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Ecological responses of squamate reptiles to nocturnal warming

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ABSTRACT

Nocturnal temperatures are increasing at a pace exceeding diurnal temperatures in most parts of the world. The role of warmer nocturnal temperatures in animal ecology has received scant attention and most studies focus on diurnal or daily descriptors of thermal environments' temporal trends. Yet, available evidence from plant and insect studies suggests that organisms can exhibit contrasting physiological responses to diurnal and nocturnal warming. Limiting studies to diurnal trends can thus result in incomplete and misleading interpretations of the ability of species to cope with global warming. Although they are expected to be impacted by warmer nocturnal temperatures, insufficient data are available regarding the night-time ecology of vertebrate ectotherms. Here, we illustrate the complex effects of nocturnal warming on squamate reptiles, a keystone group of vertebrate ectotherms. Our review includes discussion of diurnal and nocturnal ectotherms, but we mainly focus on diurnal species for which nocturnal warming affects a period dedicated to physiological recovery, and thus may perturb activity patterns and energy balance. We first summarise the physical consequences of nocturnal warming on habitats used by squamate reptiles. Second, we describe how such changes can alter the energy balance of diurnal species. We illustrate this with empirical data from the asp viper (*Vipera aspis*) and common wall lizard (*Podarcis muralis*), two diurnal species found throughout western Europe. Third, we make use of a mechanistic approach based on an energy-balance model to draw general conclusions about the effects of nocturnal temperatures. Fourth, we examine how warmer nights may affect squamates over their lifetime, with potential consequences on individual fitness and population dynamics. We review quantitative evidence for such lifetime effects using recent data derived from a range of studies on the European common lizard (*Zootoca vivipara*). Finally, we consider the broader eco-evolutionary ramifications of nocturnal warming and highlight several research questions that require future attention. Our work emphasises the importance of considering the joint influence of diurnal and nocturnal warming on the responses of vertebrate ectotherms to climate warming.

Key words: ectotherms, energy-balance model, global warming, minimum temperature, squamates, thermal performance curve.

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I. INTRODUCTION

Over the past century, mean air temperatures have been increasing across most regions of the globe, threatening numerous species and ecosystems (Pörtner *et al.*, 2022). Yet, in many parts of the world, climate warming appears to be an asymmetrical process driven by a more rapid increase of nocturnal (T_N) than diurnal air temperatures (T_D) (Dai, Trenberth & Karl, 1999; Sun *et al.*, 2000; Vose, Easterling & Gleason, 2005; Alexander *et al.*, 2006). Despite this, most studies evaluating the impact of global warming either consider temperature increments to be constant over a 24-h cycle or focus solely on diurnal patterns (e.g. maximum daily temperature), with nocturnal warming often considered an inconsequential aspect of climate change (Speights *et al.*, 2018). Ignoring nocturnal warming is however of particular concern because the available data show that organisms can exhibit different, and sometimes opposing, eco-physiological responses to T_D and T_N (Xia *et al.*, 2009; Zhao *et al.*, 2014; Freixa *et al.*, 2017; Speights & Barton, 2019). Thus, studies that focus only on diurnal warming may provide a somewhat simplified and incomplete assessment of the vulnerability and capacity of organisms to cope with climate change (Vickerman & Sunderland, 1975; Peng *et al.*, 2013; Zhao *et al.*, 2014; Speights, Harmon & Barton, 2017; Ma, Ma & Pincebourde, 2021).

Plant ecologists have been at the forefront of investigations of the impacts of nocturnal warming on functional traits and ecological interactions of organisms. For example, in an early study, Alward, Detling & Milchunas (1999) demonstrated that warmer T_N altered the composition of plant communities of the north-eastern Colorado steppes, with a decrease of the dominant C_4 grass species in favour of exotic and native C_3 forbs. Warmer T_Ns were later shown to influence vegetation productivity (Peng *et al.*, 2013; Mu *et al.*, 2015), growth (Clark, Clark & Oberbauer, 2010; Xia *et al.*, 2018) and phenology (Wang, Luo & Shafeeque, 2019). Mechanistic responses by plants to warmer T_N are complex and operate at different levels (Sadok & Krishna Jagadish, 2020). Leaf morphology and physiology appear to play a crucial role, with warmer T_Ns leading to a reduction in leaf quality and earlier senescence, which results in higher respiration rates at night and a decline in photosynthesis-dependent processes. Ultimately, these modifications can have cascading effects on plant growth, seed production and fitness (García *et al.*, 2015; Lesjak & Calderini, 2017). Recently, entomologists have begun to investigate the effects of the diel patterns of climate change. Studies focusing on insect species have revealed heterogeneous and complex responses (i.e. neutral, positive and/or negative) to warmer T_Ns, ranging from individual physiology to community dynamics (Whitney-Johnson, Thompson & Hon, 2005; Warren & Chick, 2013;

Ma, Hoffmann & Ma, 2015; Barton, 2017; Speights *et al.*, 2017; Bai *et al.*, 2019).

The susceptibility of insects to warmer T_Ns is not surprising: ectotherms rely on external heat sources to regulate their body temperature and to maintain it within a range of temperatures that optimises performance (Angilletta *et al.*, 2002; Seebacher & Franklin, 2005; Clusella-Trullas, Blackburn & Chown, 2011). The temperature dependence of physiological performance in ectotherms is classically conceptualised as a thermal performance curve (TPC; Fig. 1). The curve describes the response of a focal performance trait [e.g. activity, metabolic rate (MR), individual growth rate, locomotion, digestion, population growth rates] to changes in body temperature. Most TPCs are assumed to follow a left-skewed bell-shaped curve: the performance increases steadily from the critical thermal minimum (CT_{min}) up to a peak value attained at the optimal body temperature (T_{opt}). Above T_{opt}, performance usually exhibits a sharp decline towards the critical thermal maximum (CT_{max}). The range between CT_{min} and CT_{max} therefore defines an organism's critical thermal range for nocturnal and diurnal activities. Given the rapid decline of performance above T_{opt}, ectotherms are highly sensitive to increases in maximum environmental temperatures as these temperatures are likely to push an organism's body temperature beyond T_{opt} and towards CT_{max} (Deutsch *et al.*, 2008; Buckley, Tewksbury & Deutsch, 2013; Rohr & Palmer, 2013; Burraco *et al.*, 2020; Clusella-Trullas *et al.*, 2021). Yet patterns of activity can also be influenced by minimum temperatures: daily or seasonal increase in T_N can push organism body temperatures towards higher values, away from their CT_{min} and therefore to within an adequate thermal range for activity. An increase in minimum temperatures can, for example, facilitate the colonisation of new habitats by offering new opportunities for foraging and hunting or by increasing intrinsic physiological rates (e.g. digestion, metabolic rates) (Battisti *et al.*, 2005). Another potential consequence is the alteration of an individual's resting thermal range: warmer minimum temperatures may trigger an increase in resting physiological rates (e.g. resting MR, cellular damage reparation rates) that could increase energy consumption (Speights *et al.*, 2017; Ma *et al.*, 2020).

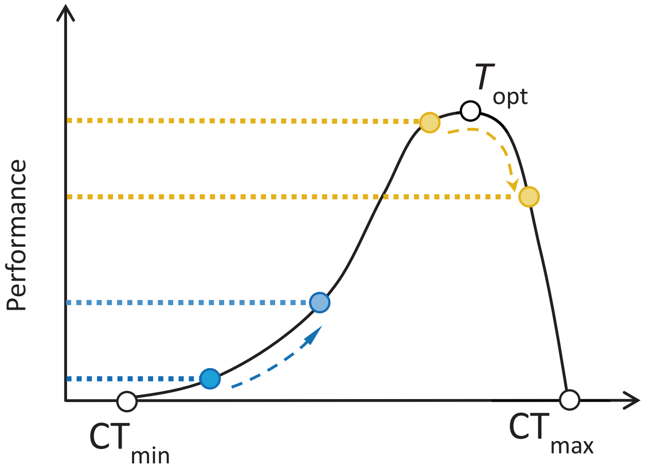

Fig. 1. Impact of warmer days and nights on individual performance. In ectotherms the temperature dependence of biological processes is conceptualised as a thermal performance curve (TPC). The curve describes the response of performance traits to changes in body temperature. Because of the left-skewed bell shape of the TPC, it is assumed that increasing temperatures near or at the critical thermal maximum (CT_{max}) have a large and negative instantaneous impact on performance (orange arrow). On the other hand, a similar increase in temperature at or near the critical thermal minimum (CT_{min}) is presumed to have a positive, but smaller, instantaneous impact on performance (blue arrow). In addition, warmer minimum temperatures during the night can push body temperature away from CT_{min} and towards the optimal body temperature (T_{opt}), hence allowing higher levels of performance. Modified from Speights *et al.* (2017).

Because research on the impact of nocturnal warming is at an early stage, our goal here is threefold. We first discuss the potential responses of vertebrate ectotherms to warmer nights. Next, we use published data, legacy data and analytical models to illustrate such responses. Finally, we propose avenues for future research studying the impact of nocturnal warming on organisms. To do so, we present a comprehensive assessment of the consequences of warmer nights on an emblematic group of vertebrate ectotherms, the order Squamata. This order includes three keystone groups (amphisbaenians, lizards and snakes) and represents the largest group of non-avian reptiles (11,549 species; Uetz *et al.*, 2023). Squamates occur in most biomes of the globe and exhibit a wide diversity of morphological, physiological, behavioural and ecological strategies (Meiri, 2018). The sensitivity of squamates to increasing maximum air temperature is well documented (Thomas *et al.*, 2004; Araújo & Rahbek, 2006; Dupoué *et al.*, 2022; Stark *et al.*, 2023; Zhang *et al.*, 2023) and one study forecasts that climate warming will lead to the extinction of almost 40% of these species by 2080 (Sinervo *et al.*, 2010). Yet little is known about the impact (positive or negative) of warmer minimum air temperatures (i.e. T_N) on this extinction rate. The well-studied group of squamates thus provides an opportunity to clarify the impacts of nocturnal warming on ectothermic vertebrates (Taylor *et al.*, 2020), and we anticipate the general conclusions drawn from our work are likely to be applicable to other taxonomic groups. Although our review discusses such impacts on both diurnal and nocturnal ectotherms (see Sections IV.2 and VI.1), we mainly focus on diurnal squamates. For diurnal species, nocturnal warming affects a period dedicated to physiological recovery, and may perturb activity patterns and energy balance in a complex manner (Fig. 2). By contrast, warmer T_N affects the primary activity period of nocturnal species and it is possible that nocturnal reptiles mainly benefit from increasing physiological performance and foraging opportunities, although there are fewer data to confirm this hypothesis.

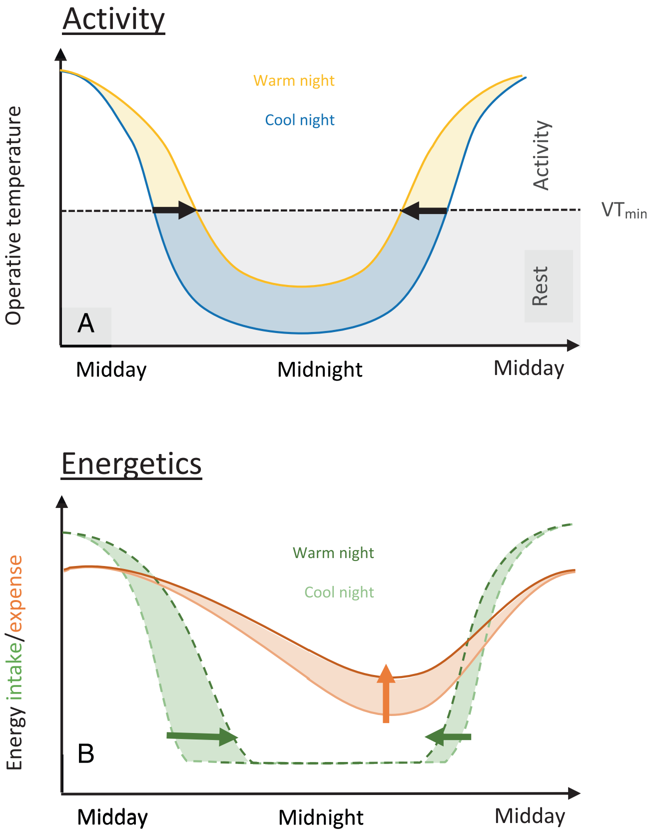

Fig. 2. Impact of warmer nocturnal temperatures on the nocturnal activity and energy budget of squamate reptiles. Warmer nocturnal temperatures are expected to modify opportunities for activity (A); as nocturnal temperatures increase, operative temperatures (*y*-axis) are likely to exceed the minimum voluntary temperature (VT_{min}) (horizontal broken line) later at night and earlier in the morning (black arrows), offering increased opportunities for foraging or physiological activity. The gain in potential activity time is represented by the yellow shaded area. This extension of activity occurs at the detriment of resting time (blue area), potentially affecting the quality of physiological recovery. From an energy budget perspective (B), compared to a cold night (pale green or pale orange), warmer nights (dark green or dark orange) may offset the balance between energy income (green lines) and metabolic expenses (orange lines). Activity extension can offer opportunities for foraging or assimilation over a larger part of the day, hence increasing the energetic intake (green shaded area). On the other hand, warmer nocturnal activity can also increase nocturnal metabolic and physiological activity, therefore raising energetic expenses over the night (orange shaded area). The overall energetic costs and benefits of warmer nocturnal temperatures will depend on the balance between these two processes.

We first discuss the physical basis of nocturnal warming and the implications of warmer nights on habitats used by squamates. Here, we emphasise the importance of legacy data to understand better the microhabitat dynamics of nocturnal warming. Second, we focus on the immediate effects of warmer nights on an individual's physiology and behaviour. In particular, we illustrate how warmer nights may change the activity window of many diurnal species while also entailing a concomitant increase in metabolic expenditure. Third, we explore the immediate energetic costs and benefits of warmer nights for a range of behavioural and foraging strategies used by ectothermic predators by extending the energy balance model of Huey & Kingsolver (2019). Fourth, we expand our discussion beyond short-term effects and consider the potential chronic implications of nocturnal warming on the physiology, life history, and population ecology of squamates. We illustrate this by synthesising extensive quantitative evidence from studies of the European common lizard (*Zootoca vivipara*) in our laboratories. Finally, we highlight the eco-evolutionary ramifications of nocturnal warming by proposing future avenues of research and emphasise the importance of considering the multifaceted aspects of climate change when studying nocturnal warming.

II. NOCTURNAL WARMING AND THE THERMAL MICROHABITATS OF SQUAMATES

(1) The asymmetry in warming between diurnal and nocturnal air temperatures

Between 1950 and 2004, T_Ns increased at a rate exceeding 1.4 times the observed change in maximum T_D on average across the world (0.204 °C vs. 0.141 °C per decade) (Karl *et al.*, 1993; Easterling *et al.*, 1997; Dai *et al.*, 1999; Vose *et al.*, 2005; Thorne *et al.*, 2016). This trend was observed over most regions of the globe (Alexander *et al.*, 2006), but is much stronger in the northern hemisphere (e.g. North America, Europe, China, Himalaya region) and Australia than in the rest of the world (e.g. India, New Zealand, parts of Africa) (Davy *et al.*, 2017; Sun *et al.*, 2018). The physical mechanisms involved in this pattern are still debated and seem to be multi-factorial. The most likely explanations include the thickening of global cloud cover (Easterling *et al.*, 1997; Dai *et al.*, 1999; Cox *et al.*, 2020), increased soil moisture and its positive effect on diurnal plant transpiration (Dai *et al.*, 1999), changes in land use due to rapid urbanisation (Small, Sloan & Nychka, 2001; Zhou *et al.*, 2009), and variation in global atmospheric circulation (Vose *et al.*, 2005) and in the planetary boundary layer thickness (Davy *et al.*, 2017). Regardless of the underlying physical reasons for the asymmetry in diel warming, this trend is expected to continue in the future. For example, the percentage of unusually warm nights recorded each year is expected to rise by 20–40% by 2100 under realistic greenhouse gas emissions scenarios (Karl *et al.*, 2008; Sillmann *et al.*, 2013).

Consequences of warmer nights are not limited to changes in air temperatures above ground. Changes in ground temperatures related to nocturnal warming have been well documented (Wu *et al.*, 2012, Shi *et al.*, 2021) and could modify the microclimatic conditions of ground shelters used by ectotherms. During the day, the organic layer of the soil (first 5 cm) intercepts solar energy that radiates to lower soil horizons (subsoil). At night, the top ground layer cools down faster than deeper ones, because of contact with cooler air temperatures. A fraction of the thermal energy accumulated in the subsoil is transferred back towards the surface, warming the top layer of the ground (Shi *et al.*, 2021). As atmospheric T_N increases due to global warming, the cooling effect from the air is reduced, without a radical change in the restoration of heat energy coming from deeper layers, which causes a disproportionate augmentation of temperature in the top soil layers. To illustrate this, field experiments using large infrared heaters suspended above the ground generated asymmetric warming patterns between daytime and night (Wu *et al.*, 2012). Minimum temperatures recorded 10 cm above the ground significantly increased from 0.65 °C to 1.33 °C (0.68 °C difference) through nocturnal warming, but were not affected by daytime warming treatments. In parallel, minimum ground temperatures significantly increased from 4.05 °C to 5.34 °C (1.29 °C difference) through the nocturnal warming treatment but, again, remained unaffected by experimental diurnal warming. Nocturnal warming at the soil surface was found to shorten significantly the development of eggs and nymphs in three grasshopper species, leading to an advance in adult emergence time by 2–6 days depending on species (Wu *et al.*, 2012).

(2) Nocturnal warming and microhabitats exploited by squamates: the value of legacy data

Squamates can be found in myriad microhabitats. They notably rely on burrows, substrate elements, canopy leaves, rock cracks, holes in trees or water to regulate their body temperature, lay their eggs, evade predators or stressful thermal conditions during their activity periods, and shelter during periods of rest and inactivity (Huey *et al.*, 1989; Goldenberg *et al.*, 2021; Mohanty *et al.*, 2022; Nordberg & McKnight, 2023). For ectotherms, appropriate selection of nesting, retreat and resting sites is key as such sites offer a variety of thermoregulatory opportunities that influence many physiological rates (e.g. developmental, metabolic and digestive rates). Alternatively, this choice may have deleterious consequences and reduce an individual's fitness if the retreat-site temperature is inappropriate (e.g. too deep or too shallow) (Huey *et al.*, 1989; Kearney, 2002; Lelièvre *et al.*, 2010; Bentley *et al.*, 2020; Chukwuka, Monks & Cree, 2020). As a consequence, the thermal quality of the habitat cannot simply be reduced to air temperature, but should rather be described by the mosaic of operative environmental temperatures (T_e, the temperature of an object with no heat capacity and resulting from both radiation and convective heat transfer) present in the environment (Bakken & Gates, 1975; Kearney, Isaac & Porter, 2014; Ma *et al.*, 2021).

Unfortunately, there are insufficient published data to provide an exhaustive description of the impact of nocturnal warming on all relevant microhabitats exploited by squamate species (e.g. ground substrates, leaf litter, boulders, rock cavities, tree trunks, branches or canopy). However, some inferences can be made from legacy data re-analysed under the prism of nocturnality (Huey, Miles & Pianka, 2021*b*). As an example, we analysed T_es originally recorded at Saguaro National Park (SNP, Arizona, USA; D. B. Miles, unpublished data) to estimate the diurnal thermal quality of the habitat exploited by the ornate tree lizard (*Urosaurus ornatus*) (see online Supporting Information, Appendix S1). This diurnal lizard species is arboreal and occupies mesquite (*Prosopis velutina*) and paloverde (*Parkinsonia aculeata*) trees. Analysis of the data shows that both the minimum T_Ns and maximum T_Ds increased over the 2001–2022 period. However, the minimum T_Ns increased faster, as indicated by the significant interaction between time (in years) and temperature parameter detected in our linear model ($F_{1,63} = 111.1$, $P < 0.005$; see Table S1 in Appendix S1) (Fig. 3). For comparison, between 2001 and 2022, minimum T_N have increased by 9.4 °C while T_Ds have increased by 5.6 °C. For *U. ornatus*, mid-late spring coincides with a critical period of reproduction: females have already mated and a clutch of eggs is developing *in utero*. Rising temperatures during this period not only have the potential to influence the phenotypic traits of hatchlings but can also impact the post-gestation state of females. We encourage re-analysis of similar historical data (Huey *et al.*, 1989; Kearney, 2002; Sabo, 2003; Lelièvre *et al.*, 2010; Gunderson *et al.*, 2019) to investigate the nocturnal thermal characteristics of other substrates and environments.

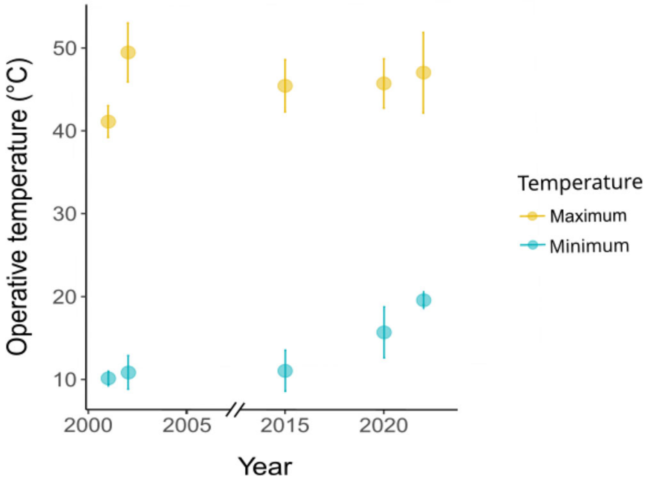

Fig. 3. Temporal pattern of diurnal and nocturnal operative temperatures recorded in mid–late spring on mesquite trees exploited by the diurnal ornate tree lizard (*Urosaurus ornatus*), in the desert of Saguaro National Park (Arizona, USA). Dots represents average minimum (blue) or average maximum (yellow) temperature recorded each year. Vertical bars represent standard deviation from the mean.

III. IMPACT OF NOCTURNAL WARMING: SHORT-TERM EFFECTS ON THE COST-TO-BENEFIT BALANCE?

(1) Increased performance and new opportunities for activity for diurnal ectotherms

At first sight, warmer nights appear beneficial for diurnal ectotherms. Based on the shape of the thermal performance curve (Fig. 1), diurnal ectotherms are expected to benefit from a passive increase in performance as warmer T_N creates a thermal environment (air or substrate) characterised by prolonged exposure to temperatures above CT_{min} (and closer to T_{opt}). For temperature-sensitive traits, such as metabolism, gut passage rate or development time, small increments in temperature can be sufficient to lead to a significant performance advantage. For example, an increase of ~1 °C in air temperature could potentially result in an 8.9% increase in metabolic expenditure of ectotherms in temperate regions (Dillon, Wang & Huey, 2010). To illustrate this passive temperature effect, we collected MR data from 65 male wall lizards (*Podarcis muralis*) at four body temperatures (30 °C, 25 °C, 20 °C and 15 °C), during both their active (day) and inactive (night) phases (see Appendix S2 for methodology). We therefore compared the resting metabolic rate (RMR) measured over the active phase with the standard metabolic rate (SMR) measured over the inactive phase, as defined in Andrews & Pough (1985). We observed lower MRs at night (i.e. SMR), regardless of air temperature (Fig. 4). We also found a positive relationship between body temperature and both RMR and SMR. The slope of this relationship was steeper for RMR (i.e. during the day) than for SMR (i.e. during the night) (see Table S2 in Appendix S2). Interestingly, we observed that despite individuals being at rest, SMR at warm T_Ns could exceed RMR recorded during the day at colder T_Ds. Further, the variance in SMR was significantly smaller than the variance in RMR at each temperature (Levene's test for homogeneity of variance; $F_{7,1594} = 221.4$, $P < 0.005$). Together, these observations confirm that, in diurnal ectotherms, increasing T_N over the resting period leads to a passive increase in physiological rates. The results also highlight a potential inability to buffer the effect of temperature on metabolic rate physiologically or behaviourally during a nocturnal period of inactivity, even where MRs are high (e.g. mean SMR at 30 °C exceeds mean RMR at 20 °C; Fig. 4).

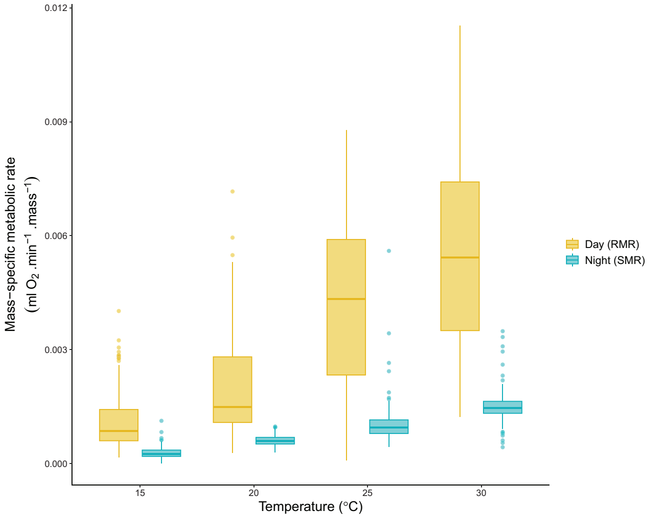

Fig. 4. Diurnal and nocturnal metabolic rates of 65 male wall lizards (*Podarcis muralis*) at four different temperatures. Resting metabolic rate (RMR) was measured three times for each individual at each temperature, at rest (no locomotor activity and in a post-prandial physiological state) during the active (diurnal) phase of the diel cycle (measurements took place between 10:00 and 16:00). Standard metabolic rate (SMR) was also measured three times for each individual at each temperature, during the inactive (nocturnal) phase of the diel cycle (measurements took place between 22:00 and 04:00). From bottom to top, horizontal lines represent the 25th percentile (Q1), the median and the 75th percentile (Q3) of each group. Vertical lines represent the minimum (Q1 − interquartile range) and maximum (Q3 + interquartile range) values. Dots represents outliers. See Appendix S2 for further details.

Another possible response of diurnal species to increased T_Ns is to extend their daily foraging activity window at dusk, dawn, and eventually over part of the night (Sperry, Ward & Weatherhead, 2013; Lara Resendiz, 2019; Levy *et al.*, 2019) (Fig. 2A). Such increased activity has been well documented in insects. For example, warmer T_Ns enhanced the opportunity for dispersal outbreaks in the pine processionary moth (*Thaumetopoea pityocampa*) in USA and Canada (Battisti *et al.*, 2005), facilitated elevational shifts in a North American ant species (*Aphaenogaster rudis*) (Warren & Chick, 2013), increased nocturnal foraging activity in different species of soil-dwelling ants (McMunn & Pepi, 2022), and augmented nocturnal hunting activity in the American nursery web spider (*Pisaurina mira*) (Barton & Schmitz, 2018) and the harlequin ladybird (*Harmonia axyridis*) (Speights & Barton, 2019). In squamates, similar patterns have been observed in ratsnakes (*Pantherophis* spp.) (Sperry *et al.*, 2013) and rock rattlesnakes (*Crotalus lepidus*) (Mata-Silva *et al.*, 2018), both diurnal species that extend their foraging activity into the night when T_Ns are favourable. Note however that, in a globally warming environment, the benefits of extension of activity into part of the night may be counterbalanced by a reduction in midday activity due to T_D exceeding CT_{max} (Vickers, Manicom & Schwarzkopf, 2011).

Together with increased foraging activity, higher physiological rates could translate into an increase in the daily opportunities for conversion or storage of energy, which may improve body growth, shorten the gestation period, and ultimately increase individual fitness (Ma *et al.*, 2020). Such positive effects of warmer nights have been documented in insects (reviewed in Ma *et al.*, 2020), where warmer T_N can reduce the development time of eggs (Wu *et al.*, 2012; Zhao *et al.*, 2014; Speights & Barton, 2019) or larvae (Whitney-Johnson *et al.*, 2005; Wu *et al.*, 2012;

Kingsolver, Higgins & Augustine, 2015). Similar results have been found for squamates, with warmer T_Ns accelerating gestation and embryonic development in lizards (Clarke & Zani, 2012; Brusch IV *et al.*, 2023) and geckos (Moore, Penniket & Cree, 2020). Warmer nights also increased hatchling size (Clarke & Zani, 2012), adult body condition (Moore *et al.*, 2020) and juvenile growth rates (Dupoué *et al.*, 2017*b*; Rutschmann *et al.*, 2021) in different squamate species.

(2) Limits to nocturnal activity for diurnal ectotherms

A key question is whether diurnal squamates always benefit from a warmer nocturnal environment, whether by switching from strict diurnal to cathemeral or nocturnal activity, or *via* an increase in their metabolic and physiological rates. Although physiological traits such as metabolic, gut passage, or assimilation rates should be faster with small increases in T_N (Dillon *et al.*, 2010), this increase in T_N might not be sufficient to initiate locomotor, foraging or hunting activities. First, even if the thermal environment becomes optimal, foraging activity at night could remain constrained by factors independent of temperature, such as higher risks of predation (Berger & Gotthard, 2008; Amadi *et al.*, 2021), or a requirement for light for visual detection of prey (Brown & Shine, 2006; Sperry *et al.*, 2013; Mukherjee & Mohan, 2022). An individual's intrinsic circadian cycle may also inhibit nocturnal activity if it is relatively inflexible (Bradshaw & Holzapfel, 2009; Tougeron & Abram, 2017; Shemesh, Cohen & Bloch, 2007; Coomans *et al.*, 2015; Krzeptowski & Hess, 2018).

Second, differences in the TPCs for different physiological traits are expected under the 'multiple performances–multiple optima' hypothesis (Huey, 1982; Clark, Sandblom & Jutfelt, 2013). Therefore, although they could increase metabolic activity, nocturnal thermal conditions may remain well below the preferred body temperature (T_{pref}) for other traits such as locomotion. T_Ns are indeed frequently lower than the thermoregulatory requirements of a species to initiate activity [i.e. voluntary minimum temperature ($\mathrm{VT}_{\mathrm{min}}$), often estimated as the 25th percentile of T_{pref}, or as the lowest recorded active body temperature when lizards first emerge from a refuge] (Kubisch *et al.*, 2016; Taylor *et al.*, 2020). For example, Kubisch *et al.* (2016) found $\mathrm{VT}_{\mathrm{min}}$ to vary from 24.6 °C to 31.3 °C in three lizard species from Patagonia. Similarly, Diele-Vegas *et al.* (2018) found $\mathrm{VT}_{\mathrm{min}}$ to vary between 19.9 °C and 32.9 °C among 27 different species of South American lizards. In both studies, the lower limit for voluntary foraging activity was quite high (*ca.* 25 °C for diurnal lizard species), hence limiting opportunities for these species to engage in foraging activities despite warm nocturnal conditions. Whether warmer nocturnal thermal conditions are sufficient to increase performance levels of all traits necessary for activity therefore will rely on an individual's thermoregulation capacities and requirements (Kearney, Shine & Porter, 2009; Vickers *et al.*, 2011). Among diurnal thermoregulators, species predominantly use heat from the sun to reach a body temperature within the range that favours performance (Angilletta, 2009; Kearney *et al.*, 2009). In the absence of solar radiation, the potential for thermoregulation is restricted to heat conduction from substrates that emit heat accumulated during the day and thus requires the use of a behavioural thermoregulation strategy based on thigmothermy rather than heliothermy (Huey *et al.*, 1989; Kearney & Predavec, 2000; Nordberg & Schwarzkopf, 2019). Despite numerous studies showing that nocturnal species are capable of exploiting such thermal opportunities (Kearney & Predavec, 2000; Vidan *et al.*, 2017), little is known about this ability in diurnal thermoregulators (see Section VI.1).

Third, the use of a favourable nocturnal thermal environment can also be constrained by diurnal activity patterns and thermoregulation preferences. For example, one field study showed that exploitation of warmer artificial shelters differed between two sympatric colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*). Such artificial shelters improved nocturnal digestion rates significantly for *H. viridiflavus* (by up to 25%) compared to *Z. longissimus* (4.4% increase) (Lelièvre *et al.*, 2010). This pattern could be explained by differences in diurnal thermal preferences between these species: *H. viridiflavus* is considered to be thermophilic, with higher preferred body temperatures (27.5–31.1 °C) relative to *Z. longissimus*. As such, *H. viridiflavus* favoured the warmer artificial refuges over natural ones during the daytime. This preferential diurnal use of artificial structures also allowed this species to benefit from warmer nocturnal conditions and therefore to increase its RMR and nocturnal digestion rate. By contrast, *Z. longissimus* favoured cooler environments (21.5–25.5 °C) and did not exploit the artificial shelters during the daytime, hence missing an opportunity to exploit a warmer nocturnal thermal habitat.

Overall, although occasional nocturnal activity (de Mesquita, Passos & Rodrigues, 2012) or prolonged switches to nocturnal and cathemeral patterns have been reported for squamates (Seifan *et al.*, 2010; Sperry *et al.*, 2013; Mata-Silva *et al.*, 2018; Lara Resendiz, 2019; Mukherjee & Mohan, 2022), there remains a need for further studies of nocturnal thermoregulation strategies of squamates and their relationship with daytime thermoregulation.

(3) Summer heatwave and nocturnal warming: a case study in a diurnal snake

To address further the impact of warm nocturnal conditions on resting body temperature and nocturnal thermoregulation, we analysed unpublished body temperature data for the asp viper (*Vipera aspis*) and T_e data from a viper biomimetic model, both collected by M. Guillon and O. Lourdais during the 2003 European mega-heatwave (Garcia-Herrera *et al.*, 2010; Russo, Sillmann & Fischer, 2015) (see Appendix S3 for details). The asp viper is a typical diurnal and heliothermic snake species. Mean ± SD T_{pref} for non-reproductive individuals is 30.6 °C ± 4.2 °C (Lorioux, Lisse & Lourdais, 2013).

At night, vipers' shelter in underground refuges to avoid predation.

During the study, 17 hot days (maximum air temperature in the shade 30°–35 °C) and 11 very hot days (>35 °C) were identified by the French national meteorological agency (Météo France; Laaïdi *et al.*, 2012) classification (Fig. 5). Daily maximum surface temperature in the enclosure (mean ± SE; 40.48 °C ± 9.27 °C) significantly influenced the minimum temperature in the refuge in the following night (19.98 °C ± 2.57 °C; ANOVA, $\beta = 0.24 \pm 0.02$, $F_{1,64} = 87.61$, $P < 0.005$; Table S3 in Appendix S3), likely due to ground thermal inertia (Rosen & Lowe, 1994). Despite extremely high operative temperatures during the daytime (Fig. 5), vipers were able to thermoregulate efficiently during the daytime: individuals avoided overheating and maintained a mean diurnal maximum body temperature of 31.8 °C ± 2.7 °C, which is very close to their T_{pref}. At night, body temperature followed closely the thermal conditions recorded in the shelters (Figs 5 and 6). Mean nocturnal body temperatures (recorded between 22:00 and 08:00) were influenced both by previous day type ($F_{2,60} = 256.95$, $P < 0.005$) and minimum shelter temperature during that night ($\beta = 0.62 \pm 0.06$, $F_{1,60} = 127.92$, $P < 0.005$; the interaction term was not significant ($F_{2,60} = 1.28$, $P = 0.28$; Table S4 in Appendix S3). Nocturnal body temperatures were higher during nights following very hot days and hot days compared to those following normal days (mean ± SE = 25.37 ± 1.14 °C and 22.42 ± 1.43 °C vs. 19.34 ± 1.51 °C, respectively). During the night, temperatures within a burrow are often warmer than temperatures at the surface (Fig. 5), allowing vipers within their overnight refuge to maintain nocturnal body temperatures sometimes exceeding the body temperature recorded for actively thermoregulating vipers during the day. This pattern was particularly pronounced during the peak of the heatwave from 1 to 12 August (Fig. 5).

Together, these observations confirm, for this heliothermic diurnal species, a 'passive' influence of nocturnal refuge conditions on body temperature. While individuals remained in their shelter we did not detect any foraging attempts (as shown by the synchrony between nocturnal body temperature and shelter temperature despite warm surface temperatures) (mean 25.97 ± 10.76 °C). Shelter use by this diurnal species may allow them to avoid predation or may result from an intrinsic circadian rhythm. It is also likely that shelter-use behaviours limit water loss and are thus important in hydroregulation, as demonstrated experimentally by Dezetter, Le Gallliard & Lourdais (2022). However, the likely increase in SMR during the warmest nights could potentially affect energy balance and lead to a loss of body condition (Zhao *et al.*, 2014; Speights *et al.*, 2017). Further, any negative impacts on body reserves during non-reproductive years in capital

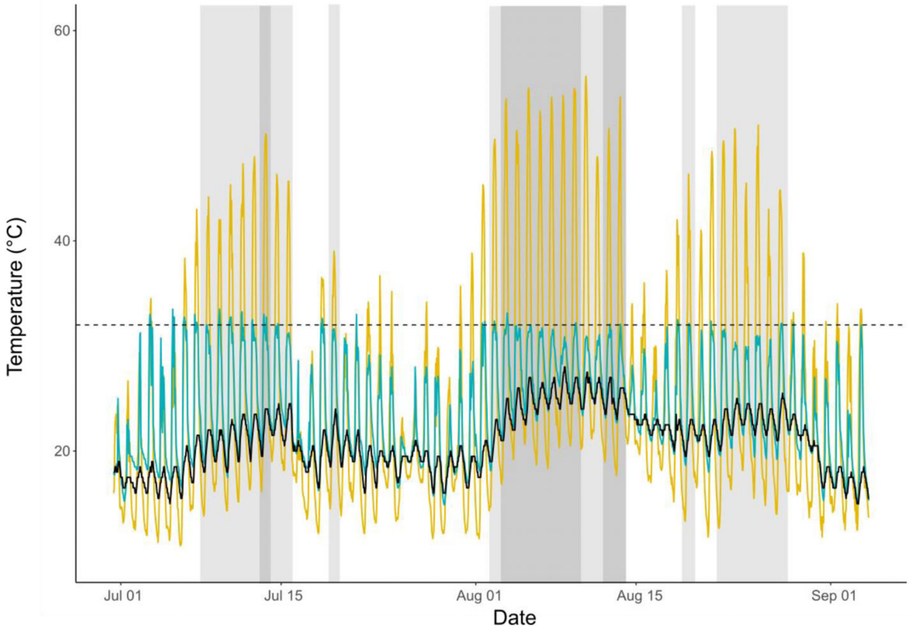

Fig. 5. Mean daily variation in body temperature in six asp vipers (*Vipera aspis*) (solid blue line) shows a close match with minimum shelter temperatures measured using biomimetic models ($N = 3$; solid black line) over the course of the night. Mean surface temperatures ($N = 3$ biomimetic models; solid yellow line) often exceeded the preferred body temperature of *V. aspis* (mean ± SD $T_{\text{pref}} = 30.63 \pm 4.22$, dashed black line; Lorioux *et al.*, 2013), highlighting the ability of this species to thermoregulate efficiently during the day while being more thermally passive in their shelter over the night. Periods of heatwaves (as defined by Météo France) are shaded in light grey (hot; $T_{\max}$ 30–35 °C) and dark grey (extremely hot; $T_{\max} > 35$ °C). Note that this classification was made at a regional level, leading to some mismatches with our data set.

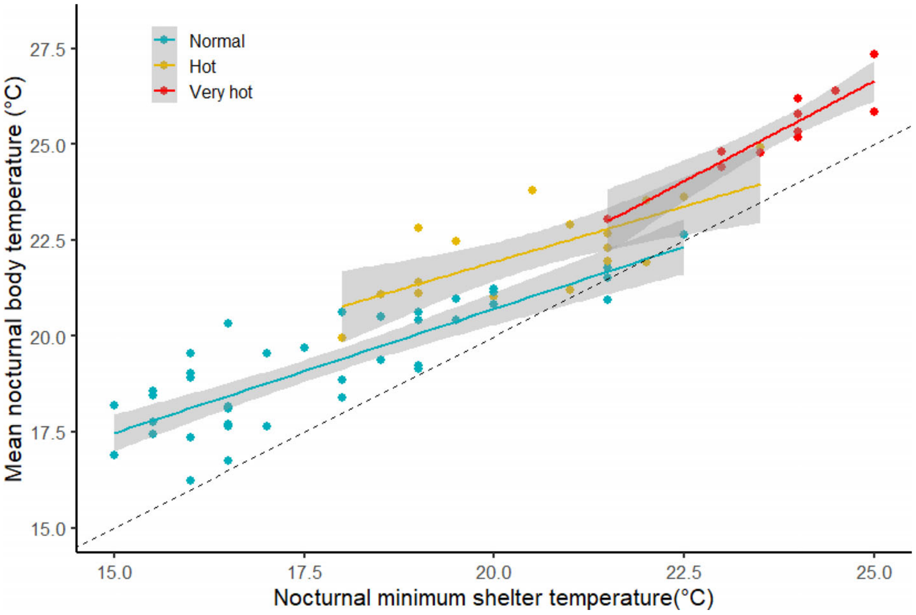

Fig. 6. Relationship between nocturnal minimum environmental temperature recorded in a shelter and mean asp viper (*Vipera aspis*) nocturnal body temperature. Nocturnal temperatures were recorded from 22:00 to 08:00. Data are plotted separately for three different categories of day according to Météo France classification: normal (maximum air temperature in the shade <30 °C; blue), hot (30–35 °C; yellow), and very hot (>35 °C; red). Solid lines represent the estimated slope and shaded regions the 95% confidence intervals. The black dashed line is $y = x$.

breeding species such as the asp viper could influence reproductive success in the following year (Lourdais *et al.*, 2002; Lourdais *et al.*, 2003; see Section VI.3).

IV. BALANCE BETWEEN COSTS AND BENEFITS: A MODELLING APPROACH

That ectotherms might be constrained in their capacity to forage at night despite warmer nocturnal conditions, themselves associated with higher SMRs, raises a second question: do warmer nights entail energetic costs that cannot be compensated by diurnal feeding activity? To answer this question and to explore the energetic costs and benefits of warmer T_Ns, we extended the energy-balance model of Huey & Kingsolver (2019) (see Appendix S4). Their original model quantifies the daily net energy gain (NEG_d) of an active, thermoconforming ectothermic predator at different environmental temperatures. Their model assumes that the net energy budget depends on energetic input from food intake and assimilation, and output from energy expenditure. By extending this model we partition an active phase [i.e. diurnal phase with positive attack rates (AR) and metabolic rates (MR)] from a resting phase (i.e. nocturnal phase with zero AR but positive MR) and disentangle the effects of warmer T_D and T_N. Note that whereas Huey & Kingsolver (2019) assumed a Type I functional response where food intake increases linearly with food density, we assume a more realistic Type II functional response (Englund *et al.*, 2011) where food intake increases with resource density at low prey availability (in proportion to AR) but saturates at high prey availability (in proportion to handling and ingestion time and satiation; see Fig. S1 in Appendix S4). Also note that we chose default parameters to match the thermal biology of an 'average' species, but our qualitative predictions should hold for different parameterisations.

(1) Model development

We provide here a brief description of our model and refer readers to Appendix S4 for a full description and the R code. The NEG_d (i.e. the energy derived from food consumption and assimilation) includes a positive input from a temperature (T)- and resource (R)-dependent functional response ($FR_{R,T}$) and a negative output (MR_T) from energy expenditure associated with basal metabolism and body maintenance. Energy input is scaled by the conversion efficiency during food assimilation α set to 69% and assumed to be independent of temperature in all simulations (Levy *et al.*, 2017). Energy output is implemented as a temperature-dependent MR (the energy expended per unit time):

$$\mathrm{NEG}_{R,T} = \alpha \times \mathrm{FR}_{R,T} - \mathrm{MR}_T \tag{1}$$

The Type II functional response ($FR_{R,T}$) is given by:

$$\mathrm{FR}_{R,T} = \frac{\mathrm{AR}_T \times R}{1 + \mathrm{AR}_T \times R/\mathrm{IR}_T} \tag{2}$$

where R denotes the resource density (arbitrarily fixed to $R = 2$ in all examples), AR_T is the temperature-dependent attack rate, and IR_T is the temperature-dependent ingestion rate. The body temperature dependence of the AR and IR were both modelled using Arrhenius-like equations as recommended by Englund *et al.* (2011). We scaled all parameters of AR and IR (see equations S6 and S7 in Appendix S4) to have a unimodal relationship with body temperature and a maximum of 1 at an optimal body temperature [T_{opt}; here, $T_{\mathrm{opt}} = 30$ °C, which is within the range of optimal temperatures for locomotion and food consumption in lizards (Clusella-Trullas & Chown, 2014)], and used empirical data from the meta-analysis of Englund *et al.* (2011) to derive parameters for these equations (see Fig. S2 in Appendix S4). We first set a default metabolic rate with a basal value of 1 at 20 °C (DMR_{20}) and assumed that it would increase exponentially with the inverse of body temperature (in °K) according to equation S10. Note that in our simulations, DMR_{20} was then set to 1, 5, 10 or 15% of the maximum energy intake at 20 °C (Andrews & Pough, 1985). At each time-step, the air temperature T was estimated using an asymmetric 24-h periodic function that provides a good description of diel cycles in above-ground air temperature (Parton & Logan, 1981) (see Fig. S3 in Appendix S4). Because our focus was on nocturnal warming, we kept maximum diurnal temperatures ($T_{\mathrm{D,max}}$) constant (40 °C) across all simulations, while varying minimum nocturnal temperatures ($T_{\mathrm{N,min}}$) from 0 to 30 °C (Fig. S3).

We computed the net energy gain for each hour (NEG_{h}), summing these over the 24-h cycle to obtain NEG_{d}. All simulations and statistical analyses were performed with R statistical software (version 3.3.2, R Development Core Team, 2023).

(2) Modelled scenarios: nocturnal temperature and thermoregulation pattern

To validate our model, we first (Scenario 0, see Appendix S4) simulated a perfect thermoconformer (i.e. an animal that spends no time or metabolic energy on behavioural thermoregulation). Unlike other scenarios, Scenario 0 was set in an environment with variations in $T_{\mathrm{D,max}}$ and in resource density, but no variations in $T_{\mathrm{N,min}}$. As in Huey & Kingsolver (2019), this model highlighted that reduced resource levels in warmer diurnal environments trigger a 'metabolic meltdown', i.e. declining energy intake paired with increased energetic expenditure and a reduced activity opportunity due to warmer diurnal maximum temperatures in the middle of the day.

We then compared five alternative scenarios to investigate the impacts of warmer nights (i.e. $T_{\mathrm{N,min}}$) on species with different thermoregulation strategies and foraging styles (Table 1). In Scenario 1, we assumed a thermoconforming ectotherm with 24 h foraging activity. This allowed us to investigate effects of minimum T_{N} in the absence of time partitioning of activity and of any behavioural control of body temperature. In Scenario 2, we extended the model to the case of a thermoconforming ectotherm with an activity cycle based on photoperiod. This organism was active during the day (07:00–20:00) and inactive over the night (21:00–06:00). To make this tractable without explicitly modelling kinematics of handling, gut passage time and assimilation of food (Levy *et al.*, 2017), we assumed that foraging behaviour (i.e. AR) was only possible between 07:00 and 20:00 (AR, IR & MR all >0); IR and MR were calculated all over the full 24-h period ($AR = 0$ while IR & MR >0). In Scenario 3, we applied the model to a perfectly thermoregulating ectotherm (i.e. a species that maintains body temperature within a range of temperatures optimal for performance) for which the activity window was possible over the 24-h daily cycle but limited by environmental temperatures. This scenario thus represents an ectothermic predator able to extend its foraging activity into the night when environmental temperatures are suitable. Here, we assumed that AR was limited by a lower (18 °C) and upper threshold (40 °C) corresponding to typical values of VT_{min} and VT_{max} for foraging in many terrestrial lizards [see Rozen-Rechels *et al.* (2020) for an example]. Moreover, as the organism was able to thermoregulate, we assumed that it could maintain a body temperature of 30 °C matching the T_{opt} for foraging whenever environmental temperatures exceeded T_{opt}. Scenario 4 illustrates the case of a perfect thermoregulator with an activity window delimited by both temperature and photoperiod. As in Scenario 2, AR was limited by daylight, while IR and MR were dependent only on body temperature. As in Scenario 3, this scenario assumes body temperature during

Table 1. Summary of the scenarios tested using our energy balance model. AR, attack rate; IR, ingestion rate; MR, metabolic rate. All rates (AR, IR and MR) were dependent on temperature. Depending on the scenario, AR was either positive throughout the 24 h diel cycle, only diurnal (positive from 07:00 to 20:00), only nocturnal (positive from 20:00 to 07:00) or constrained by a temperature window (e.g. positive when $T \geq 18$ °C and $T \leq 40$ °C). See Section IV.2 and Appendix S4 for detailed description of each scenario.

Scenario	Thermoregulation strategy	Temperature variation	AR	IR and MR
0	Thermoconforming	$T_{\mathrm{D,max}}$	24 h	24 h
1	Thermoconforming	$T_{\mathrm{N,min}}$	24 h	24 h
2	Thermoconforming	$T_{\mathrm{N,min}}$	Diurnal	24 h
3	Thermoregulating	$T_{\mathrm{N,min}}$	24 h & $T \in$ [18–40 °C]	24 h
4	Thermoregulating	$T_{\mathrm{N,min}}$	Diurnal & $T \in$ [18–40 °C]	24 h
5	Thermoregulating	$T_{\mathrm{N,min}}$	Nocturnal & $T \in$ [15–35 °C]	24 h

daytime was 30 °C whenever environmental temperatures exceeded 30 °C (i.e. efficient behavioural thermoregulation). The final scenario (Scenario 5) describes a nocturnal thermoregulator, with a foraging activity window strictly delimited to the night (20:00–07:00). For this scenario, AR was positive at night and depended on body temperature, while IR and MR depend only on body temperature. We assume the species is capable of selecting retreat sites to maintain a diurnal body temperature close to 30 °C (T_{pref}) whenever diurnal environmental temperatures exceeded 30 °C (Kearney & Predavec, 2000; Tan & Schwanz, 2015; Chukwuka *et al.*, 2021). At night, foraging activity is delimited by $\mathrm{VT}_{\mathrm{min}}$ and $\mathrm{VT}_{\mathrm{max}}$, which are fixed at 15 °C and 35 °C because those values are typically lower in nocturnal than diurnal ectotherm species.

For all scenarios (with the exception of Scenario 0), we evaluated the response of $\mathrm{NEG}_{\mathrm{d}}$ to varying minimum T_{N}s ranging from 0 to 30 °C. We also evaluated varying resting metabolic expenditure by using DMR_{20} values of 0.01, 0.05, 0.1, and 0.15 (Andrews & Pough, 1985) to allow us to characterise the effects of nocturnal warming on species with increasing resting metabolic rates.

(3) Results and conclusions

The model highlights that the consequences of nocturnal warming for an organism's daily energy budget depend on a species' thermoregulatory behaviour and activity patterns. First, the model shows that, for diurnal species, for a given foraging activity window and regardless of the thermal ecology of the species (Scenarios 1–4), a higher DMR_{20} (lower lines in blue and green on Fig. 7) involves a lower net energy gain. In natural conditions, this difference could be compensated by increased food intake provided that sufficient resources are available in the environment and until the required amount of energy exceeds the satiation point in the case of a Type II functional response (Huey & Kingsolver, 2019).

Second, in all scenarios the model has an optimal T_{N} ($T_{\mathrm{N,opt}}$) for the $\mathrm{NEG}_{\mathrm{d}}$ (Fig. 7, circles). Below this optimum, an increase of T_{N} increases $\mathrm{NEG}_{\mathrm{d}}$. Above it, $\mathrm{NEG}_{\mathrm{d}}$ decreases and, in some cases, even becomes negative (Scenario 2). Thus, whenever T_{N} exceeds the $T_{\mathrm{N,opt}}$, the concomitant increase in MR is not compensated by the AR, resulting in an energetic debt. Note that for higher DMR_{20} (and more restricted activity patterns), $T_{\mathrm{N,opt}}$ is lower. To compensate for this, we expect foraging effort to increase in ectotherms with higher energy demands when T_{N} is higher in the absence of specific constraints on nocturnal foraging activity (i.e. Scenarios 2 & 4; see Section III.2). Such a change in foraging effort driven by nocturnal warming could have important consequences on food-web dynamics (see Section VI.4) as already demonstrated by several studies on insects (Barton & Schmitz, 2018; Ma *et al.*, 2020). It is also possible that changes of DMR *via* metabolic plasticity (Norin, Malte & Clark, 2016; Sun *et al.*, 2022) would help individuals to acclimatise to warmer T_{N}. Similarly, inter-individual variation in DMR may facilitate adaptation to higher T_{N} by lowering DMR in the population through natural selection.

Third, comparing different activity patterns and thermoregulation strategies, we found that species limited only by temperature in their activity (Scenarios 1 and 3) generally performed better than species also limited by daylight (Scenarios 2 and 4), even when T_{N}s were high. This confirms the idea that ectotherms with flexible daily activity patterns should benefit (up to a certain point) from warmer T_{N}, whereas strictly diurnal species are likely to be more constrained. Furthermore, compared to thermoconformers (Scenarios 1 and 2), the ability of thermoregulators (Scenarios 3 and 4) to optimise their body temperature over a larger part of the daytime provides a buffer against the negative energetic impacts of warmer nights beyond the $T_{\mathrm{N,opt}}$ for $\mathrm{NEG}_{\mathrm{d}}$ (i.e. slopes are less negative beyond $T_{\mathrm{N,opt}}$). This is not surprising as efficient thermoregulators can maintain a higher foraging rate despite diurnal environmental temperatures exceeding T_{opt}, and can therefore reduce the cost of a higher metabolism during the warmest part of the day.

Finally, nocturnal species (Scenario 5) show the greatest relative energetic benefit from warmer nights, as illustrated by the largest amplitude of $\mathrm{NEG}_{\mathrm{d}}$ gained at warmer nocturnal temperatures compared to diurnal species (Fig. 7). From low to intermediate minimum temperatures, $\mathrm{NEG}_{\mathrm{d}}$ benefits exponentially from increased ARs with increasing temperatures. Once minimum T_{N} reaches $\mathrm{VT}_{\mathrm{min}}$, the increase in $\mathrm{NEG}_{\mathrm{d}}$ plateaus until it reaches $T_{\mathrm{N,opt}}$. There are two possible explanations for this pattern. First, foraging activity (AR) may be maximal and therefore there is no further opportunity to increase energetic income. Second, with increasing minimum T_{N} thermal conditions will exceed $\mathrm{VT}_{\mathrm{max}}$ over a larger part of the night, reducing AR and energetic income. Above $T_{\mathrm{N,opt}}$, minimum temperature exceeds $\mathrm{VT}_{\mathrm{max}}$ for the majority of the night and foraging is highly restricted, resulting in an drop in $\mathrm{NEG}_{\mathrm{d}}$. Also note that for the highest DMR_{20}, $\mathrm{NEG}_{\mathrm{d}}$ is only positive over a short range of temperature in nocturnal species. This result may be related to our parameterisation of the model where we decided not to modify the AR functions for the nocturnal species. Instead, several studies have reported higher efficiency of locomotion at low temperatures in nocturnal squamates, which would translate to a higher AR at low temperatures (Autumn *et al.*, 1999; Hare *et al.*, 2007) (see Fig. S15 in Appendix S4). Similarly, a higher MR efficiency at low temperatures is a common assumption for such species (Autumn *et al.*, 1999; Kearney & Porter, 2004). Adjusting these two characteristics could reduce $T_{\mathrm{N,opt}}$ and thereby increase the benefit of warmer nights for nocturnal species (see Scenario 5 in Appendix S4 for an illustration). Whether warmer nights will benefit all nocturnal species yet remains to be confirmed. Nocturnal ectotherms are rarely active over the entire night and temperatures below $\mathrm{VT}_{\mathrm{min}}$ also represent thermal refugia for these species (Kearney & Porter, 2004). A reduction in the time dedicated to rest and

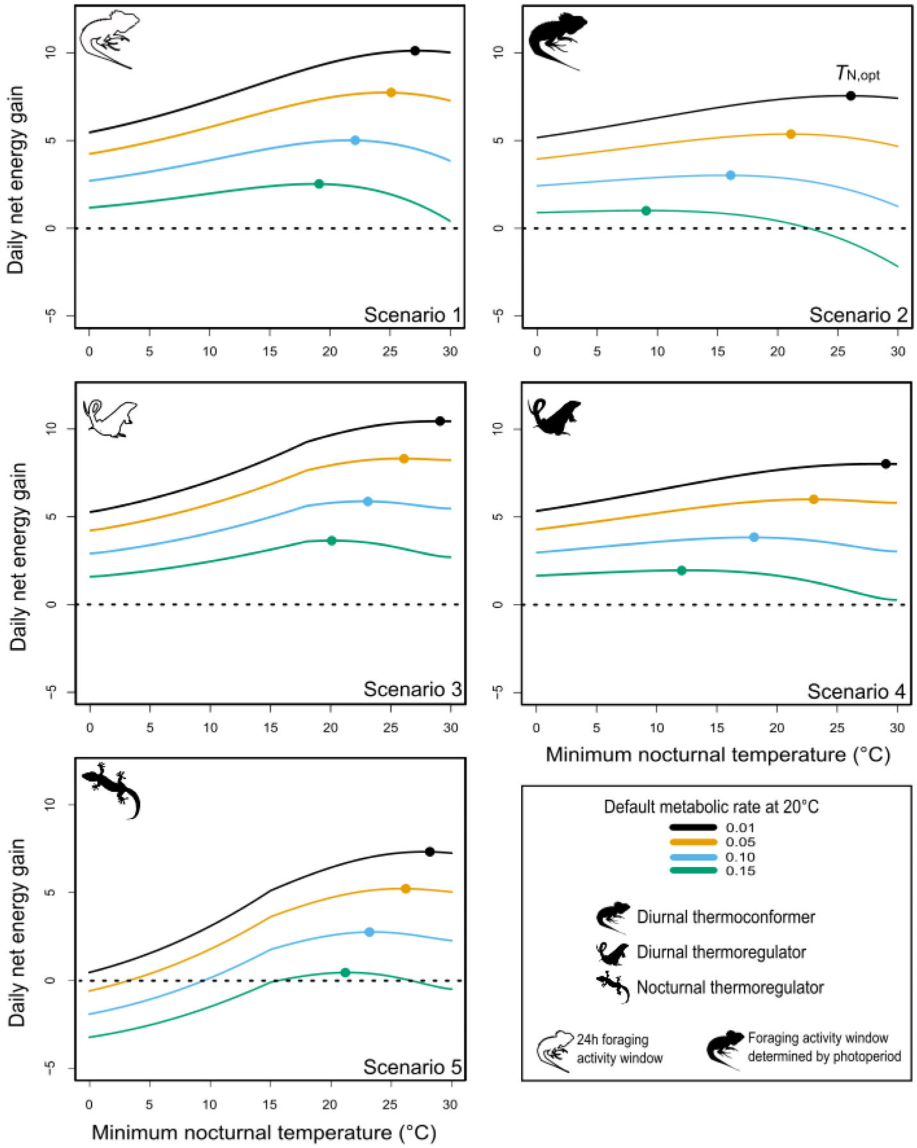

Fig. 7. Daily net energy gain (NEG$_d$) predicted by our energy budget model for different thermoregulation behaviours (thermoconformer vs. thermoregulator), ecological behaviours (diurnal vs. nocturnal) and default metabolic rates at 20 °C (DMR$_{20}$). For each increment of daily minimum nocturnal temperature tested (0–30 °C), a daily temperature cycle was created (see Fig. S3). NEG was then calculated hourly for each temperature cycle, before being integrated over 24 h to obtain one NEG$_d$ value for each minimum nocturnal temperature. Scenario 1 represents a thermoconforming ectotherm with no time constraints on activity. Scenario 2 represents a thermoconforming ectotherm with strictly diurnal foraging activity. Scenario 3 represents a thermoregulator (preferred temperature $T_{\text{pref}} = 30$ °C) with a 24 h active phase bounded by voluntary thermal limits (18–40 °C). Scenario 4 represents a perfect thermoregulator ($T_{\text{pref}} = 30$ °C), bounded by voluntary thermal limits and with a strict diurnal activity phase. Scenario 5 represents a perfect thermoregulator ($T_{\text{pref}} = 30$ °C) with a nocturnal activity phase, bounded by voluntary thermal limits (15–35 °C). The different colours represent curves for different DMR$_{20}$ values. DMR$_{20}$ is expressed as a percentage of the daily maximum energy intake, and can be interpreted as a proxy for animal size, with larger animals having a lower metabolic rate. Circles show the optimum minimum nocturnal temperature ($T_{\text{N,opt}}$) and represent a tipping point between positive and negative effects of nocturnal temperature on daily net energy gain. Pictograms indicate the ecological and thermoregulatory characteristics of the simulated ectotherms.

recovery thus could entail negative fitness effects in nocturnal ectotherms too (see Section VI.1).

Altogether, our model confirms that approaches based only on instantaneous TPCs will provide an incomplete picture, by failing to consider the temporal dynamics and trade-offs of different performances involved in maintenance, foraging, digestion and energy balance. Energetic intake and expenditure must be integrated over the entire day, and potentially over an individual's lifetime to measure the actual cost–benefit balance of warmer nights. This point has been made previously in other recent studies using TPCs to make predictions about the temperature dependence of fitness traits (Kingsolver & Woods, 2016; Sinclair *et al.*, 2016).

(4) Empirical analysis of energy balance in the European common lizard

Testing our model's predictions would require empirical data on food intake and energy balance in ectotherms at different T_Ns with different activity and foraging patterns, as well as different thermoregulation strategies. Suitable unpublished information about food intake and energy balance was recorded by Brusch IV *et al.* (2023) in an experiment designed to quantify the effects of T_N, T_D and water availability on the costs of reproduction and reproductive success in European common lizards (see Appendix S5 for details). Female common lizards use mixed income and capital breeding strategies and feed during reproduction to fuel their energy investment during mating, vitellogenesis (i.e. yolk formation) and gestation (Bleu *et al.*, 2013; Brusch IV *et al.*, 2023). In this experiment, body mass of females increased during gestation (+1.8 g during 40–60 days) due to an increase in somatic mass at the beginning of gestation and to egg growth at the end of gestation, mostly from water uptake. In addition, there was a temporal pattern in mass change with a rapid increase in body mass during the first two-thirds of gestation followed by a plateau in the last third of gestation (Brusch IV *et al.*, 2023). The average weekly mass gain of gravid females correlated positively with their weekly food intake with a food mass to body mass conversion rate of 0.31 (linear regression, $F_{1,631} = 311.6$, $P < 0.001$, $\beta \pm SE = 0.31 \pm 0.02$). The best repeated measures model describing the weekly food mass to body mass conversion revealed a positive interaction term between T_D and time ($F_{1,498} = 12.2$, $P < 0.005$; Table S5 in Appendix S5) but a negative effect of T_N ($F_{1,128} = 4.05$, $P = 0.046$, $\beta \pm SE = -0.55 \pm 0.02$), thus confirming our models' predictions of potential negative effects of night-time warming on energy balance. In addition, it was found that females had lower post-parturition body condition in hot- than in cold-night conditions (see Brusch IV *et al.*, 2023). Together, these results indicate asymmetric effects of nocturnal and daytime warming on the energy budget of a strictly diurnal species, unable to extend its activity and foraging into the night (see also Section VI.3).

V. CHRONIC EFFECTS OF NOCTURNAL WARMING

(1) Warmer nights entail delayed costs in diurnal species

In an experimental study, Zhao *et al.* (2014) demonstrated that nocturnal warming significantly enhanced the development rate of English grain aphid (*Sitobion avenae*) nymphs. However, chronic exposure to warmer T_Ns also resulted in a dramatic reduction in the survival and reproductive performance of adults, leading to a 30% decrease in population growth rate. These results highlight the importance of considering the lifetime and chronic consequences of warmer nights. To explore this in more detail, we first review different mechanisms by which warmer nights could entail long-term fitness costs, before illustrating these costs using the common lizard as a model species.

First, warmer nocturnal environments are known to affect sleep quality and therefore to compromise rest and recovery (Tougeron & Abram, 2017) (Fig. 2). During the sleep phase, metabolism usually decreases, providing an opportunity to repair cellular or tissue damage (Didomenico, Bugaisky & Lindquist, 1982) and to modulate immune responses, cognition (e.g. memory consolidation) and waste clearance (e.g. reactive oxygen species, ROS) (Sharma & Kavuru, 2010). For young individuals (e.g. neonates) sleep is also important for brain maturation and neuromuscular development in reptiles (Libourel & Herrel, 2016). In insects, warmer nights affect the central oscillator complex (i.e. a transcription–translation feedback loop of five genes regulating circadian rhythms) (Saunders *et al.*, 2002; Beck, 2012) and perturb the internal clock (Dunlap, 1999). In both cases, the end result is desynchronisation of the photo- and thermoperiod, forcing an active state when individuals are typically asleep (Kayser, Yue & Sehgal, 2014).

Examples of costs related to sleep disturbance for vertebrate ectotherms are rare in the literature. Yet, an indirect demonstration of such costs comes from studies of warming effects on the resistance of amphibians to environmental stressors such as heavy metal pollution (Hallman & Brooks, 2015) or pathogenic contamination (Neely *et al.*, 2020). In both cases, experimental reduction of T_Ns (hence, a better resting environment) significantly increased the survival potential of individuals to the stressor, especially for cold-adapted species. In other words, the higher the quantity of resources mobilised to cope with a nocturnal heat stress and the lower the resting quality, the fewer resources remained to cope with the contaminant.

Another long-term cost of warmer nights may be the accumulation of metabolic by-products resulting from nocturnal activity. In squamates, the maintenance of active metabolic rates below T_{opt} (i.e. typical scenario during warmer nights; Fig. 1) can be particularly challenging. Physiological activity at suboptimal temperatures (i.e. below the thermal performance optimum) may induce stronger oxidative stress *via* sustained mitochondrial activities and associated ROS production, while also impeding antioxidant defences and lowering repair capabilities [see Ritchie & Friesen (2022) for a review]. Eventually, chronic exposure to warmer conditions at night and the resulting oxidative stress may affect individual life-history trajectories by trading off higher investments in immediate physiological activities (and in the management of their by-products) against longevity and/or lifetime reproductive success (Monaghan, Metcalfe & Torres, 2009; Speakman *et al.*, 2015). Among the cellular mechanisms involved in such a response, oxidative stress can favour telomere erosion (i.e. the protective DNA sequences capping the end of chromosomes), accelerate aging rates and hasten senescence (Reichert, Stier & Stier, 2017; Chatelain, Drobniak & Szulkin, 2020; Burraco *et al*., 2022). To illustrate this, a recent conceptual model (i.e. the 'aging loop hypothesis') was developed from empirical evidence on the European common lizard (Dupoué *et al*., 2022). This mechanistic model investigated the effects of increasing temperatures, physiological stress and population dynamics and posited that warmer conditions during resting phases can accelerate the pace of life of a diurnal ectotherm, with deleterious effects accumulating across generations through biomarkers such as telomeric DNA, leading eventually to population collapse.

Several other short-term benefits associated with increased metabolic activity (e.g. faster growth rate, higher gut-passage rates, earlier onset of reproduction) may require trade-offs in energy allocation between maintenance, growth or reproduction and survival, ultimately imposing long-term costs that reduce an individual's fitness (see Section VI.3) (Metcalfe, Monaghan & Metcalfe, 2001; Bestion *et al*., 2015; Dupoué *et al*., 2017*b*). It is thus clear that it will only be possible to understand the impacts of nocturnal warming by integrating its effects over the entire life of an individual, rather than by focusing only on short-term positive effects (Zhao *et al*., 2014; Rutschmann *et al*., 2021).

(2) Can diurnal ectotherms mitigate the impacts of chronic nocturnal warming?

Without further empirical studies, it is difficult to evaluate to what extent long-term effects of warmer T_N will impact ectotherms in natural conditions, or whether some species have the capacity to mitigate at least some of the chronic costs associated with nocturnal warming, and thus maintain high fitness (Battisti *et al*., 2005; Clarke & Zani, 2012; Moore *et al*., 2020). One potential way to mitigate energetic costs associated with warmer nocturnal environments lies in the capacity of squamates to select cooler refugia when usual resting environments are too warm. Yet limited data are available regarding the ability of diurnal thermoregulators to extend their thermoregulatory behaviour overnight. A common assumption is that such capacities are limited, because T_Ns are uniformly low among thermal refugia, i.e. natural selection operating on nocturnal thermoregulation (which depends on the spatial thermal heterogeneity of retreat sites) is likely to be weak for diurnal species (Huey *et al*., 2021*a*). Recent studies have reported previously undocumented nocturnal basking activity for tropical crocodilians and turtles (McKnight *et al*., 2023; Nordberg & McKnight, 2023). While individuals normally rest in water at night, occurrences of terrestrial nocturnal basking were recorded in nights with high water surface temperatures. One hypothesis is that air temperatures offer a cool thermal refuge from waters exceeding T_{pref} (e.g. >30 °C). Such nocturnal basking behaviour was however seen in only 13 of the 29 freshwater turtle species studied by McKnight *et al*. (2023), highlighting heterogeneity in the ability of diurnal species to alter their nocturnal behaviour in a context of warming nights.

Further, because warmer nocturnal environments come with some immediate benefits (e.g. digestion, growth), it is difficult to confirm whether organisms seek cooler resting temperatures *via* thermoregulation behaviour and thus forfeit such benefits to avoid potential long-term fitness costs. Most studies focusing on the responses of individuals to immediate benefits *versus* long-term costs suggest that animals favour short-term over long-term consequences (Drent & Daan, 1980; Metcalfe *et al*., 2001; Stephens & Anderson, 2001; Stephens, Kerr & Ferna, 2004; Stevens & Stephens, 2010).

Another possible route for diurnal ectotherms to cope with warmer T_N is through plasticity of their diurnal behaviour or physiology (Sun *et al*., 2022) so as to limit the negative effects of exposure to warmer T_N. Studies on the European common lizard found correlations among several physiological traits and warmer nocturnal environments, implying that plasticity may serve as a buffer to nocturnal warming (see Section V.3 for detailed examples). It is also possible that, despite costs associated with foraging and exploring a nocturnal environment (e.g. predation risk, absence of light, adjustments to internal clock), individuals could adopt an energetically conservative hunting behaviour at night such as 'sit-and-wait' or 'sit-and-pursue' strategies rather than active foraging–hunting (Kruse, Toft & Suncerland, 2008; Schmitz & Barton, 2014), although this requires empirical investigation.

(3) Quantitative insights from the European common lizard

To illustrate the chronic effects of warming nights, we gathered published data collected by our laboratories on the European common lizard (see Fig. 8). This species has a broad geographic distribution, extending across Europe and Asia, and evolved in cold mesic environments. The common lizard has been a key model squamate species used to understand the responses of vertebrate ectotherms to global warming (Chamaille-Jammes *et al*., 2006; Bestion *et al*., 2015; Massot *et al*., 2017; Rozen-Rechels *et al*., 2020; Horreo & Fitze, 2022).

As expected, experimental and comparative studies have highlighted positive effects of warmer nights. Notably, lizards exposed to warmer T_N showed increased growth rates and a shorter gestation time. For example, a 40 day-long experimental exposure to warmer nights (+5 °C) increased mean body growth rate in yearling individuals by almost 20% (Rutschmann *et al*., 2021). Furthermore, both experimental and comparative studies reported positive effects on female reproductive phenology, with warmer nights (+5 °C) accelerating gestation time by almost 30% (Brusch IV *et al*., 2023). Other studies identified potential costs of warmer T_N. First, energy allocation to rapid growth involves a trade-

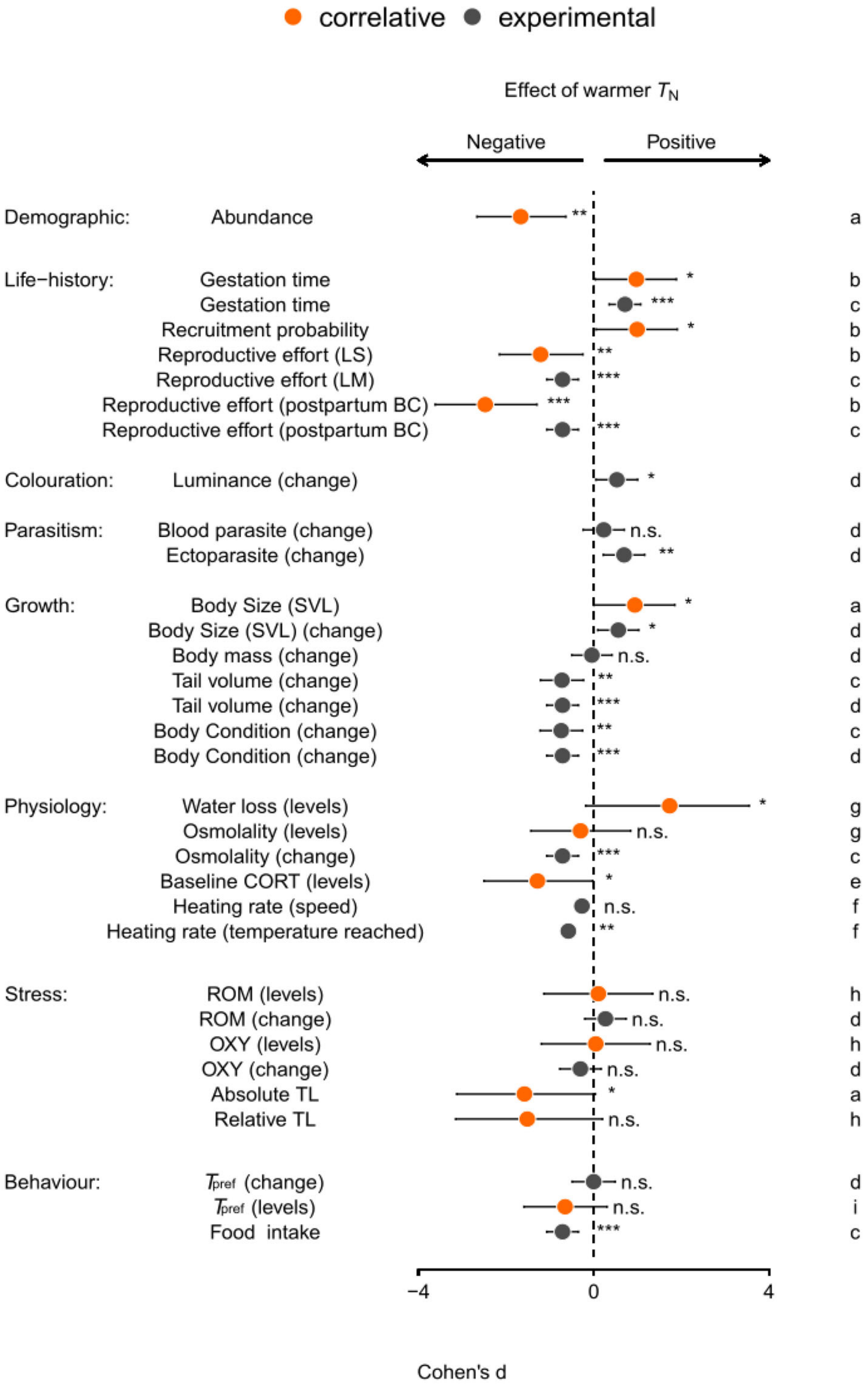

Fig. 8. Plot of effect sizes (Cohen's *d*) for the effects of warmer nocturnal temperatures (T_N) on phenotypic traits of the common lizard (*Zootoca vivipara*). Correlative studies are shown in orange and experimental studies in grey. Stars indicate significance level (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$). Cohen's *d* and associated 95% confidence intervals were estimated using the *t_to_d* function in R (*effectsize* package; Ben-Shachar *et al.*, 2020) for all traits other than the heating rates variables, for which non-linear mixed effect models were used (*lme.dscore* function in *EMAtools* R package; Kleiman, 2022) and confidence intervals could not be calculated. BC, body condition; CORT, corticosterone; LM, litter mass; LS, litter size; OXY, oxygen metabolites; ROM, non-enzymatic antioxidant capacity; SVL, snout–vent length; TL, telomere length; T_{pref}, preferred body temperature. 'Levels' indicates measures from comparative studies. 'Change' indicates measures implying an experimental design where levels were compared before and after treatments. List of publications: a. Dupoué *et al.* (2017*b*); b. A. Dupoué *et al.* (in preparation); c. Brusch IV *et al.* (2023); d. Rutschmann *et al.* (2021); e. Dupoué *et al.* (2018); f. Rutschmann *et al.* (2020); g. Dupoué *et al.* (2017*c*); h. Dupoué *et al.* (2020); i. Rozen-Rechels *et al.* (2021).

off with energy reserves (i.e. energy storage). For example, yearling lizards exposed to warmer T_N during 38 days displayed higher growth rates, but also lower body condition and lower levels of fat reserves (i.e. tail volume) than yearlings in the control treatment (Rutschmann *et al.*, 2021). Similarly, in females, earlier parturition in a warmer nocturnal treatment was associated with a smaller litter size (∼5 vs. 6 juveniles per litter) (Brusch IV *et al.*, 2023; A. Dupoué *et al.*, in preparation), lower litter mass (∼33% reduction in mass per juvenile) and lower *postpartum* body condition (Brusch IV *et al.*, 2023). In both cases, it appears that significant quantities of energy had to be mobilised to compensate for the accelerated pace of life, potentially reducing the amount of energy available for other critical maintenance functions, such as immunity (e.g. ectoparasite infestations; Rutschmann *et al.*, 2021). Contrary to our previous predictions regarding enhanced generation of ROS from elevated metabolic rates, warmer T_N did not result in higher levels of oxidative stress (no significant effect on oxygen metabolites and non-enzymatic antioxidant capacity; Fig. 8) (Dupoué *et al.*, 2020; Rutschmann *et al.*, 2021). It remains difficult to conclude whether the absence of an oxidative stress response reflects an actual absence of stress, whether individuals managed to mitigate this acute stress, or whether the markers analysed were not appropriate to characterise the oxidative stress related to increased resting metabolic activity and/or sleep deprivation (Zhang *et al.*, 2023). In fact, in a comparative study across 10 populations, telomere length (an integrative measure of cellular aging) was found to decrease at higher T_N (no effect of T_D was detected), confirming that common lizards are physiologically challenged in warmer nocturnal environments (Dupoué *et al.*, 2017*b*). This finding also confirms that T_N-related stresses can have chronic effects. This conclusion was strengthened by a non-linear correlation between T_N and the extinction risk of a population: collapsing populations experienced warmer minimum T_N (Dupoué *et al.*, 2017*b*).

Other indirect arguments supporting a detrimental impact of warmer nights come from the many relationships found between T_N and physiological and behavioural traits of common lizards. There was a negative relationship between minimum T_N and baseline corticosterone levels (a glucocorticoid-type hormone involved in energy regulation, immune reactions and stress responses) of adult and yearling females (Dupoué *et al.*, 2018), with warmer nights correlated with lower baseline corticosterone levels. The authors suggested that high T_N may exacerbate chronic stress such that individuals regularly exposed to increased T_N downregulate corticosterone secretion to reduce activity levels, mitigate maintenance costs, and ultimately conserve energy and water. Other physiological parameters such as osmolality changes (Brusch IV *et al.*, 2023), evaporative water loss (Dupoué *et al.*, 2017*c*), heating rates (Rutschmann *et al.*, 2020), prey consumption rate (Brusch IV *et al.*, 2023) or changes in dorsal colouration (Rutschmann *et al.*, 2021) were all correlated with T_N consistently with buffering of the impact of warmer nights (Fig. 8). Note however that no behavioural adjustment *via* thermoregulation preferences has been detected so far for the common lizard (Rutschmann *et al.*, 2021; Rozen-Rechels *et al.*, 2021). Rather, unpublished results show an opposite pattern: male common lizards favoured relatively warm nocturnal body temperatures when exposed to a temperature gradient (10–50 °C) in thermal preference laboratory tests (mean ± SE: diurnal $T_{\mathrm{pref}} = 29.9\ °\mathrm{C} \pm 2.35\ °\mathrm{C}$; nocturnal $T_{\mathrm{pref}} = 26.7\ °\mathrm{C} \pm 3.3\ °\mathrm{C}$; C. Perry & J. Cote, unpublished observations).

VI. NOCTURNAL WARMING: OPEN QUESTIONS AND FUTURE RESEARCH

Above we considered both immediate and long-term costs and benefits of nocturnal warming. It may also have wider eco-evolutionary ramifications and many other questions remain unaddressed. Below we consider five questions that could be explored in future research.

(1) Are the effects of warmer nights similar for diurnal and nocturnal species?

The diel activity pattern describes when a species is most active during the day–night cycle (i.e. diurnal, nocturnal or crepuscular), or whether it exhibits activity during both day and night (i.e. cathemeral species) or whether it shows flexibility between different activity strategies. It is thought that the ancestral state in reptiles was strict nocturnality. Yet, diurnality is now the dominant pattern for many lizard species (around 70%) with heterogeneous frequencies among clades (Kearney & Predavec, 2000; Gamble *et al.*, 2015; Vidan *et al.*, 2017; Slavenko *et al.*, 2022). In snakes, ancestral clades are mostly nocturnal, with the exception of derived species within the family Colubridae, which are mainly diurnal (Gibbons & Semlitsch, 1987; Anderson & Wiens, 2017). In general, crepuscular or cathemeral species are rarer in reptiles (254 species identified in a recent review of the literature; Cox & Gaston, 2023), and examples of intra-specific flexibility in daily activity patterns are scarce (Abom *et al.*, 2012; Degregorio *et al.*, 2014; Vidan *et al.*, 2017). Reasons for this lack of flexibility include sensory constraints, the role of predation or resource availability, and adaptations to nocturnal life, including more efficient performance at low than high temperatures, especially for locomotion (Autumn *et al.*, 1999; Llewelyn, Shine & Webb, 2005; Ibargüengoytía *et al.*, 2007; Anderson & Wiens, 2017; Dayananda, Jeffree & Webb, 2020). Thus, most species might be constrained by their strict diurnal or nocturnal lifestyles, with only a minority able to adjust their activity to warmer nocturnal climates (McCain & King, 2014).

In nocturnal species, which can be good thermoregulators (Kearney & Predavec, 2000; Nordberg & Schwarzkopf, 2019; Chukwuka *et al.*, 2021), metabolism, physiological performance, locomotor activity and prey capture are generally constrained by low T_N (Autumn *et al.*, 1999; Kruse *et al.*, 2008; Hare *et al.*, 2010). As long as they do not exceed CT_{max} (Sunday *et al.*, 2014; Garcia-Robledo *et al.*, 2018), warmer T_Ns should therefore favour these species by extending their opportunities for activity and foraging (Kearney & Porter, 2004; Scenario 5 in Fig. 7). For example, Kearney & Porter (2004) estimated that food consumption dedicated to maintenance in the Australian nocturnal gecko *Heteronotia binoei* would differ by 6.3 g per night between the coldest (2.2 g) and warmest (8.5 g) part of the species distribution. On warmer nights, the encounter rate necessary to fulfil such requirements was calculated to be relatively low (0.03 g/h), because the activity window is large. On colder nights, due to activity restrictions, this encounter rate was estimated to be almost six times higher (0.17 g/h). This example illustrates how warmer nights can increase activity opportunities and facilitate resource acquisition in nocturnal reptiles.

However, just as for diurnal species, an extension of activity into longer periods of the night does not necessarily translate into fitness benefits in all nocturnal species. First, greater opportunities for nocturnal activity can be limited by an increased risk of encountering predators. Apart from nocturnal predators (which could also see their activity period enlarged), diurnal predators could show a switch towards nocturnal activity and act as new agents of selection. Second, as seen in *H. binoei* higher MRs during warmer nights need to be balanced by higher resource acquisition. If prey activity does not match nocturnal predators' increase in activity, encounter rates could decrease and nocturnal predators could face metabolic meltdown (Huey & Kingsolver, 2019). Finally, for nocturnal species subject to increasing T_N, the time spent at low temperatures ($T_e < VT_{min}$) will be restricted to shorter portions of the late night. Over the day, temperatures are often high enough to allow thermoregulation and physiological activity, even within diurnal refuges (Kearney & Predavec, 2000; Croak *et al.*, 2012; Chukwuka *et al.*, 2020). Thus, the time window available for metabolic recovery may be limited and could shrink further in a context of nocturnal warming, leading to long-term negative effects.

The long-term effects of nocturnal warming on nocturnal species are however difficult to predict without further data. We suggest that a formal framework for comparing different modes of activity should take into account differences in exposure to nocturnal warming (i.e. modes are not evenly distributed across the globe) and in thermal sensitivity (especially using the formalism of TPCs). We also suggest that future research focuses on nocturnal thermoregulatory abilities and nocturnal heating and cooling rates of diurnal species (Lelièvre *et al.*, 2010). The analysis of species with flexible diel activity patterns, such as some snakes and lizards, or comparisons of closely related taxa that display a diversity of diel activity patterns (e.g. Gekkonidae or Scincidae) could represent a promising research perspective.

(2) Are the effects of warmer nights similar in tropical, arid and temperate areas?

One major difference between climate zones is the magnitude of temperature variation at annual, seasonal and diel scales (Janzen, 1967). Temperate-zone climates are highly seasonal, with a pronounced difference in daily maximum and minimum temperatures during the activity seasons of squamate reptiles (spring and summer). Daily temperature variation can be higher in mediterranean, arid and semi-arid environments where the difference between daily maximum and minimum T_e during summer often exceeds 30 °C. By contrast, tropical environments, notably tropical forests, tend to exhibit low annual mean thermal oscillations, even at high elevations (e.g. Janzen, 1967). As a consequence, the majority of tropical squamate species tend to be thermal specialists (stenothermic) [see Van Berkum (1986) and de Souza Terra, Ortega & Ferreira (2018) for tropical savannas] because of the low seasonality in temperature and the relative homogeneity of their thermal environment (Tewksbury, Huey & Deutsch, 2008; Huey *et al.*, 2009). By contrast, high heterogeneity in the thermal landscape across temperate or arid habitats has favoured the evolution of heliothermy, which allows squamates to regulate their body temperature over a wide thermal tolerance range. It is therefore likely that the effect of warmer nights on squamate reptiles will vary across biomes because of differences in exposure and behavioural sensitivity to nocturnal warming.

It is crucial also to consider physiological adaptations to climatic zones. So far, we have mainly focused our attention on species inhabiting temperate zones. Cold-adapted squamates are often strictly diurnal and have higher SMRs than warm-adapted species (Lourdais *et al.*, 2013; Dupoué, Brischoux & Lourdais, 2017*a*; Sun *et al.*, 2022), which may be particularly disadvantageous in the context of a passive resting temperature increase induced by nocturnal warming. On the other hand, tropical squamates often show lower CT_{max} and narrower TPCs (Garcia-Robledo *et al.*, 2018) than squamates from temperate climate zones. Because nights are already warm in tropical environments, an increase in T_N should not impact the low-temperature region of the TPC, but could affect its upper region, moving individuals closer to their CT_{max}. One consequence of this is that the effects of warmer nights could vary across biomes: being chronic and long-term in some areas (e.g. temperature zone), whereas acute and immediate in others (e.g. tropics).

Finally, rising T_Ds may depress the activity of squamates during the hottest part of the day, leading to a larger number of hours of restricted activity (Vickers *et al.*, 2011), and this may differ among tropical, temperate and arid areas (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey, Losos & Moritz, 2010). The expected result is a switch of activity towards early morning and early evening, which may be facilitated by warmer T_N. However, as previously discussed, it is not certain that this reduction in diurnal activity and consequent lost feeding opportunities can be offset by increased nocturnal activity. We encourage future research to compare the responses of species from different climatic zones to assess whether warming nights have similar impacts across the globe.

(3) Will warmer nocturnal temperatures shift life-history strategies?

Because of seasonal variation, fluctuations in prey density or predation risk, reptiles face constraints on their ability to acquire, store and spend energy (Sinervo & Licht, 1991; Bleu *et al.*, 2013; Arnall *et al.*, 2019), and there will be multiple trade-offs in energy allocation among maintenance, growth, reproduction and survival. Such trade-offs among life-history traits are known to vary with individual characteristics, but also with local conditions (Ernande *et al.*, 2004; Sgrò & Hoffmann, 2004; Rutschmann *et al.*, 2016). Through its contrasting influence on different physiological and behavioural processes (Clark *et al.*, 2013), nocturnal warming may also affect these life-history trade-offs (e.g. levy their intensity or shift their relative importance). For example, nocturnal warming alters energy allocation rules in juvenile common lizards, with individuals exposed to warmer T_Ns being more likely to invest in immediate growth rather than long-term reserves (Rutschmann *et al.*, 2021). How this could influence winter survival and next-season reproduction is yet to be explored (Bestion *et al.*, 2015). In the same species, T_N also influenced energy allocation in adult females (Brusch IV *et al.*, 2023), with colder T_N resulting in lower litter mass and longer gestation. Interestingly, warmer days had the opposite effect, highlighting the contrasting impacts of T_D and T_N (Speights & Barton, 2019).

Another illustration of life-history shifts driven by warmer T_N comes from the nocturnal *Woodworthia* 'Otago/Southland' gecko species from southern New Zealand. This species classically reproduces biennially, with embryos retained *in utero* over winter (Cree & Guillette, 1995). However, experimental exposure to warmer T_N during late summer was shown to advance the parturition season to the autumn, leading to changes in female life history (e.g. doubling reproductive rate) and population dynamics (Moore *et al.*, 2020). Further work is needed to explore the long-term implications of nocturnal warming on life-history trade-offs and strategies of energy investment.

(4) Will warmer nights alter interactions between squamates and other species?

Squamates are keystone species in their ecosystems and are engaged in numerous predator–prey relationships. Thus, by affecting the ecology of ectotherms, warmer T_N may also perturb the trophic networks in which they are embedded. Further, because the thermal preferences and TPCs of prey and predator species do not usually overlap (Bennett *et al.*, 2018), it is unlikely that all elements of a trophic network will respond uniformly to warmer nights. Thus, one might expect the destabilisation of prey–predator systems or the emergence of new ones, leading to a potential reorganisation of trophic communities. For example, extension of the activity window in insects has been shown to increase the top-down effects of insects on plants (see review by Ma *et al.*, 2020). Similarly, bottom-up effects have been documented to be altered through modified nectar production in plants (Mu *et al.*, 2015) or through altered nutrient allocation within plants (Jing *et al.*, 2016). Community-level studies specifically focusing on vertebrate ectotherms are still rare but it has already been shown that shifts from diurnal towards cathemeral/nocturnal activity during periods of warmer temperatures (i.e. summer or heatwaves) can result in diet and microhabitat-use changes (Sperry *et al.*, 2013; Mata-Silva *et al.*, 2018; Lara Resendiz, 2019).

Further, ectothermic vertebrates are frequently involved in mutualistic associations with symbionts and microbiota crucial for digestion or nutrient acquisition (Shigenobu, Watanabe & Hattori, 2000). The microbiome also plays essential roles in behaviour, immunity, and life history (Macke *et al.*, 2016). Whether effects of nocturnal warming on an individual's microbiota differ from effects of diurnal warming (Bestion *et al.*, 2017; Moeller *et al.*, 2020) is difficult to determine. However, the dynamics of the microbiome is shaped both by the thermal tolerance capacities of the symbionts and by the temperature-dependent immune responses of the individual hosts (Ferguson, Heinrichs & Sinclair, 2016; Goessling & Mendonça, 2016; Abram & Dixon, 2017). By affecting the body temperature or the thermoregulatory behaviour of the host, warmer nights therefore have the potential to affect microbiome dynamics and ultimately to impact the fitness of the ectotherm (Burke *et al.*, 2010; Higashi, Barton & Oliver, 2020).

(5) Will interactions between warmer nights and other climatic factors alter squamate ecology?

Global change is undoubtedly multi-factorial and, among other parameters, warmer T_Ns are likely to be accompanied by changing precipitation and snow regimes (Yang *et al.*, 2016; Dai, Zhao & Chen, 2018), water temperatures (Nordberg & McKnight, 2023), heatwave intensity and frequency (Meehl & Tebaldi, 2004; Sanderson, Hemming & Betts, 2011; Murali *et al.*, 2023), or habitat quality and diversity (Hoekstra *et al.*, 2005). Nocturnal warming is likely to reduce the quality of rest periods for diurnal species and their ability to recover from diurnal stressors. Thus, it could exacerbate the already detrimental effects of other diurnal environmental changes. For example, warmer T_Ns have been found to reduce the longevity and fecundity of English grain aphids when combined with warm T_Ds (Zhao *et al.*, 2014). Warmer nocturnal temperatures were also reported to exacerbate the detrimental effects of metallic pollutants on amphibian species (Hallman & Brooks, 2015) and to interact with light pollution to alter the food-chain dynamics of aphids and ladybirds (Miller *et al.*, 2017). Further research investigating interactions between distinct components of global change and nocturnal warming could provide a more complete picture of how ectotherms will respond to future modifications of their environment.

VII. CONCLUSIONS

(1) Nocturnal warming is an understudied aspect of global warming. Using diurnal squamates as a model taxon, we demonstrated that impacts of warmer nights can be very different from those of T_D increases.
(2) Because they affect the coldest hours of the diel cycle, usually dedicated to rest in diurnal species, warmer T_Ns have the potential to alter the time budget dedicated to the different activity phases of diurnal ectotherms. Whether warmer nights are beneficial or detrimental will ultimately depend on the balance between energy acquisition and expenditure.
(3) Because warmer nights allow an increase in performance, they may have positive effects as long as they also allow species to (*i*) acquire sufficient energy to meet their increased metabolism, and (*ii*) rest sufficiently to recover and eliminate metabolic stressors produced by elevated metabolic activity. If individuals cannot fulfil these conditions, warmer nights could be deleterious.
(4) Because T_Ns are far from upper $\mathrm{CT}_{\max}$, any effects of increasing T_N are not as immediate as effects of warmer maximum T_D. Instead, warmer nights may impose chronic costs accumulating over an individual's lifetime and leading to a reduction in lifetime fitness. Whether such negative effects can be compensated by behavioural or physiological adjustments is yet to be evaluated for most ectothermic species.
(5) Many important questions remain unanswered, including whether there are differences among species with different behavioural strategies, differences between climate zones and effects on ecological interactions between squamates and their prey, predators and microbiome. New research programs and new protocols will be necessary to explore nocturnal warming as a key element of global warming. While legacy data can be re-analysed to answer some of these questions, others will require novel explorations of the night-time behaviour, physiology and population ecology of reptiles.

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IX. AUTHOR CONTRIBUTIONS

A. R. drafted the manuscript, performed the literature review and supervised the project. C. P. helped with the literature review, carried out the experiment for Section III.1 and analysed data together with A. R. J-F. L. G. designed the model and scenarios for Sections IV.1–3 and performed computation (together with A. R.), analysed data (collected by G. B.) and drafted Sections IV.4 and VI.1. A. D. performed the statistical analyses for Section V.3 and drafted that section. M. G. collected data for Section III.3 under the supervision of O. L. who analysed data and drafted that section. M. R., J. Co., and J. Cl. helped discuss the results and provided critical feedback on the manuscript. D. B. M. collected data for Section II.3, analysed the data and drafted that section, helped with the literature review and drafted Sections VI.2 and VI.3. A. R., A. D., J. Cl., and D. B. M. conceived the original idea of the project. All authors contributed to the final version.

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XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Saguaro National Park legacy operative environmental temperature data.

Appendix S2. Diurnal and nocturnal metabolic rates of *Podarcis muralis*.

Appendix S3. Summer heatwave and nocturnal warming: a case study in a diurnal snake.

Appendix S4. Bioenergetic modelling of energy balance.

Appendix S5. Empirical analysis of energy balance.