performance (Dawson 1975; Bennett 1980; Stevenson 1985; Bauwens et al. 1995; but see Angilletta et al. 2002b; Martin and Huey 2008) and is key to determining the efficiency of thermoregulation and hence the focus of numerous studies on T_p ($\sim$230 published studies were compiled by Clusella-

Trullas et al. 2011). The large availability of T_p data enables the study of patterns of variation of this trait at several scales.

Preferred body temperatures

In most lizards, T_p follows diel cycles, with higher T_p found during the photophase than the scotophase. These patterns have been found in both diurnal (e.g. Rismiller and Heldmaier 1982; Sievert and Paulissen 1996; Tosini and Menaker 1996; Ellis et al. 2006) and nocturnal (e.g. Andrews and Kenney 1990; Cortes et al. 1994; Refinetti and Susalka 1997) species. Some exceptions include a lack of T_p variation in several nocturnal gecko species (Autumn and De Nardo 1995; Angilletta and Werner 1998) and the opposite pattern in a few cases. For example, Sievert and Hutchison (1988) found that the nocturnal *Gekko gecko* had higher T_p during the activity period of the scotophase than during the photophase. This pattern was also found for the diurnal *Cordylus vittifer* (Skinner 1991). In general, however, the highest T_p of diurnal lizards is found during the active phases/periods of the day, and for crepuscular species and those living in hot environments, activity periods can be restricted to the evenings or extend to the start of the scotophase (Engbretson and Hutchison 1976; Gil et al. 1994; Ellis et al. 2006).

Several studies have demonstrated that the diel cycles of behavioural thermoregulation are true circadian rhythms, i.e. these cycles remain even under constant darkness (e.g. nocturnal lizard: Refinetti and Susalka 1997; diurnal lizards: Cowgell and Underwood 1979; Innocenti et al. 1993; Tosini and Menaker 1996; Ellis et al. 2006, 2008). Mechanisms underlying circadian rhythms such as melatonin production and the role of the pineal complex for thermoregulation have been reviewed elsewhere and will not be repeated here (see Underwood 1992; Tosini 1997; Lutterschmidt et al. 2003). Diel cycles of T_p can be modified with changes in photoperiod (Spellerberg 1974; Rismiller and Heldmaier 1982; Sievert and Hutchison 1991), light treatment/position in the thermal gradient (e.g. uniform vs focus light at one side of the gradient; Sievert and Hutchison 1988, 1989, 1991) and season (Rismiller and Heldmaier 1988; Sievert and Hutchison 1989; Andrews 1994; Firth and Belan 1998; Ellis et al. 2008). For seasonal effects, it is the amplitude (maximum minus minimum T_p) of the daily rhythm that mostly differs across seasons and these differences are mostly influenced by changes in the minimum mean T_p (Firth and Belan 1998).

Most lizards in a thermal gradient voluntarily choose lower body temperatures during the scotophase despite the availability of a wide range of temperatures, possibly reflecting the need to limit energetic costs during non-active periods (Regal 1967). Among lizards that do not

hibernate and that show a diel cycle, the amplitude calculated from the mean maximum and minimum T_p in thermal gradients monitored for 24 h ranged from 1.6 °C for the scincid *Tiliqua rugosa* in the spring (Firth and Belan 1998) to 10.1 °C for *Lacerta viridis* in the fall (Rismiller and Heldmaier 1982), with an overall mean (±SD) of 6.1 ± 2.8 °C (data compiled for 12 species from 13 studies in the literature; the season with highest diurnal amplitude per species was used to calculate the overall mean when several seasons or studies where available, Fig. 2).

Although several studies have monitored T_p for several days (up to 15 days; e.g. DeWitt 1967; Hutchison and Kosh 1974; Engbretson and Hutchison 1976), few have tested for significant differences across days. In general, the extent of thermoregulation (mean and daily amplitude of T_p) for each individual is similar on successive days. For example, Angilletta et al. (1999) found that the mean T_p of five species of nocturnal geckos did not differ between two consecutive days and Clusella-Trullas et al. (2007a) found no effect of day on the T_p of cordylid lizards measured for 3 days prior and after an acclimation treatment of 7 days at 20 °C (although interaction effects of individual, time of day and day on T_p and low repeatability of T_p within and among days were found). However, variation across days may depend on the species, acclimation treatment and time scale investigated (e.g. Engbretson and Hutchison 1976),

but current data are not sufficient to detect any consistent patterns.

Several studies have investigated the effects of season on T_p. For studies that include winter and summer seasons, the majority of comparisons indicate that summer T_p estimated from active and freshly collected individuals is higher than winter T_p (e.g. Tocher 1992; Christian et al. 1998). This trend is maintained for species in tropical regions (dry winter vs wet summer seasons; e.g. Christian and Bedford 1995; Navarro-García et al. 2008) and deserts (e.g. Case 1976). Data from 11 studies and 13 species indicate that the magnitude of change in mean T_p between winter and summer varied from 0.4 (Christian et al. 1999) to 3.6 °C (Vickers et al. 2011) (Fig. 2). Although this pattern is consistent across studies, the mean T_p is in a few cases not significantly different between seasons (e.g. Baez and Cortes 1990; Christian et al. 1999). As for diurnal rhythms, the mean alone may not reflect the shape and spread of the frequency distribution of T_p selected within a season and parameters such as maximum, minimum and range of T_p might be what vary between seasons (e.g. Díaz et al. 2006). For example, Firth and Belan (1998) found little interseasonal differences in mean daily T_p but noted a significant seasonal variation of daily T_p rhythm, reflected by increased amplitude of the rhythm in late spring and summer compared to winter.
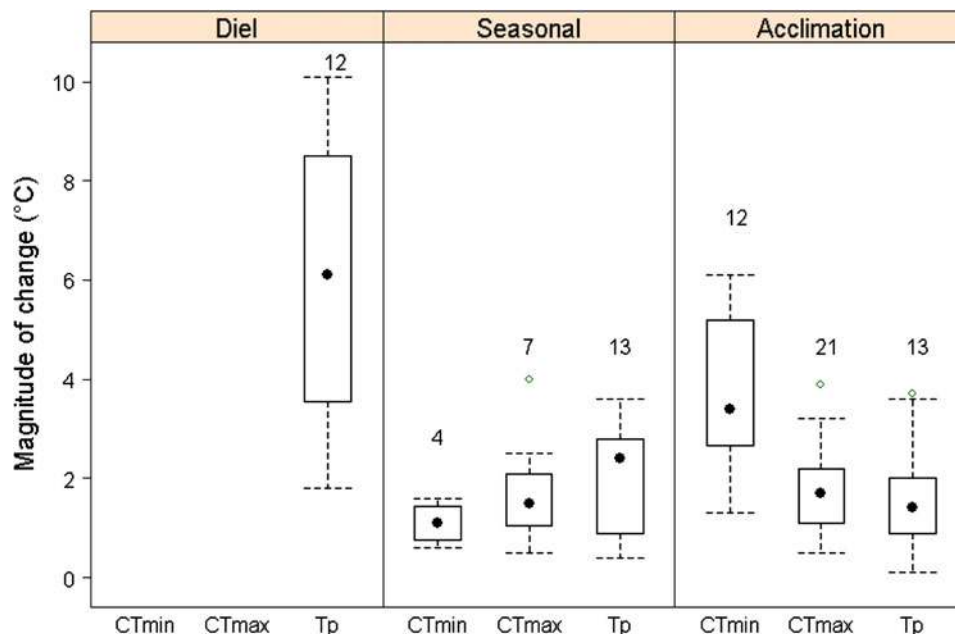

Fig. 2 Magnitude of change of critical thermal minima (CT$_{min}$), critical thermal maxima (CT$_{max}$) and preferred body temperatures (T_p) for lizard species at three temporal scales (*diel*, *seasonal* and *acclimation*). The magnitude of change was calculated as the highest difference in the trait of interest between day and night for diel effects, between summer/dry and winter/wet seasons for seasonal effects and between temperature treatments for acclimation. When several data were available for the same species, the highest magnitude of change was used. *Boxplots* provide the median (*black dot*), the 25 and 75th percentiles (*box lower* and *upper sides*) and outliers (*empty circles*). The number of species (*n*) is given above each *boxplot*. Diel data were not available for CT$_{min}$ and CT$_{max}$

Differences in T_p across seasons do not reflect constraints from the experimental environment given that T_p measurements are typically performed using the same methods and thermal gradients offer a broad range of temperatures for thermoregulation. Therefore, seasonal shifts likely reflect an acclimatization response and/or an endogenous seasonal cycle (for a review of mechanisms see Underwood 1992). Acclimatization responses may have evolved to compensate for changes in physiological state across seasons (e.g. spermiogenesis, development of ova, embryos, performance such as the temperature sensitivity of muscle contraction speed) or to lengthen activity times, reduce energetic costs and increase water conservation (e.g. Patterson and Davies 1978a, b; Van Damme et al. 1986; Christian and Bedford 1995; Díaz et al. 2006). The detailed causes and benefits of seasonal shifts in T_p are difficult to discern as several underlying mechanisms may be at play and most studies to date have been correlative. For example, gravid females of *Lacerta vivipara* select low T_p during summer, which likely favours successful embryo development while males maintain high temperatures in late summer and spring, coinciding with spermiogenesis (Patterson and Davies 1978a; Van Damme et al. 1986). Both photoperiod and temperature seem to influence T_p shifts across seasons (e.g. Rismiller and Heldmaier 1988), but additional studies are needed to establish if both factors contribute equally across taxonomic groups and at different latitudes or regions. While temperature and photoperiod are reliable parameters of seasonal cueing in temperate zones, lizards in tropical regions may use other or additional cues. Interestingly, Gundy et al. (1975) showed that lizard species that lack a parietal eye, which is thought to have a role in thermoregulatory rhythms (Underwood 1992), are restricted to low latitudes, whereas species that have a parietal eye occur in a wide range of latitudes, including high latitudes.

While seasonal changes reported above may reflect acclimatization to various environmental changes, studies that investigate acclimation effects on T_p, a form of reversible phenotypic plasticity, do so under controlled laboratory conditions that mostly expose the organism to variation in a single environmental parameter, generally temperature. Typically, the exposure to a new temperature treatment lasts several days or weeks, and, therefore, acclimation reflects a potential response to a temperature change of a shorter timeframe than an acclimatization response. Studies that investigate the effects of thermal acclimation on T_p are not common and have given mixed results. Out of ten studies, six found significant effects of thermal acclimation on T_p, and in general, mean T_p increases at higher acclimation temperatures (e.g. Kauffmann and Bennett 1989; Patterson 1991; Tocher 1992; Yang et al. 2008). However, some species select lower T_p at the highest temperature treatment, and in these cases, the exposure temperature is generally higher than the average T_p (Wilhoft and Anderson 1960; Li et al. 2009). For the 13 species investigated thus far, the maximum magnitude of change in T_p, given the acclimation treatments used in each study, ranged from 0.1 (Wheeler 1986) to 3.7 °C (Tocher 1992) (Fig. 2). If these changes are adjusted by the amount of temperature variation between acclimation treatments (i.e. the acclimation response ratio (ARR, Claussen 1977), and see also the similar 'acclimation flexibility', Levins 1969; Kingsolver and Huey 1998) and assuming a linear relationship between T_p and acclimation temperature, the mean rate of change is 0.15 ± 0.08 °C per degree acclimation (Fig. 3). Overall, the ability to acclimate in the laboratory is in line with acclimatization effects reported in the literature. However, several factors can interact with acclimation effects and its variation across studies and species. For example,

Fig. 3 Mean acclimation response ratio (ARR) for critical thermal minimum (CT$_{min}$, $n = 12$), critical thermal maximum (CT$_{max}$, $n = 21$ species) and preferred body temperature (T_p, $n = 13$). ARR reflects the differences in CT$_{max}$ relative to the difference in temperature of acclimation treatments. When several data were available for the same species, the highest magnitude of change was used. *Boxplots* provide the median (*thick horizontal line*), the 25th and 75th percentiles (*box lower and upper sides*) and outliers (*empty circles*)
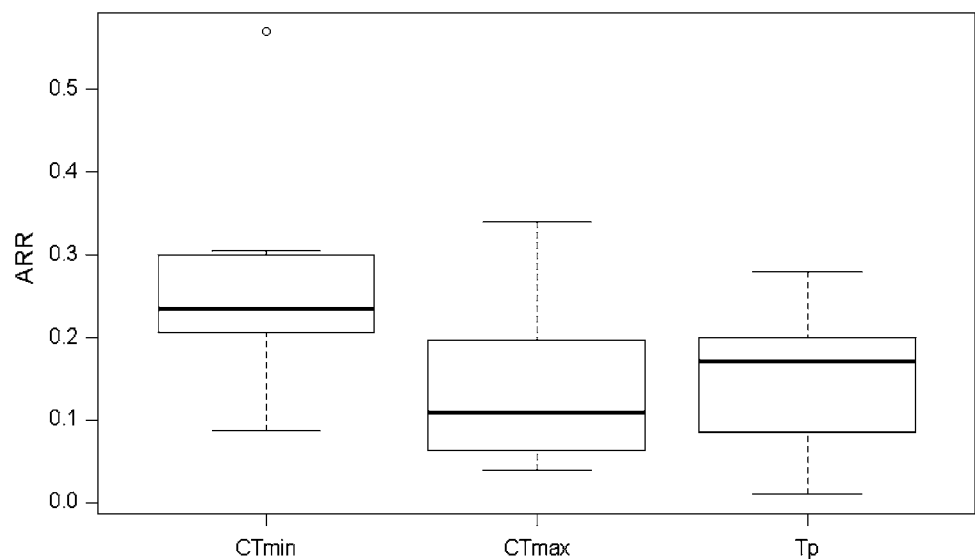
methodological differences such as the acclimation exposure duration, temperature (constant vs fluctuating regime) (Licht 1968; and see Gvoždík 2011) and photoperiod profiles (Licht 1968; Ballinger et al. 1969) and the season at time of capture may all affect the ability to acclimate. The potential effects of ontogeny/age, sex, feeding and reproductive status on the ability to acclimate T_p have been little explored, even though these factors are known to affect T_p (e.g. Regal 1966; Van Damme et al. 1986; Paulissen 1988; Rock et al. 2002). Similarly, to our knowledge, the time course of acclimation of T_p has not been investigated in lizards despite its essential role in establishing if acclimation regimes used in experimental trials or climate fluctuations in the environment are long enough to elicit an acclimatory response.

Temperature tolerance

The parameters of temperature tolerance reviewed here refer to sub-lethal temperature thresholds (such as those described by Cowles and Bogert (1944) and Lutterschmidt and Hutchison (1997)): the critical thermal maximum (CT_{max}) which is generally associated with the loss of righting response (LRR), or the onset of muscle spasms (OS) and the critical thermal minimum (CT_{min}) which corresponds to a LRR or the end-point of locomotory function. Few studies of diel effects on thermal tolerance have been undertaken on lizards, unlike for other taxonomic groups (e.g. amphibians, fish and insects; Johnson 1972, 1976; Kelty and Lee 2001). For CT_{max}, Chong et al. (1973) found that the panting threshold, the body temperature at which the mouth first opens to lower T_b via evaporative effects (Heatwole et al. 1973), fluctuated daily with lowest thresholds at night in the agamid *Amphibolorus muricatus* (heating ramping rate of 1 °C/min). However, no significant differences were found during daytime trial periods. Kosh and Hutchison (1972) demonstrated daily variation of CT_{max} (determined as the OS temperature) in *Anolis carolinensis* after several acclimation regimes that varied in photoperiodic cycle. Overall, no clear indication of a consistent effect across acclimation treatments was found, but cyclic/fluctuating thermal regimes resulted in higher CT_{max} than constant temperature regimes. For CT_{min}, a circadian rhythm was found in *Podarcis sicula* exposed to several temperature and light regimes, with the highest amplitude occurring in lizards experiencing natural variations of light and temperature compared with a light dark cycle at constant temperature or with a constant light-temperature cycle (Spellerberg and Hoffmann 1972).

Critical thermal tolerance has generally been found to change significantly across seasons. However, studies that examine seasonal acclimatization are few and most rather address the plasticity of CT_{max} and/or CT_{min} under controlled laboratory conditions (but see Tsuji 1988 for both seasonal and acclimation effects on metabolic rate and CT_{min}). For acclimatization (lizards taken from the field), both CT_{max} and CT_{min} are higher during summer than winter seasons, or during warmer months with an average increase of 1.8 ± 1.2 °C for CT_{max} ($n = 7$ spp., range = 0.5–4 °C) and 1.1 ± 0.4 °C for CT_{min} ($n = 4$, range = 0.6–1.6 °C) (Larson 1961; Ballinger et al. 1969; Spellerberg 1972a, b; Smith and Ballinger 1994; Fig. 2). For acclimation effects, the greatest magnitude of change ranges from 0.5 to 3.9 °C for CT_{max} ($n = 21$ spp., 12 studies) and from 1.3 to 6.1 °C ($n = 12$ spp., 6 studies) for CT_{min} (Fig. 2). When adjusted by the magnitude of acclimation temperature variation (ARR), the mean rate of change for CT_{max} and CT_{min} are 0.13 ± 0.08 °C and 0.26 ± 0.13 per degree acclimation, respectively (Fig. 3). These results accord with the lower flexibility of upper lethal temperature compared with lower thermal temperature in fish (Kingsolver and Huey 1998, data from Brett 1956). However, the comparison of plasticity within or among species exposed to different acclimation temperatures should be made with caution as the acclimation temperature and tolerance response may not follow a linear relationship depending on the temperature treatments used in the experiments (Fig. 4). In addition, the time course of CT_{max} acclimation may vary among species or acclimation temperatures despite typically having a hyperbolic curve (Ballinger and Schrank 1970; Art and Claussen 1982; and see Hutchison and Maness 1979 for amphibians). For example, the acclimation of CT_{max} in the lizard *Phrynosoma cornutum* maintained initially at 5 °C and then exposed to 27 °C occurred within 18 h whereas it took at least 30 h to acclimate to 40 °C (Ballinger and Schrank 1970). Art and Claussen (1982) found that CT_{max} acclimation for *Anolis carolinensis* moved from 15 to 35 °C was completed within 12 h. For CT_{min}, 10 Australian lizard species examined by Spellerberg (1972b) had similar rate of change when exposed to an acclimation temperature 1° below their mean summer CT_{min}, with a fast rate of change in the first 24 h which then plateaued over the following 10 days. Despite these few studies, further research is needed to explore the time-course of acclimation in lizards and what factors may affect the ability to acclimate (see Weldon et al. 2011 for insects).

Spatial scales

Altitude

From a total of 15 studies encompassing 23 species, field active T_b did not differ with altitude for 10 species, but these were mostly examined at high altitudes (*Liolaemus*
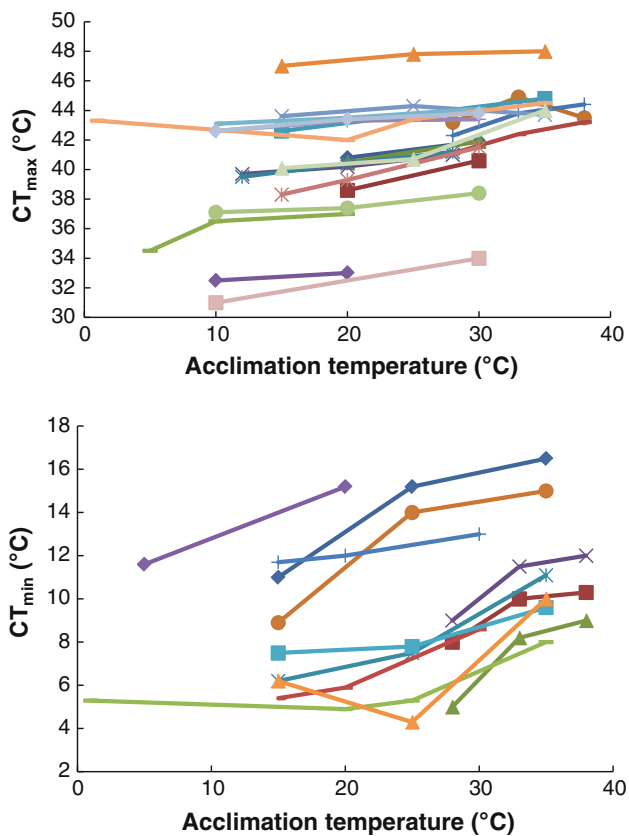
Fig. 4 Tolerance responses (CT_{max} and CT_{min}) in relation to temperature acclimation treatments for several lizard species compiled from the literature. Acclimation periods ranged from 1 to 4 weeks (mean ± SD = 2.2 ± 0.7 weeks). *Each colour* corresponds to one species (colour figure online)

characteristics such as body size and skin reflectance (Ashton and Feldman 2003; Clusella-Trullas et al. 2007b) and/or differences in thermal performance curve parameters, in particular thermal tolerance limits (see next section). In addition, patterns of T_b during inactivity and altitude (or latitude) have not been examined. For T_p measured in thermal gradients, little or no altitudinal variation has been reported (Labra 1998; Van Damme et al. 1989, 1990; Díaz 1997; Gvoždík and Castilla 2001; Gutierrez et al. 2010). The explanation for such conserved T_p across altitudes is not entirely clear and may include one or several of the following mechanisms: T_p is evolutionary conserved (i.e. responds slowly to directional selection), behaviour dampens selection on T_p (Bogert 1949; Huey et al. 2003) or 'warmer is better' scenario (selection favours a high T_p despite reductions in activity time; Angilletta 2009), high gene flow across populations prevents local adaptation (e.g. King and Lawson 1995; Lenormand 2002), and/or other mechanisms such as genetic correlations.

Studies that compare closely related species of lizards inhabiting different altitudes have found mixed support for an altitudinal effect on active T_b (Carothers et al. 1998; Andrews 2008). For example, Brattstrom (1965) reanalysed data from 10 species of *Sceloporus* lizards presented by Bogert (1949) and found that species at higher altitudes had lower active T_b. By contrast, Andrews (1998) found that there was no relationship between T_b and altitude for multiple populations and species of *Sceloporus* in temperate areas whereas a significant negative relationship was found for tropical species. This difference may have originated from species in the tropics being distributed higher in altitude and remaining active throughout the year, while in temperate areas, larger fluctuations in temperature typically shorten lizard activity periods. In addition, sampling location or latitude (and associated environmental variables such as light and climate variables) and phylogeny may confound inter-specific analyses (e.g. Clark and Kroll 1974). Studies including T_p of closely related species that occur along the same altitudinal gradient or inter-specific analyses that incorporate partitioning of variance explained by altitude in addition to geographic location and phylogeny have to our knowledge, not been undertaken.

As for T_b and T_p, the outcomes of studies examining the intra-specific effects of altitude on CT_{max} have been mixed, with slight changes in CT_{max} when found significant (mean difference is 0.3 ± 0.2 °C/100 m and ranges from 0.1 to 0.5 °C/100 m, $n = 5$ *Anolis* and 1 *Sceloporus* spp.; Hertz 1979, 1981; Hertz et al. 1979; Lemos-Espinal and Ballinger 1995; no effects found in Spellerberg 1972a; Huey and Webster 1976; Hertz and Huey 1981; Hertz and Nevo 1981; Gvoždík and Castilla 2001). Surprisingly, little has been done with regard to CT_{min} variation along altitudinal

and *Sceloporus* spp., Burns 1970; Carothers et al. 1998; Lemos-Espinal and Ballinger 1995), and field T_b decreased with altitude for the remaining species (including anoles, agamids and lacertids, e.g. Huey and Webster 1976; Van Damme et al. 1989; Waltner 1991). Therefore, most species (except for high altitude species) are not able to maintain similar active T_b along altitudinal gradients despite known thermoregulatory behaviours (habitat site selection, basking frequency, times of activity) that can raise T_b closer to operative temperatures at higher altitudes (e.g. Hertz and Huey 1981; Grant and Dunham 1990; Díaz 1997). Although most species are constrained by cold and are not able to compensate entirely for climate changes, differences in T_b across altitudes are fairly small (from the highest to lowest altitude, the mean difference is 0.6 ± 0.7 °C/100 m and ranges from 0.13 to 2.40 °C/100 m, $n = 10$ spp.) and are generally much lower than differences in operative temperatures across sites (Adolph 1990; Huey et al. 2003). In addition to behavioural compensation, physiological and genetic responses can be at play. Most often, local adaptations along an altitudinal gradient are reflected by variation in morphological

gradients (Spellerberg 1972a; Hertz and Nevo 1981; Gvoždík and Castilla 2001) and to our knowledge, no significant effects have been found to date. Inter-specific studies examining altitudinal effects suffer from the same confounding effects as per T_b and T_p. Although most studies specify the end-point used for scoring critical limits, much less attention has generally been given to differentiating between acclimatization to different altitudes versus genetic underpinnings (e.g. employing common-garden approaches).

Latitude and phylogeny

Most studies examining the relationship between field active T_b or preferred body temperature (T_p) and latitude have been undertaken inter-specifically or using closely related species, mostly because the geographical extent of a single species is limited (e.g. Medina et al. 2009). In general, there are no consistent patterns of T_b or T_p with latitude (T_b: *Sceloporus* spp. (Bogert 1949; Andrews 1998), *Chameleo* spp. (Andrews 2008), T_p: *Phymaturus* spp. (Cruz et al. 2009), *Liolaemus* spp. (Medina et al. 2009)). Clark and Kroll (1974) found a significant positive relationship between T_b of 28 anole populations (encompassing several species) and latitude (~0–30°N), while Medina et al. (2009) found a negative relationship between T_b of 55 populations of *Liolaemus* (encompassing 34 species) and latitude (~19–46°S). Using a broader taxonomic scope, Brattstrom (1965) indicated that tropical forms do not appear to have a higher T_p than temperate species while Ruibal (1961) pointed out that the distinction between heliothermic (open site and forest edge dwellers) and non-heliothermic (forest dwellers) tropical species needs to be made to explore inter-specific comparisons in tropical areas. However, most analyses to date have not included covariates that may confound examination of these patterns (e.g. basking behaviour (heliotherms vs non-basking spp.) or habitat use (forest vs open-habitat dwellers, altitude), climate variables and phylogenetic relatedness among species). An exception is the study by Huey et al. (2009) in which T_b of 70 lizard species was not related to latitude once basking behaviour and family membership were taken into account. In fact, when examined, the phylogenetic signal for field active T_b and T_p is typically strong and significant (Blomberg et al. 2003; Huey et al. 2009; Clu-sella-Trullas et al. 2011; Grigg and Buckley 2013) and in line with the general view of these traits' conservatism (Licht et al. 1966; van Damme et al. 1990). Although some variation in T_b and T_p may exist within taxonomic families, there is striking differentiation across families (see Table 1) and these phylogenetic patterns are likely associated with life-style (e.g. fossorial vs terrestrial spp., baskers vs non-baskers; Brattstrom 1965; Avery 1982;

Table 1 Variation of field active body temperature (T_b) and preferred body temperature in a thermal gradient (T_p) among families of lizards

Family	$T_b \pm$ SD	N	$T_p \pm$ SD	N
Agamidae	33.9 ± 3.5	23	35.2 ± 3.3	20
Amphisbaenidae	23.6	1	21.3 ± 0.1	2
Anguidae	27.4 ± 5.2	6	30.0	2
Anniielliidae	21	1	24.5	1
Carphodactylidae	23.4 ± 2.95	5	26.1 ± 1.6	2
Chamaeleonidae	28.0 ± 3.7	10	31.1 ± 2.4	11
Cordylidae	28.4 ± 0.9	5	32.7 ± 0.9	7
Corytophanidae	30.8 ± 4.5	3	–	–
Crotaphytidae	37.8 ± 0.3	3	33.5	1
Diplodactylidae	25.4 ± 5.1	15	31.9 ± 3.6	6
Eublepharidae	26.1 ± 2.1	5	27.0 ± 3.4	9
Gekkonidae	28.5 ± 4.9	13	29.8 ± 3.3	15
Gerrhosauridae	32.2 ± 1.9	3	–	–
Gymnophthalmidae	27.0 ± 2.6	9	–	–
Helodermatidae	29.8 ± 0.6	2	28.7	1
Iguanidae	37.5 ± 1.8	7	35.8 ± 2.6	7
Lacertidae	34.9 ± 2.9	31	34.1 ± 1.7	24
Lanthanotidae	28.0	1	–	–
Leiocephalidae	36.3	1	–	–
Liolaemidae	33.8 ± 2.4	74	34.3 ± 2.1	13
Opluridae	38.2 ± 2.2	2	–	–
Phrynosomatidae	34.9 ± 2.1	59	35.1 ± 2.2	20
Phyllodactylidae	25.7 ± 4.4	11	31.5 ± 1.9	5
Polychrotidae	29.4 ± 2.6	44	29.3 ± 2.7	10
Pygopodidae	24.9	1	–	–
Scincidae	31.4 ± 4.0	72	31.0 ± 3.3	58
Sphaerodactylidae	30.4 ± 4.2	9	–	–
Sphenodontidae	14.5	1	–	–
Teiidae	37.7 ± 2.3	36	37.0 ± 2.2	7
Trogonophidae	22.0	1	22.5	1
Tropiduridae	33.6 ± 2.7	21	34.6 ± 1.6	11
Varanidae	35.0 ± 2.7	19	35.0 ± 1.6	8
Xantusidae	23.6 ± 3.1	4	28.9 ± 2.0	3
Xenosauridae	23.0 ± 1.9	4	–	–
Mean ± SD	32.2 ± 4.8	502	32.4 ± 3.8	244
Minimum[a]	14.5		21.1	
Maximum[a]	41.6		39.8	

Mean T_b was calculated using data from references included in the supplementary materials of Sinervo et al. (2010) and T_p from Clu-sella-Trullas et al. (2011)

N number of species

[a] Minimum and maximum correspond to the min and max means of individual species means

Huey 1982; Pianka and Vitt 2003) and evolutionary conservatism (Grigg and Buckley 2013). Furthermore, the weak evidence of latitudinal patterns of T_p and T_b does not mean that environmental variation does not influence these

Table 2 Variation of critical thermal maximum (CT_{max}) and minimum (CT_{min}) among lizard taxonomic families

Family	$CT_{max} \pm$ SD	N	$CT_{min} \pm$ SD	N
Agamidae	44.9 ± 2.3	13	6.3 ± 4.3	7
Anguidae	39.7 ± 0.8	2	–	–
Anniellidae	34.0	1	–	–
Chamaeleonidae	41.8 ± 1.0	6	4.5 ± 2.0	6
Cordylidae	42.0 ± 1.9	4	8.0 ± 1.5	5
Corytophanidae	43.1	1	–	–
Crotaphytidae	46.5	1	11.6	1
Eublepharidae	42.3 ± 1.0	2	8.0 ± 0.6	2
Gekkonidae	40.8 ± 2.2	14	10.6 ± 1.7	11
Iguanidae	46.4 ± 0.7	3	14.0	1
Lacertidae	44.0 ± 1.2	21	3.5 ± 2.2	5
Liolaemidae	39.6 ± 0.4	2	5.4 ± 2.7	13
Phrynosomatidae	43.9 ± 1.7	20	8.3 ± 3.6	9
Phyllodactylidae	42.2	1	8.0	1
Polychrotidae	37.7 ± 2.3	28	11.2 ± 2.8	9
Scincidae	41.1 ± 2.9	77	6.1 ± 3.2	34
Sphaerodactylidae			8.9	1
Teiidae	47.1 ± 3.4	3	10.5	1
Varanidae	43.6 ± 0.1	2	5.0	1
Xantusiidae	38.1 ± 2.9	3	5.5 ± 1.5	2
Mean ± SD	41.6 ± 3.3	204	7.2 ± 3.6	109
Minimum[a]	33.1		1	
Maximum[a]	51		15.4	

Mean CT_{max} and CT_{min} were calculated from supplementary materials in Clusella-Trullas et al. (2011)

N number of species

[a] Minimum and maximum correspond to the min and max of individual species means

traits. Indeed, using 396 species of squamate reptiles, Clusella-Trullas et al. (2011) demonstrated that precipitation and temperature variation were the best predictors of T_p and CT_{max} across global scales, respectively, suggesting that microsite selection likely plays a larger role than mean ambient temperature (and probably latitude) in shaping performance curve parameters.

Among lizard species, the variation of CT_{max} is generally lower than that of CT_{min} across geographical regions and latitudes (although this difference is small; Hoffmann et al. 2013; Spellerberg 1972b; van Berkum 1988), perhaps due to limited evolutionary potential of CT_{max} (Kellermann et al. 2009; Grigg and Buckley 2013). Several studies have investigated the relationship between CTs and latitude. Van Berkum (1988) found that within taxonomic groups (*Anolis* spp., *Sceloporus* spp., Teiids and Xantusiids), tropical lizards had slightly lower CT_{max} and higher CT_{min} than their temperate counterparts. Huey et al. (2009) found that after adjusting the data for phylogenetic relatedness among 70 species, CT_{max} was not related to latitude but CT_{min} decreased significantly

with latitude. As for T_p and T_b, CT_{max} and CT_{min} have generally strong phylogenetic signal (Huey et al. 2009; Clusella-Trullas et al. 2011; but see Labra et al. 2009; Grigg and Buckley 2013) and life history explains at least part of the variation observed (Table 2). For example, viviparous species have lower CT_{max} and CT_{min} than oviparous ones, and basking species have higher CT_{max} than non-baskers (Ruibal 1961; Huey et al. 2009; Clusella-Trullas et al. 2011).

Synthesis and future directions

The implications of the present state of knowledge on reptile thermal biology are potentially wide-ranging of which three strike us as perhaps most significant. First are the consequences of variation in these traits for forecasting the potential impacts of habitat alterations and climate change (Kearney et al. 2009; Clusella-Trullas et al. 2011; Huey et al. 2012), which are likely to play out at both local and regional scales. Habitat alterations include changing patterns of shade and moisture availability as vegetation change proceeds, owing both to direct human modification and change in atmospheric CO_2 and fire regimes (e.g. Chown 2010; Gonzalez et al. 2010; Buitenwerf et al. 2012; Ellison et al. 2012). In addition, these traits and their patterns across known phylogenetic associations can provide much insight into the nature of evolutionary constraints, or on the other hand evolutionary potential (significance for evolutionary rescue, see, e.g. Sgrò et al. 2011; Gonzalez et al. 2012). For example, it appears that the plasticity of thermal performance curve parameters is relatively small in magnitude (Figs. 2, 3) and that these traits are phylogenetically conserved. This type of information has direct implications for predictions of adaptability and management for the conservation of sensitive species. Moreover, it is presently largely unclear what the role of phenotypic plasticity relative to evolutionary change might be (i.e. is plasticity correlated with basal trait variation). Insights into the nature of, or constraints on, these relationships are of direct value in integrating adaptability into risk assessments, relative to the rate of environmental change (e.g. Chevin et al. 2010, 2012). Perhaps the largest constraint in obtaining these insights and indeed in forecasting the likely risks of given changes to reptiles in general, is a lack of information on their heritability and genetic architecture. These are key aspects for understanding evolutionary responses (Blows and Hoffmann 2005), with genetic covariance among traits and life stages being especially significant (see, e.g. McGuigan and Blows 2010; Marshall and Morgan 2011). Nonetheless, appropriate investigations for reptiles are largely absent (but see Sinervo 1990, and related approaches by, e.g. Tsuji et al. 1989; Sorci et al. 1995; Revell et al. 2010), perhaps reflecting the difficulties
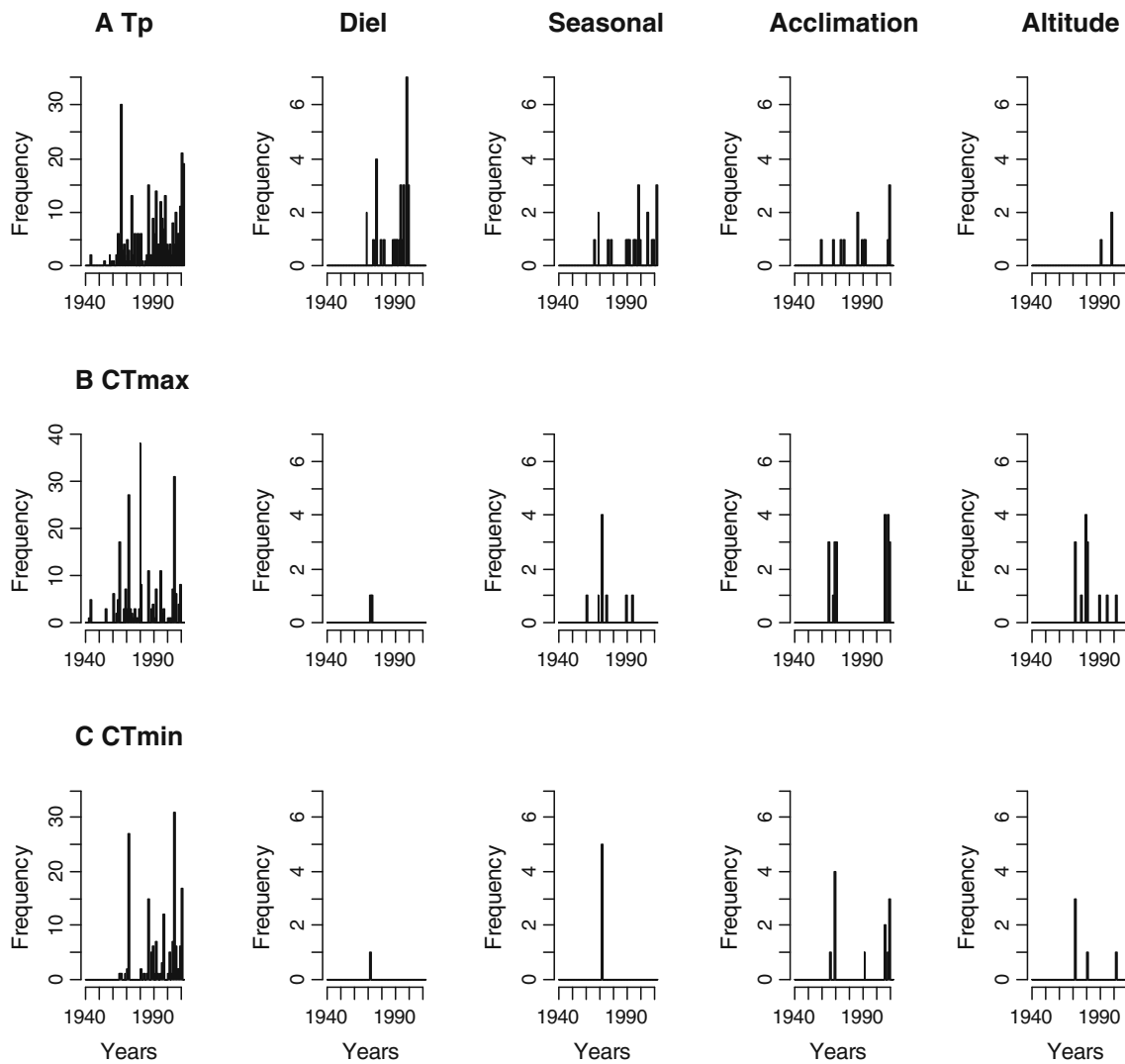
Fig. 5 Number of species examined per year for **a** preferred body temperature (T_p), **b** critical thermal maximum (CT_{max}) and **c** critical thermal minimum (CT_{min}), from 1940 to 2011. Each *panel row* includes from *left* to *right*: the frequency of species examined for the trait and for the effects of time of day, season, acclimation and altitude on this trait

associated with undertaking such work on the group, despite the significance of doing so.

Second, it is possible to consider thermal trait variation in the context of a species by sites ecological matrix type-approach to understand the evolution of trait diversity within and among species (Chown 2012). Such an approach explicitly documents spatial physiological variation within and among species and may enable a forecasting approach at the assemblage (i.e. groups of species at a given spatial location) level. It may also further the potential for exploring the impact of environmental change on diversity (Chown et al. 2010b) and on species interactions (e.g. frequency-dependent models of thermal adaptation, Mitchell and Angilletta 2009), especially if interacting species are ectotherms with competing thermal niche requirements, by explicitly incorporating the effects

of traits on abundances or occupancy. However, to be less subject to potential constraints associated with variation in experimental approaches (e.g. Terblanche et al. 2011), such a macrophysiological approach requires new investigations of a range of species and populations undertaken using the same methods. Such approaches are not yet common for reptiles, but are developing rapidly for other taxa (e.g. Kellermann et al. 2012).

Finally, it is increasingly clear that physiological information (in particular traits of thermal biology) has come to play a significant role in the conservation of reptile species (Tracy et al. 2006; Seebacher and Franklin 2012). Nonetheless, the number of studies that investigate thermal traits and their variation is minimal and has increased at a slow pace in the past 70 years (Fig. 5). Planning of conservation areas may well need to consider landscape-level thermal

opportunities and variation of thermal traits (including evolutionary change) within this landscape (Sgrò et al. 2011). This is of central importance, for example, as climates warm and risk of thermal stress increases into the future (Kearney et al. 2009). Given some of the limitations of correlative models of species distributions to predict future species' range and vulnerability, knowledge of species' thermal trait variation in time and space will be increasingly needed for integrative models that incorporate phenotypic plasticity (Chevin et al. 2010), niche requirements (Kearney et al. 2013) and evolutionary potential (Schoener 2011; Sgrò et al. 2011) to forecast population dynamics and species occurrences (Crozier and Dwyer 2006; Jankowski et al. 2013).

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