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1 **Ecological responses of squamate reptiles to nocturnal warming**

2

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30

31 ABSTRACT

32 Nocturnal temperatures are increasing at a pace exceeding diurnal temperatures in most parts
33 of the world. The role of warmer nocturnal temperatures in animal ecology has received scant
34 attention and most studies focus on diurnal or daily descriptors of thermal environments'
35 temporal trends. Yet, available evidence from plant and insect studies suggests that organisms
36 can exhibit contrasting physiological responses to diurnal and nocturnal warming. Limiting
37 studies to diurnal trends can thus result in incomplete and misleading interpretations of the
38 ability of species to cope with global warming. Although they are expected to be impacted by
39 warmer nocturnal temperatures, insufficient data are available regarding the night-time
40 ecology of vertebrate ectotherms. Here, we illustrate the complex effects of nocturnal
41 warming on squamate reptiles, a keystone group of vertebrate ectotherms. Our review
42 includes discussion of diurnal and nocturnal ectotherms, but we mainly focus on diurnal
43 species for which nocturnal warming affects a period dedicated to physiological recovery,
44 and thus may perturb activity patterns and energy balance. We first summarise the physical
45 consequences of nocturnal warming on habitats used by squamate reptiles. Second, we
46 describe how such changes can alter the energy balance of diurnal species. We illustrate this
47 with empirical data from the asp viper (*Vipera aspis*) and common wall lizard (*Podarcis*
48 *muralis*), two diurnal species found throughout western Europe. Third, we make use of a
49 mechanistic approach based on an energy-balance model to draw general conclusions about

50 the effects of nocturnal temperatures. Fourth, we examine how warmer nights may affect
51 squamates over their lifetime, with potential consequences on individual fitness and
52 population dynamics. We review quantitative evidence for such lifetime effects using recent
53 data derived from a range of studies on the European common lizard (*Zootoca vivipara*).
54 Finally, we consider the broader eco-evolutionary ramifications of nocturnal warming and
55 highlight several research questions that require future attention. Our work emphasises the
56 importance of considering the joint influence of diurnal and nocturnal warming on the
57 responses of vertebrate ectotherms to climate warming.

58

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

61

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93 I. INTRODUCTION

94 Over the past century, mean air temperatures have been increasing across most regions of the
95 globe, threatening numerous species and ecosystems (Pörtner *et al.*, 2022). Yet, in many parts
96 of the world, climate warming appears to be an asymmetrical process driven by a more rapid
97 increase of nocturnal (T_N) than diurnal air temperatures (T_D) (Dai, Trenberth & Karl, 1999;
98 Sun *et al.*, 2000; Vose, Easterling & Gleason, 2005; Alexander *et al.*, 2006). Despite this,
99 most studies evaluating the impact of global warming either consider temperature increments

100 to be constant over a 24-h cycle or focus solely on diurnal patterns (e.g. maximum daily
101 temperature), with nocturnal warming often considered an inconsequential aspect of climate
102 change (Speights *et al.*, 2018). Ignoring nocturnal warming is however of particular concern
103 because the available data show that organisms can exhibit different, and sometimes
104 opposing, eco-physiological responses to T_D and T_N (Xia *et al.*, 2009; Zhao *et al.*, 2014;
105 Freixa *et al.*, 2017; Speights & Barton, 2019). Thus, studies that focus only on diurnal
106 warming may provide a somewhat simplified and incomplete assessment of the vulnerability
107 and capacity of organisms to cope with climate change (Vickerman & Sunderland, 1975;
108 Peng *et al.*, 2013; Zhao *et al.*, 2014; Speights, Harmon & Barton, 2017; Ma, Ma &
109 Pincebourde, 2021).

110 Plant ecologists have been at the forefront of investigations of the impacts of nocturnal
111 warming on functional traits and ecological interactions of organisms. For example, in an
112 early study, Alward, Detling & Milchunas (1999) demonstrated that warmer T_N altered the
113 composition of plant communities of the north-eastern Colorado steppes, with a decrease of
114 the dominant C_4 grass species in favour of exotic and native C_3 forbs. Warmer T_{NS} were later
115 shown to influence vegetation productivity (Peng *et al.*, 2013; Mu *et al.*, 2015), growth
116 (Clark, Clark & Oberbauer, 2010; Xia *et al.*, 2018) and phenology (Wang, Luo & Shafeeqe,
117 2019). Mechanistic responses by plants to warmer T_N are complex and operate at different
118 levels (Sadok & Krishna Jagadish, 2020). Leaf morphology and physiology appear to play a
119 crucial role, with warmer T_{NS} leading to a reduction in leaf quality and earlier senescence,
120 which results in higher respiration rates at night and a decline in photosynthesis-dependent
121 processes. Ultimately, these modifications can have cascading effects on plant growth, seed
122 production and fitness (García *et al.*, 2015; Lesjak & Calderini, 2017). Recently,
123 entomologists have begun to investigate the effects of the diel patterns of climate change.
124 Studies focusing on insect species have revealed heterogeneous and complex responses (i.e.

125 neutral, positive and/or negative) to warmer T_{NS} , ranging from individual physiology to
126 community dynamics (Whitney-Johnson, Thompson & Hon, 2005; Warren & Chick, 2013;
127 Ma, Hoffmann & Ma, 2015; Barton, 2017; Speights *et al.*, 2017; Bai *et al.*, 2019).

128 The susceptibility of insects to warmer T_{NS} is not surprising: ectotherms rely on external
129 heat sources to regulate their body temperature and to maintain it within a range of
130 temperatures that optimises performance (Angilletta *et al.*, 2002; Seebacher & Franklin,
131 2005; Clusella-Trullas, Blackburn & Chown, 2011). The temperature dependence of
132 physiological performance in ectotherms is classically conceptualised as a thermal
133 performance curve (TPC; Fig. 1). The curve describes the response of a focal performance
134 trait [e.g. activity, metabolic rate (MR), individual growth rate, locomotion, digestion,
135 population growth rates] to changes in body temperature. Most TPCs are assumed to follow a
136 left-skewed bell-shaped curve: the performance increases steadily from the critical thermal
137 minimum (CT_{min}) up to a peak value attained at the optimal body temperature (T_{opt}). Above
138 T_{opt} , performance usually exhibits a sharp decline towards the critical thermal maximum
139 (CT_{max}). The range between CT_{min} and CT_{max} therefore defines an organism's critical thermal
140 range for nocturnal and diurnal activities. Given the rapid decline of performance above T_{opt} ,
141 ectotherms are highly sensitive to increases in maximum environmental temperatures as these
142 temperatures are likely to push an organism's body temperature beyond T_{opt} and towards
143 CT_{max} (Deutsch *et al.*, 2008; Buckley, Tewksbury & Deutsch, 2013; Rohr & Palmer, 2013;
144 Burraco *et al.*, 2020; Clusella-Trullas *et al.*, 2021). Yet patterns of activity can also be
145 influenced by minimum temperatures: daily or seasonal increase in T_N can push organism
146 body temperatures towards higher values, away from their CT_{min} and therefore to within an
147 adequate thermal range for activity. An increase in minimum temperatures can, for example,
148 facilitate the colonisation of new habitats by offering new opportunities for foraging and
149 hunting or by increasing intrinsic physiological rates (e.g. digestion, metabolic rates) (Battisti

150 *et al.*, 2005). Another potential consequence is the alteration of an individual's resting
151 thermal range: warmer minimum temperatures may trigger an increase in resting
152 physiological rates (e.g. resting MR, cellular damage reparation rates) that could increase
153 energy consumption (Speights *et al.*, 2017; Ma *et al.*, 2020).

154 Because research on the impact of nocturnal warming is at an early stage, our goal here is
155 threefold. We first discuss the potential responses of vertebrate ectotherms to warmer nights.
156 Next, we use published data, legacy data and analytical models to illustrate such responses.
157 Finally, we propose avenues for future research studying the impact of nocturnal warming on
158 organisms. To do so, we present a comprehensive assessment of the consequences of warmer
159 nights on an emblematic group of vertebrate ectotherms, the order Squamata. This order
160 includes three keystone groups (amphisbaenians, lizards and snakes) and represents the
161 largest group of non-avian reptiles (11,549 species; Uetz *et al.*, 2023). Squamates occur in
162 most biomes of the globe and exhibit a wide diversity of morphological, physiological,
163 behavioural and ecological strategies (Meiri, 2018). The sensitivity of squamates to
164 increasing maximum air temperature is well documented (Thomas *et al.*, 2004; Araújo &
165 Rahbek, 2006; Dupoué *et al.*, 2022; Stark *et al.*, 2023; Zhang *et al.*, 2023) and one study
166 forecasts that climate warming will lead to the extinction of almost 40% of these species by
167 2080 (Sinervo *et al.*, 2010). Yet little is known about the impact (positive or negative) of
168 warmer minimum air temperatures (i.e. T_N) on this extinction rate. The well-studied group of
169 squamates thus provides an opportunity to clarify the impacts of nocturnal warming on
170 ectothermic vertebrates (Taylor *et al.*, 2020), and we anticipate the general conclusions drawn
171 from our work are likely to be applicable to other taxonomic groups. Although our review
172 discusses such impacts on both diurnal and nocturnal ectotherms (see Sections IV.2 and
173 VI.1), we mainly focus on diurnal squamates. For diurnal species, nocturnal warming affects
174 a period dedicated to physiological recovery, and may perturb activity patterns and energy

175 balance in a complex manner (Fig. 2). By contrast, warmer T_N affects the primary activity
176 period of nocturnal species and it is possible that nocturnal reptiles mainly benefit from
177 increasing physiological performance and foraging opportunities, although there are fewer
178 data to confirm this hypothesis.

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

195 **II. NOCTURNAL WARMING AND THE THERMAL MICROHABITATS OF** 196 **SQUAMATES**

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

198 Between 1950 and 2004, T_{NS} increased at a rate exceeding 1.4 times the observed change in
199 maximum T_D on average across the world (0.204 versus 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

225 disproportionate augmentation of temperature in the top soil layers. To illustrate this, field
226 experiments using large infrared heaters suspended above the ground generated asymmetric
227 warming patterns between daytime and night (Wu *et al.*, 2012). Minimum temperatures
228 recorded 10 cm above the ground significantly increased from 0.65 °C to 1.33 °C (0.68 °C
229 difference) through nocturnal warming, but were not affected by daytime warming
230 treatments. In parallel, minimum ground temperatures significantly increased from 4.05 °C to
231 5.34 °C (1.29 °C difference) through the nocturnal warming treatment but, again, remained
232 unaffected by experimental diurnal warming. Nocturnal warming at the soil surface was
233 found to shorten significantly the development of eggs and nymphs in three grasshopper
234 species, leading to an advance in adult emergence time by 2–6 days depending on species
235 (Wu *et al.*, 2012).

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

238 Squamates can be found in myriad microhabitats. They notably rely on burrows, substrate
239 elements, canopy leaves, rock cracks, holes in trees or water to regulate their body
240 temperature, lay their eggs, evade predators or stressful thermal conditions during their
241 activity periods, and shelter during periods of rest and inactivity (Huey *et al.*, 1989;
242 Goldenberg *et al.*, 2021; Mohanty *et al.*, 2022; Nordberg & McKnight, 2023). For
243 ectotherms, appropriate selection of nesting, retreat and resting sites is key as such sites offer
244 a variety of thermoregulatory opportunities that influence many physiological rates (e.g.
245 developmental, metabolic and digestive rates). Alternatively, this choice may have
246 deleterious consequences and reduce an individual's fitness if the retreat-site temperature is
247 inappropriate (e.g. too deep or too shallow) (Huey *et al.*, 1989; Kearney, 2002; Lelièvre *et al.*,
248 2010; Bentley *et al.*, 2020; Chukwuka, Monks & Cree, 2020). As a consequence, the thermal
249 quality of the habitat cannot simply be reduced to air temperature, but should rather be

250 described by the mosaic of operative environmental temperatures (T_e , the temperature of an
251 object with no heat capacity and resulting from both radiation and convective heat transfer)
252 present in the environment (Bakken & Gates, 1975; Kearney, Isaac & Porter, 2014; Ma *et al.*,
253 2021).

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

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

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

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

300 potential inability to buffer the effect of temperature on metabolic rate physiologically or
301 behaviourally during a nocturnal period of inactivity, even where MRs are high (e.g. mean
302 SMR at 30 °C exceeds mean RMR at 20 °C; Fig. 4).

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

319 Together with increased foraging activity, higher physiological rates could translate into
320 an increase in the daily opportunities for conversion or storage of energy, which may improve
321 body growth, shorten the gestation period, and ultimately increase individual fitness (Ma *et*
322 *al.*, 2020). Such positive effects of warmer nights have been documented in insects (reviewed
323 in Ma *et al.*, 2020), where warmer T_N can reduce the development time of eggs (Wu *et al.*,
324 2012; Zhao *et al.*, 2014; Speights & Barton, 2019) or larvae (Whitney-Johnson *et al.*, 2005;

325 Wu *et al.*, 2012; Kingsolver, Higgins & Augustine, 2015). Similar results have been found
326 for squamates, with warmer T_{NS} accelerating gestation and embryonic development in lizards
327 (Clarke & Zani, 2012; Bruschi *et al.*, 2023) and geckos (Moore, Penniket & Cree, 2020).
328 Warmer nights also increased hatchling size (Clarke & Zani, 2012), adult body condition
329 (Moore *et al.*, 2020) and juvenile growth rates (Dupoué *et al.*, 2017b; Rutschmann *et al.*,
330 2021) in different squamate species.

331 (2) Limits to nocturnal activity for diurnal ectotherms

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

344 Second, differences in the TPCs for different physiological traits are expected under the
345 'multiple performances–multiple optima' hypothesis (Huey, 1982; Clark, Sandblom &
346 Jutfelt, 2013). Therefore, although they could increase metabolic activity, nocturnal thermal
347 conditions may remain well below the preferred body temperature (T_{pref}) for other traits such
348 as locomotion. T_{NS} are indeed frequently lower than the thermoregulatory requirements of a
349 species to initiate activity [i.e. voluntary minimum temperature (VT_{min}), often estimated as

350 the 25th percentile of T_{pref} , or as the lowest recorded active body temperature when lizards
351 first emerge from a refuge] (Kubisch *et al.*, 2016; Taylor *et al.*, 2020). For example, Kubisch
352 *et al.* (2016) found VT_{min} to vary from 24.6 to 31.3 °C in three lizard species from Patagonia.
353 Similarly, Diele-Vegas *et al.* (2018) found VT_{min} to vary between 19.9 and 32.9 °C among 27
354 different species of South American lizards. In both studies, the lower limit for voluntary
355 foraging activity was quite high (*ca.* 25 °C for diurnal lizard species), hence limiting
356 opportunities for these species to engage in foraging activities despite warm nocturnal
357 conditions. Whether warmer nocturnal thermal conditions are sufficient to increase
358 performance levels of all traits necessary for activity therefore will rely on an individual's
359 thermoregulation capacities and requirements (Kearney, Shine & Porter, 2009; Vickers *et al.*,
360 2011). Among diurnal thermoregulators, species predominantly use heat from the sun to
361 reach a body temperature within the range that favours performance (Angilletta, 2009;
362 Kearney *et al.*, 2009). In the absence of solar radiation, the potential for thermoregulation is
363 restricted to heat conduction from substrates that emit heat accumulated during the day and
364 thus requires the use of a behavioural thermoregulation strategy based on thigmothermy
365 rather than heliothermy (Huey *et al.*, 1989; Kearney & Predavec, 2000; Nordberg &
366 Schwarzkopf, 2019). Despite numerous studies showing that nocturnal species are capable of
367 exploiting such thermal opportunities (Kearney & Predavec, 2000; Vidan *et al.*, 2017), little
368 is known about this ability in diurnal thermoregulators (see Section VI.1).

369 Third, the use of a favourable nocturnal thermal environment can also be constrained by
370 diurnal activity patterns and thermoregulation preferences. For example, one field study
371 showed that exploitation of warmer artificial shelters differed between two sympatric
372 colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*). Such artificial shelters
373 improved nocturnal digestion rates significantly for *H. viridiflavus* (by up to 25%) compared
374 to *Z. longissimus* (4.4% increase) (Lelièvre *et al.*, 2010). This pattern could be explained by

375 differences in diurnal thermal preferences between these species: *H. viridiflavus* is considered
376 to be thermophilic, with higher preferred body temperatures (27.5–31.1 °C) relative to *Z.*
377 *longissimus*. As such, *H. viridiflavus* favoured the warmer artificial refuges over natural ones
378 during the daytime. This preferential diurnal use of artificial structures also allowed this
379 species to benefit from warmer nocturnal conditions and therefore to increase its RMR and
380 nocturnal digestion rate. By contrast, *Z. longissimus* favoured cooler environments (21.5–
381 25.5 °C) and did not exploit the artificial shelters during the daytime, hence missing an
382 opportunity to exploit a warmer nocturnal thermal habitat.

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

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

390 To address further the impact of warm nocturnal conditions on resting body temperature and
391 nocturnal thermoregulation, we analysed unpublished body temperature data for the asp viper
392 (*Vipera aspis*) and T_e data from a viper biomimetic model, both collected by M. Guillon and
393 O. Lourdais during the 2003 European mega-heatwave (Garcia-Herrera *et al.*, 2010; Russo,
394 Sillmann & Fischer, 2015) (see Appendix S3 for details). The asp viper is a typical diurnal
395 and heliothermic snake species. Mean \pm SD T_{pref} for non-reproductive individuals is $30.6 \pm$
396 4.2 °C (Lorioux, Lisse & Lourdais, 2013). At night, vipers' shelter in underground refuges to
397 avoid predation.

398 During the study, seventeen hot days (maximum air temperature in the shade 30–35 °C)
399 and eleven very hot days (>35 °C) were identified by the French national meteorological

400 agency (Météo France) classification (Fig. 5). Daily maximum surface temperature in the
401 enclosure (mean \pm SE; 40.48 ± 9.27 °C) significantly influenced the minimum temperature in
402 the refuge in the following night (19.98 ± 2.57 °C; ANOVA, $\beta = 0.24 \pm 0.02$, $F_{1,64} = 87.61$,
403 $P < 0.005$; Table S3 in Appendix S3), likely due to ground thermal inertia (Rosen & Lowe,
404 1994). Despite extremely high operative temperatures during the daytime (Fig. 5), vipers
405 were able to thermoregulate efficiently during the daytime: individuals avoided overheating
406 and maintained a mean diurnal maximum body temperature of 31.8 ± 2.7 °C, which is very
407 close to their T_{pref} . At night, body temperature followed closely the thermal conditions
408 recorded in the shelters (Figs 5 and 6). Mean nocturnal body temperatures (recorded between
409 22:00 and 08:00) were influenced both by previous day type ($F_{2,60} = 256.95$, $P < 0.005$) and
410 minimum shelter temperature during that night ($\beta = 0.62 \pm 0.06$, $F_{1,60} = 127.92$, $P < 0.005$; the
411 interaction term was not significant ($F_{2,60} = 1.28$, $P = 0.28$; Table S4 in Appendix S3).
412 Nocturnal body temperatures were higher during nights following very hot days and hot days
413 compared to those following normal days (mean \pm SE = 25.37 ± 1.14 °C and 22.42 ± 1.43 °C
414 *versus* 19.34 ± 1.51 °C, respectively). During the night, temperatures within a burrow are
415 often warmer than temperatures at the surface (Fig. 5), allowing vipers within their overnight
416 refuge to maintain nocturnal body temperatures sometimes exceeding the body temperature
417 recorded for actively thermoregulating vipers during the day. This pattern was particularly
418 pronounced during the peak of the heatwave from 1 to 12 August (Fig. 5).

419 Together, these observations confirm, for this heliothermic diurnal species, a ‘passive’
420 influence of nocturnal refuge conditions on body temperature. While individuals remained in
421 their shelter we did not detect any foraging attempts (as shown by the synchrony between
422 nocturnal body temperature and shelter temperature despite warm surface temperatures)
423 (mean 25.97 ± 10.76 °C). Shelter use by this diurnal species may allow them to avoid
424 predation or may result from an intrinsic circadian rhythm. It is also likely that shelter-use

425 behaviours limit water loss and are thus important in hydoregulation, as demonstrated
426 experimentally by Dezetter, Le Galliard & Lourdais (2022). However, the likely increase in
427 SMR during the warmest nights could potentially affect energy balance and lead to a loss of
428 body condition (Zhao *et al.*, 2014; Speights *et al.*, 2017). Further, any negative impacts on
429 body reserves during non-reproductive years in capital breeding species such as the asp viper
430 could influence reproductive success in the following year (Lourdais *et al.*, 2002; Lourdais *et*
431 *al.*, 2003; see Section VI.3).

432 **IV. BALANCE BETWEEN COSTS AND BENEFITS: A MODELLING APPROACH**

433 That ectotherms might be constrained in their capacity to forage at night despite warmer
434 nocturnal conditions, themselves associated with higher SMRs, raises a second question: do
435 warmer nights entail energetic costs that cannot be compensated by diurnal feeding activity?
436 To answer this question and to explore the energetic costs and benefits of warmer T_{NS} , we
437 extended the energy-balance model of Huey & Kingsolver (2019) (see Appendix S4). Their
438 original model quantifies the daily net energy gain (NEG_d) of an active, thermoconforming
439 ectothermic predator at different environmental temperatures. Their model assumes that the
440 net energy budget depends on energetic input from food intake and assimilation, and output
441 from energy expenditure. By extending this model we partition an active phase [i.e. diurnal
442 phase with positive attack rates (AR) and metabolic rates (MR)] from a resting phase (i.e.
443 nocturnal phase with zero AR but positive MR) and disentangle the effects of warmer T_D and
444 T_N . Note that whereas Huey & Kingsolver (2019) assumed a Type I functional response
445 where food intake increases linearly with food density, we assume a more realistic Type II
446 functional response (Englund *et al.*, 2011) where food intake increases with resource density
447 at low prey availability (in proportion to AR) but saturates at high prey availability (in
448 proportion to handling and ingestion time and satiation; see Fig. S1 in Appendix S4). Also

449 note that we chose default parameters to match the thermal biology of an “average” species,
450 but our qualitative predictions should hold for different parameterisations.

451 (1) Model development

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

$$460 \quad NEG_{R,T} = \alpha * FR_{R,T} - MR_T \quad (1)$$

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

$$462 \quad FR_{R,T} = \frac{AR_T * R}{1 + AR_T * R / IR_T} \quad (2)$$

463 where R denotes the resource density (arbitrarily fixed to $R = 2$ in all examples), AR_T is the
464 temperature-dependent attack rate, and IR_T is the temperature-dependent ingestion rate. The
465 body temperature dependence of the AR and IR were both modelled using Arrhenius-like
466 equations as recommended by Englund *et al.* (2011). We scaled all parameters of AR and IR
467 (see equations S6 and S7 in Appendix S4) to have a unimodal relationship with body
468 temperature and a maximum of 1 at an optimal body temperature [T_{opt} ; here, $T_{opt} = 30$ °C,
469 which is within the range of optimal temperatures for locomotion and food consumption in
470 lizards (Clusella-Trullas & Chown, 2014)], and used empirical data from the meta-analysis of
471 Englund *et al.* (2011) to derive parameters for these equations (see Fig. S2 in Appendix S4).
472 We first set a default metabolic rate with a basal value of 1 at 20 °C (DMR_{20}) and assumed
473 that it would increase exponentially with the inverse of body temperature (in °K) according to

474 equation S10. Note that in our simulations, DMR_{20} was then set to 1, 5, 10 or 15% of the
475 maximum energy intake at 20 °C (Andrews & Pough, 1985). At each time-step, the air
476 temperature T was estimated using an asymmetric 24-h periodic function that provides a good
477 description of diel cycles in above-ground air temperature (Parton & Logan, 1981) (see Fig.
478 S3 in Appendix S4). Because our focus was on nocturnal warming, we kept maximum
479 diurnal temperatures ($T_{D, \max}$) constant (40 °C) across all simulations, while varying minimum
480 nocturnal temperatures ($T_{N, \min}$) from 0 to 30 °C (Fig. S3).

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

484 **(2) Modelled scenarios: nocturnal temperature and thermoregulation pattern**

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

493 We then compared five alternative scenarios to investigate the impacts of warmer nights (i.e.
494 $T_{N, \min}$) on species with different thermoregulation strategies and foraging styles (Table 1). In
495 Scenario 1, we assumed a thermoconforming ectotherm with 24 h foraging activity. This
496 allowed us to investigate effects of minimum T_N in the absence of time partitioning of
497 activity and of any behavioural control of body temperature. In Scenario 2, we extended the
498 model to the case of a thermoconforming ectotherm with an activity cycle based on

499 photoperiod. This organism was active during the day (07:00 to 20:00) and inactive over the
500 night (21:00 to 06:00). To make this tractable without explicitly modelling kinematics of
501 handling, gut passage time and assimilation of food (Levy *et al.*, 2017), we assumed that
502 foraging behaviour (i.e. AR) was only possible between 07:00 and 20:00 (AR, IR & MR all
503 >0); IR and MR were calculated all over the full 24-h period (AR = 0 while IR & MR >0). In
504 Scenario 3, we applied the model to a perfectly thermoregulating ectotherm (i.e. a species
505 that maintains body temperature within a range of temperatures optimal for performance) for
506 which the activity window was possible over the 24-h daily cycle but limited by
507 environmental temperatures. This scenario thus represents an ectothermic predator able to
508 extend its foraging activity into the night when environmental temperatures are suitable.
509 Here, we assumed that AR was limited by a lower (18 °C) and upper threshold (40 °C)
510 corresponding to typical values of VT_{min} and VT_{max} for foraging in many terrestrial lizards
511 [see Rozen-Rechels *et al.* (2020) for an example]. Moreover, as the organism was able to
512 thermoregulate, we assumed that it could maintain a body temperature of 30 °C matching the
513 T_{opt} for foraging whenever environmental temperatures exceeded T_{opt} . Scenario 4 illustrates
514 the case of a perfect thermoregulator with an activity window delimited by both temperature
515 and photoperiod. As in Scenario 2, AR was limited by daylight, while IR and MR were
516 dependent only on body temperature. As in Scenario 3, this scenario assumes body
517 temperature during daytime was 30 °C whenever environmental temperatures exceeded 30°C
518 (i.e. efficient behavioural thermoregulation). The final scenario (Scenario 5) describes a
519 nocturnal thermoregulator, with a foraging activity window strictly delimited to the night
520 (20:00 to 07:00). For this scenario, AR was positive at night and depended on body
521 temperature, while IR and MR depend only on body temperature. We assume the species is
522 capable of selecting retreat sites to maintain a diurnal body temperature close to 30 °C (T_{pref})
523 whenever diurnal environmental temperatures exceeded 30 °C (Kearney & Predavec, 2000;

524 Tan & Schwanz, 2015; Chukwuka *et al.*, 2021). At night, foraging activity is delimited by
525 VT_{\min} and VT_{\max} , which are fixed at 15 °C and 35 °C because those values are typically
526 lower in nocturnal than diurnal ectotherm species.

527 For all scenarios (with the exception of Scenario 0), we evaluated the response of NEG_d to
528 varying minimum T_N s ranging from 0 to 30 °C. We also evaluated varying resting metabolic
529 expenditure by using DMR_{20} values of 0.01, 0.05, 0.1, and 0.15 (Andrews & Pough, 1985) to
530 allow us to characterise the effects of nocturnal warming on species with increasing resting
531 metabolic rates.

532 (3) Results and conclusions

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

541 Second, in all scenarios the model has an optimal T_N ($T_{N,opt}$) for the NEG_d (Fig. 7, circles).
542 Below this optimum, an increase of T_N increases NEG_d . Above it, NEG_d decreases and, in
543 some cases, even becomes negative (Scenario 2). Thus, whenever T_N exceeds the $T_{N,opt}$, the
544 concomitant increase in MR is not compensated by the AR, resulting in an energetic debt.
545 Note that for higher DMR_{20} (and more restricted activity patterns), $T_{N,opt}$ is lower. To
546 compensate for this, we expect foraging effort to increase in ectotherms with higher energy
547 demands when T_N is higher in the absence of specific constraints on nocturnal foraging
548 activity (i.e. Scenarios 2 & 4; see Section III.2). Such a change in foraging effort driven by

549 nocturnal warming could have important consequences on food-web dynamics (see Section
550 VI.4) as already demonstrated by several studies on insects (Barton & Schmitz, 2018; Ma *et*
551 *al.*, 2020). It is also possible that changes of DMR *via* metabolic plasticity (Norin, Malte &
552 Clark, 2016; Sun *et al.*, 2022) would help individuals to acclimatise to warmer T_N . Similarly,
553 inter-individual variation in DMR may facilitate adaptation to higher T_N by lowering DMR in
554 the population through natural selection.

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

567 Finally, nocturnal species (Scenario 5) show the greatest relative energetic benefit from
568 warmer nights, as illustrated by the largest amplitude of NEG_d gained at warmer nocturnal
569 temperatures compared to diurnal species (Fig. 7). From low to intermediate minimum
570 temperatures, NEG_d benefits exponentially from increased ARs with increasing temperatures.
571 Once minimum T_N reaches VT_{min} , the increase in NEG_d plateaus until it reaches $T_{N,opt}$. There
572 are two possible explanations for this pattern. First, foraging activity (AR) may be maximal
573 and therefore there is no further opportunity to increase energetic income. Second, with

574 increasing minimum T_N thermal conditions will exceed VT_{\max} over a larger part of the night,
575 reducing AR and energetic income. Above $T_{N,\text{opt}}$, minimum temperature exceeds VT_{\max} for
576 the majority of the night and foraging is highly restricted, resulting in an drop in NEG_d . Also
577 note that for the highest DMR_{20} , NEG_d is only positive over a short range of temperature in
578 nocturnal species. This result may be related to our parameterisation of the model where we
579 decided not to modify the AR functions for the nocturnal species. Instead, several studies
580 have reported higher efficiency of locomotion at low temperatures in nocturnal squamates,
581 which would translate to a higher AR at low temperatures (Autumn *et al.*, 1999; Hare *et al.*,
582 2007) (see Fig. S15 in Appendix S4). Similarly, a higher MR efficiency at low temperatures
583 is a common assumption for such species (Autumn *et al.*, 1999; Kearney & Porter, 2004).
584 Adjusting these two characteristics could reduce $T_{N,\text{opt}}$ and thereby increase the benefit of
585 warmer nights for nocturnal species (see Scenario 5 in Appendix S4 for an illustration).
586 Whether warmer nights will benefit all nocturnal species yet remains to be confirmed.
587 Nocturnal ectotherms are rarely active over the entire night and temperatures below VT_{\min}
588 also represent thermal refugia for these species (Kearney & Porter, 2004). A reduction in the
589 time dedicated to rest and recovery thus could entail negative fitness effects in nocturnal
590 ectotherms too (see Section VI.1).

591 Altogether, our model confirms that approaches based only on instantaneous TPCs will
592 provide an incomplete picture, by failing to consider the temporal dynamics and trade-offs of
593 different performances involved in maintenance, foraging, digestion and energy balance.
594 Energetic intake and expenditure must be integrated over the entire day, and potentially over
595 an individual's lifetime to measure the actual cost–benefit balance of warmer nights. This
596 point has been made previously in other recent studies using TPCs to make predictions about
597 the temperature dependence of fitness traits (Kingsolver & Woods, 2016; Sinclair *et al.*,
598 2016).

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

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

623 of a strictly diurnal species, unable to extend its activity and foraging into the night (see also
624 Section VI.3).

625 **V. CHRONIC EFFECTS OF NOCTURNAL WARMING**

626 **(1) Warmer nights entail delayed costs in diurnal species**

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

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

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

656 Another long-term cost of warmer nights may be the accumulation of metabolic by-
657 products resulting from nocturnal activity. In squamates, the maintenance of active metabolic
658 rates below T_{opt} (i.e. typical scenario during warmer nights; Fig. 1) can be particularly
659 challenging. Physiological activity at suboptimal temperatures (i.e. below the thermal
660 performance optimum) may induce stronger oxidative stress *via* sustained mitochondrial
661 activities and associated ROS production, while also impeding antioxidant defences and
662 lowering repair capabilities [see Ritchie & Friesen (2022) for a review]. Eventually, chronic
663 exposure to warmer conditions at night and the resulting oxidative stress may affect
664 individual life-history trajectories by trading off higher investments in immediate
665 physiological activities (and in the management of their by-products) against longevity and/or
666 lifetime reproductive success (Monaghan, Metcalfe & Torres, 2009; Speakman *et al.*, 2015).
667 Among the cellular mechanisms involved in such a response, oxidative stress can favour
668 telomere erosion (i.e. the protective DNA sequences capping the end of chromosomes),
669 accelerate aging rates and hasten senescence (Reichert, Stier & Stier, 2017; Chatelain,
670 Drobniak & Szulkin, 2020; Burraco *et al.*, 2022). To illustrate this, a recent conceptual model
671 (i.e. the ‘aging loop hypothesis’) was developed from empirical evidence on the European

672 common lizard (Dupoué *et al.*, 2022). This mechanistic model investigated the effects of
673 increasing temperatures, physiological stress and population dynamics and posited that
674 warmer conditions during resting phases can accelerate the pace of life of a diurnal
675 ectotherm, with deleterious effects accumulating across generations through biomarkers such
676 as telomeric DNA, leading eventually to population collapse.

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

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

686 Without further empirical studies, it is difficult to evaluate to what extent long-term effects of
687 warmer T_N will impact ectotherms in natural conditions, or whether some species have the
688 capacity to mitigate at least some of the chronic costs associated with nocturnal warming, and
689 thus maintain high fitness (Battisti *et al.*, 2005; Clarke & Zani, 2012; Moore *et al.*, 2020).

690 One potential way to mitigate energetic costs associated with warmer nocturnal environments
691 lies in the capacity of squamates to select cooler refugia when usual resting environments are
692 too warm. Yet limited data are available regarding the ability of diurnal thermoregulators to
693 extend their thermoregulatory behaviour overnight. A common assumption is that such
694 capacities are limited, because T_{NS} are uniformly low among thermal refugia, i.e. natural
695 selection operating on nocturnal thermoregulation (which depends on the spatial thermal
696 heterogeneity of retreat sites) is likely to be weak for diurnal species (Huey *et al.*, 2021a).

697 Recent studies have reported previously undocumented nocturnal basking activity for tropical
698 crocodilians and turtles (McKnight *et al.*, 2023; Nordberg & McKnight, 2023). While
699 individuals normally rest in water at night, occurrences of terrestrial nocturnal basking were
700 recorded in nights with high water surface temperatures. One hypothesis is that air
701 temperatures offer a cool thermal refuge from waters exceeding T_{pref} (e.g. $> 30\text{ }^{\circ}\text{C}$). Such
702 nocturnal basking behaviour was however seen in only 13 of the 29 freshwater turtle species
703 studied by McKnight *et al.* (2023), highlighting heterogeneity in the ability of diurnal species
704 to alter their nocturnal behaviour in a context of warming nights.

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

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

722 (3) Quantitative insights from the European common lizard

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

729 As expected, experimental and comparative studies have highlighted positive effects of
730 warmer nights. Notably, lizards exposed to warmer T_N showed increased growth rates and a
731 shorter gestation time. For example, a 40 day-long experimental exposure to warmer nights
732 (+5 °C) increased mean body growth rate in yearling individuals by almost 20%
733 (Rutschmann *et al.*, 2021). Furthermore, both experimental and comparative studies reported
734 positive effects on female reproductive phenology, with warmer nights (+5 °C) accelerating
735 gestation time by almost 30% (Brusch IV *et al.*, 2023). Other studies identified potential costs
736 of warmer T_N . First, energy allocation to rapid growth involves a trade-off with energy
737 reserves (i.e. energy storage). For example, yearling lizards exposed to warmer T_N during 38
738 days displayed higher growth rates, but also lower body condition and lower levels of fat
739 reserves (i.e. tail volume) than yearlings in the control treatment (Rutschmann *et al.*, 2021).
740 Similarly, in females, earlier parturition in a warmer nocturnal treatment was associated with
741 a smaller litter size (~5 versus 6 juveniles per litter) (Brusch IV *et al.*, 2023, Dupoué *et al.*, in
742 preparation), lower litter mass (~33% reduction in mass per juvenile) and lower *postpartum*
743 body condition (Brusch IV *et al.*, 2023). In both cases, it appears that significant quantities of
744 energy had to be mobilised to compensate for the accelerated pace of life, potentially
745 reducing the amount of energy available for other critical maintenance functions, such as
746 immunity (e.g. ectoparasite infestations; Rutschmann *et al.*, 2021). Contrary to our previous

747 predictions regarding enhanced generation of ROS from elevated metabolic rates, warmer T_N
748 did not result in higher levels of oxidative stress (no significant effect on oxygen metabolites
749 and non-enzymatic antioxidant capacity; Fig. 8) (Dupoué *et al.*, 2020; Rutschmann *et al.*,
750 2021). It remains difficult to conclude whether the absence of an oxidative stress response
751 reflects an actual absence of stress, whether individuals managed to mitigate this acute stress,
752 or whether the markers analysed were not appropriate to characterise the oxidative stress
753 related to increased resting metabolic activity and/or sleep deprivation (Zhang *et al.*, 2023).
754 In fact, in a comparative study across 10 populations, telomere length (an integrative measure
755 of cellular aging) was found to decrease at higher T_N (no effect of T_D was detected),
756 confirming that common lizards are physiologically challenged in warmer nocturnal
757 environments (Dupoué *et al.*, 2017b). This finding also confirms that T_N -related stresses can
758 have chronic effects. This conclusion was strengthened by a non-linear correlation between
759 T_N and the extinction risk of a population: collapsing populations experienced warmer
760 minimum T_N (Dupoué *et al.*, 2017b).

761 Other indirect arguments supporting a detrimental impact of warmer nights come from the
762 many relationships found between T_N and physiological and behavioural traits of common
763 lizards. There was a negative relationship between minimum T_N and baseline corticosterone
764 levels (a glucocorticoid-type hormone involved in energy regulation, immune reactions and
765 stress responses) of adult and yearling females (Dupoué *et al.*, 2018), with warmer nights
766 correlated with lower baseline corticosterone levels. The authors suggested that high T_N may
767 exacerbate chronic stress such that individuals regularly exposed to increased T_N
768 downregulate corticosterone secretion to reduce activity levels, mitigate maintenance costs,
769 and ultimately conserve energy and water. Other physiological parameters such as osmolality
770 changes (Brusch IV *et al.*, 2023), evaporative water loss (Dupoué *et al.*, 2017c), heating rates
771 (Rutschmann *et al.*, 2020), prey consumption rate (Brusch IV *et al.*, 2023) or changes in

772 dorsal colouration (Rutschmann *et al.*, 2021) were all correlated with T_N consistently with
773 buffering of the impact of warmer nights (Fig. 8). Note however that no behavioural
774 adjustment *via* thermoregulation preferences has been detected so far for the common lizard
775 (Rutschmann *et al.*, 2021; Rozen-Rechels *et al.*, 2021). Rather, unpublished results show an
776 opposite pattern: male common lizards favoured relatively warm nocturnal body temperatures
777 when exposed to a temperature gradient (10–50 °C) in thermal preference laboratory tests
778 (mean \pm SE: diurnal $T_{\text{pref}} = 29.9 \pm 2.35$ °C; nocturnal $T_{\text{pref}} = 26.7 \pm 3.3$ °C; C. Perry & J. Cote,
779 unpublished observations).

780 **VI. NOCTURNAL WARMING: OPEN QUESTIONS AND FUTURE RESEARCH**

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

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

785 The diel activity pattern describes when a species is most active during the day–night cycle
786 (i.e. diurnal, nocturnal or crepuscular), or whether it exhibits activity during both day and
787 night (i.e. cathemeral species) or whether it shows flexibility between different activity
788 strategies. It is thought that the ancestral state in reptiles was strict nocturnality. Yet,
789 diurnality is now the dominant pattern for many lizard species (around 70%) with
790 heterogeneous frequencies among clades (Kearney & Predavec, 2000; Gamble *et al.*, 2015;
791 Vidan *et al.*, 2017; Slavenko *et al.*, 2022). In snakes, ancestral clades are mostly nocturnal,
792 with the exception of derived species within the family Colubridae, which are mainly diurnal
793 (Gibbons & Semlitsch, 1987; Anderson & Wiens, 2017). In general, crepuscular or
794 cathemeral species are rarer in reptiles (i.e. 254 species identified in a recent review of the
795 literature; Cox & Gaston, 2023), and examples of intra-specific flexibility in daily activity
796 patterns are scarce (Abom *et al.*, 2012; Degregorio *et al.*, 2014; Vidan *et al.*, 2017). Reasons

797 for this lack of flexibility include sensory constraints, the role of predation or resource
798 availability, and adaptations to nocturnal life, including more efficient performance at low
799 than high temperatures, especially for locomotion (Autumn *et al.*, 1999; Llewelyn, Shine &
800 Webb, 2005; Ibarzüengoytía *et al.*, 2007; Anderson & Wiens, 2017; Dayananda, Jeffree &
801 Webb, 2020). Thus, most species might be constrained by their strict diurnal or nocturnal
802 lifestyles, with only a minority able to adjust their activity to warmer nocturnal climates
803 (McCain & King, 2014).

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

818 However, just as for diurnal species, an extension of activity into longer periods of the
819 night does not necessarily translate into fitness benefits in all nocturnal species. First, greater
820 opportunities for nocturnal activity can be limited by an increased risk of encountering
821 predators. Apart from nocturnal predators (which could also see their activity period

822 enlarged), diurnal predators could show a switch towards nocturnal activity and act as new
823 agents of selection. Second, as seen in *H. binoei* higher MRs during warmer nights need to be
824 balanced by higher resource acquisition. If prey activity does not match nocturnal predators'
825 increase in activity, encounter rates could decrease and nocturnal predators could face
826 metabolic meltdown (Huey & Kingsolver, 2019). Finally, for nocturnal species subject to
827 increasing T_N , the time spent at low temperatures ($T_e < VT_{\min}$) will be restricted to shorter
828 portions of the late night. Over the day, temperatures are often high enough to allow
829 thermoregulation and physiological activity, even within diurnal refuges (Kearney &
830 Predavec, 2000; Croak *et al.*, 2012; Chukwuka *et al.*, 2020). Thus, the time window available
831 for metabolic recovery may be limited and could shrink further in a context of nocturnal
832 warming, leading to long-term negative effects.

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

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

843 One major difference between climate zones is the magnitude of temperature variation at
844 annual, seasonal and diel scales (Janzen, 1967). Temperate-zone climates are highly seasonal,
845 with a pronounced difference in daily maximum and minimum temperatures during the
846 activity seasons of squamate reptiles (spring and summer). Daily temperature variation can be

847 higher in mediterranean, arid and semi-arid environments where the difference between daily
848 maximum and minimum T_e during summer often exceeds 30 °C. By contrast, tropical
849 environments, notably tropical forests, tend to exhibit low annual mean thermal oscillations,
850 even at high elevations (e.g. Janzen, 1967). As a consequence, the majority of tropical
851 squamate species tend to be thermal specialists (stenothermic) [see Van Berkum (1986) and
852 de Souza Terra, Ortega & Ferreira (2018) for tropical savannas] because of the low
853 seasonality in temperature and the relative homogeneity of their thermal environment
854 (Tewksbury, Huey & Deutsch, 2008; Huey *et al.*, 2009). By contrast, high heterogeneity in
855 the thermal landscape across temperate or arid habitats has favoured the evolution of
856 heliothermy, which allows squamates to regulate their body temperature over a wide thermal
857 tolerance range. It is therefore likely that the effect of warmer nights on squamate reptiles
858 will vary across biomes because of differences in exposure and behavioural sensitivity to
859 nocturnal warming.

860 It is crucial also to consider physiological adaptations to climatic zones. So far, we have
861 mainly focused our attention on species inhabiting temperate zones. Cold-adapted squamates
862 are often strictly diurnal and have higher SMRs than warm-adapted species (Lourdais *et al.*,
863 2013; Dupoué, Brischoux & Lourdais, 2017a; Sun *et al.*, 2022), which may be particularly
864 disadvantageous in the context of a passive resting temperature increase induced by nocturnal
865 warming. On the other hand, tropical squamates often show lower CT_{max} and narrower TPCs
866 (Garcia-Robledo *et al.*, 2018) than squamates from temperate climate zones. Because nights
867 are already warm in tropical environments, an increase in T_N should not impact the low-
868 temperature region of the TPC, but could affect its upper region, moving individuals closer to
869 their CT_{max} . One consequence of this is that the effects of warmer nights could vary across
870 biomes: being chronic and long-term in some areas (e.g. temperate zone), whereas acute
871 and immediate in others (e.g. tropics).

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

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

882 Because of seasonal variation, fluctuations in prey density or predation risk, reptiles face
883 constraints on their ability to acquire, store and spend energy (Sinervo & Licht, 1991; Bleu *et al.*
884 *al.*, 2013; Arnall *et al.*, 2019), and there will be multiple trade-offs in energy allocation
885 among maintenance, growth, reproduction and survival. Such trade-offs among life-history
886 traits are known to vary with individual characteristics, but also with local conditions
887 (Ernande *et al.*, 2004; Sgrò & Hoffmann, 2004; Rutschmann *et al.*, 2016). Through its
888 contrasting influence on different physiological and behavioural processes (Clark *et al.*,
889 2013), nocturnal warming may also affect these life-history trade-offs (e.g. levy their
890 intensity or shift their relative importance). For example, nocturnal warming alters energy
891 allocation rules in juvenile common lizards, with individuals exposed to warmer T_{NS} being
892 more likely to invest in immediate growth rather than long-term reserves (Rutschmann *et al.*,
893 2021). How this could influence winter survival and next-season reproduction is yet to be
894 explored (Bestion *et al.*, 2015). In the same species, T_N also influenced energy allocation in
895 adult females (Brusch IV *et al.*, 2023), with colder T_N resulting in lower litter mass and

896 longer gestation. Interestingly, warmer days had the opposite effect, highlighting the
897 contrasting impacts of T_D and T_N (Speights & Barton, 2019).

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

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

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

920 summer or heatwaves) can result in diet and microhabitat-use changes (Sperry *et al.*, 2013;
921 Mata-Silva *et al.*, 2018; Lara Resendiz, 2019).

922 Further, ectothermic vertebrates are frequently involved in mutualistic associations with
923 symbionts and microbiota crucial for digestion or nutrient acquisition (Shigenobu, Watanabe
924 & Hattori, 2000). The microbiome also plays essential roles in behaviour, immunity, and life
925 history (Macke *et al.*, 2016). Whether effects of nocturnal warming on an individual's
926 microbiota differ from effects of diurnal warming (Bestion *et al.*, 2017; Moeller *et al.*, 2020)
927 is difficult to determine. However, the dynamics of the microbiome is shaped both by the
928 thermal tolerance capacities of the symbionts and by the temperature-dependent immune
929 responses of the individual hosts (Ferguson, Heinrichs & Sinclair, 2016; Goessling &
930 Mendonça, 2016; Abram & Dixon, 2017). By affecting the body temperature or the
931 thermoregulatory behaviour of the host, warmer nights therefore have the potential to affect
932 microbiome dynamics and ultimately to impact the fitness of the ectotherm (Burke *et al.*,
933 2010; Higashi, Barton & Oliver, 2020).

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

936 Global change is undoubtedly multi-factorial and, among other parameters, warmer T_{NS} are
937 likely to be accompanied by changing precipitation and snow regimes (Yang *et al.*, 2016;
938 Dai, Zhao & Chen, 2018), water temperatures (Nordberg & McKnight, 2023), heatwave
939 intensity and frequency (Meehl & Tebaldi, 2004; Sanderson, Hemming & Betts, 2011;
940 Murali *et al.*, 2023), or habitat quality and diversity (Hoekstra *et al.*, 2005). Nocturnal
941 warming is likely to reduce the quality of rest periods for diurnal species and their ability to
942 recover from diurnal stressors. Thus, it could exacerbate the already detrimental effects of
943 other diurnal environmental changes. For example, warmer T_{NS} have been found to reduce
944 the longevity and fecundity of English grain aphids when combined with warm T_{DS} (Zhao *et*

945 *al.*, 2014). Warmer nocturnal temperatures were also reported to exacerbate the detrimental
946 effects of metallic pollutants on amphibian species (Hallman & Brooks, 2015) and to interact
947 with light pollution to alter the food-chain dynamics of aphids and ladybirds (Miller *et al.*,
948 2017). Further research investigating interactions between distinct components of global
949 change and nocturnal warming could provide a more complete picture of how ectotherms will
950 respond to future modifications of their environment.

951 **VII. CONCLUSIONS**

952 (1) Nocturnal warming is an understudied aspect of global warming. Using diurnal squamates
953 as a model taxon, we demonstrated that impacts of warmer nights can be very different from
954 those of T_D increases.

955 (2) Because they affect the coldest hours of the diel cycle, usually dedicated to rest in diurnal
956 species, warmer T_{NS} have the potential to alter the time budget dedicated to the different
957 activity phases of diurnal ectotherms. Whether warmer nights are beneficial or detrimental
958 will ultimately depend on the balance between energy acquisition and expenditure.

959 (3) Because warmer nights allow an increase in performance, they may have positive effects
960 as long as they also allow species to (i) acquire sufficient energy to meet their increased
961 metabolism, and (ii) rest sufficiently to recover and eliminate metabolic stressors produced
962 by elevated metabolic activity. If individuals cannot fulfil these conditions, warmer nights
963 could be deleterious.

964 (4) Because T_{NS} are far from upper CT_{max} , any effects of increasing T_N are not as immediate
965 as effects of warmer maximum T_D . Instead, warmer nights may impose chronic costs
966 accumulating over an individual's lifetime and leading to a reduction in lifetime fitness.
967 Whether such negative effects can be compensated by behavioural or physiological
968 adjustments is yet to be evaluated for most ectothermic species.

969 (5) Many important questions remain unanswered, including whether there are differences
970 among species with different behavioural strategies, differences between climate zones and
971 effects on ecological interactions between squamates and their prey, predators and
972 microbiome. New research programs and new protocols will be necessary to explore
973 nocturnal warming as a key element of global warming. While legacy data can be re-analysed
974 to answer some of these questions, others will require novel explorations of the night-time
975 behaviour, physiology and population ecology of reptiles.

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991 **IX. AUTHOR CONTRIBUTIONS**

992 A.R. drafted the manuscript, performed the literature review and supervised the project. C.P.
993 helped with the literature review, carried out the experiment for Section III.1 and analysed

994 data together with A.R. J.F.I.G. designed the model and scenarios for Sections IV.1–3 and
995 performed computation together with A.R., analysed data (collected by G.B.) and drafted
996 Sections IV.4 and VI.1. A.D. performed the statistical analyses for Section V.3 and drafted
997 that section. M.G. collected data for Section III.3 under the supervision of O.L. who analysed
998 data and drafted that section. M.R., J.Co. and J.Cl. helped discuss the results and provided
999 critical feedback on the manuscript. D.B.M. collected data for Section II.3, analysed the data
1000 and drafted that section, helped with the literature review and drafted Sections VI.2 and VI.3.
1001 A.R., A.D., J.Cl. and D.B.M. conceived the original idea of the project. All authors
1002 contributed to the final version.

1003 **X. REFERENCES**

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1005 information.

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1620 **XI. SUPPORTING INFORMATION**

1621 Additional supporting information may be found online in the Supporting Information section
1622 at the end of the article.

1623 **Appendix S1.** Saguaro National Park legacy operative environmental temperature data.

1624 **Appendix S2.** Diurnal and nocturnal metabolic rates of *Podarcis muralis*.

1625 **Appendix S3.** Summer heatwave and nocturnal warming: a case study in a diurnal snake.

1626 **Appendix S4.** Bioenergetic modelling of energy balance.

1627 **Appendix S5.** Empirical analysis of energy balance.

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1630 FIGURE CAPTIONS

1631 **Fig. 1.** Impact of warmer days and nights on individual performance. In ectotherms the
1632 temperature dependence of biological processes is conceptualised as a thermal performance
1633 curve (TPC). The curve describes the response of performance traits to changes in body
1634 temperature. Because of the left-skewed bell shape of the TPC, it is assumed that increasing
1635 temperatures near or at the critical thermal maximum (CT_{max}) have a large and negative
1636 instantaneous impact on performance (orange arrow). On the other hand, a similar increase in
1637 temperature at or near the critical thermal minimum (CT_{min}) is presumed to have a positive,
1638 but smaller, instantaneous impact on performance (blue arrow). In addition, warmer
1639 minimum temperatures during the night can push body temperature away from CT_{min} and
1640 towards the optimal body temperature (T_{opt}), hence allowing higher levels of performance.
1641 Modified from Speights *et al.* (2017).

1642

1643 **Fig. 2.** Impact of warmer nocturnal temperatures on the nocturnal activity and energy budget
1644 of squamate reptiles. Warmer nocturnal temperatures are expected to modify opportunities
1645 for activity (A); as nocturnal temperatures increase, operative temperatures (y-axis) are likely
1646 to exceed the minimum voluntary temperature (VT_{min}) (horizontal broken line) later at night
1647 and earlier in the morning (black arrows), offering increased opportunities for foraging or
1648 physiological activity. The gain in potential activity time is represented by the yellow shaded
1649 area. This extension of activity occurs at the detriment of resting time (blue area), potentially
1650 affecting the quality of physiological recovery. From an energy budget perspective (B),
1651 compared to a cold night (pale green or pale orange), warmer nights (dark green or dark
1652 orange) may offset the balance between energy income (green lines) and metabolic expenses
1653 (orange lines). Activity extension can offer opportunities for foraging or assimilation over a

1654 larger part of the day, hence increasing the energetic intake (green shaded area). On the other
1655 hand, warmer nocturnal activity can also increase nocturnal metabolic and physiological
1656 activity, therefore raising energetic expenses over the night (orange shaded area). The overall
1657 energetic costs and benefits of warmer nocturnal temperatures will depend on the balance
1658 between these two processes.

1659

1660 **Fig. 3.** Temporal pattern of diurnal and nocturnal operative temperatures recorded in mid-late
1661 spring on mesquite trees exploited by the diurnal ornate tree lizard (*Urosaurus ornatus*), in
1662 the desert of Saguaro National Park (Arizona, USA). Dots represents average minimum
1663 (blue) or average maximum (yellow) temperature recorded each year. Vertical bars represent
1664 standard deviation from the mean.

1665

1666 **Fig. 4.** Diurnal and nocturnal metabolic rates of 65 male wall lizards (*Podarcis muralis*) at
1667 four different temperatures. Resting metabolic rate (RMR) was measured three times for each
1668 individual at each temperature, at rest (no locomotor activity and in a post-prandial
1669 physiological state) during the active (diurnal) phase of the diel cycle (measurements took
1670 place between 10:00 and 16:00). Standard metabolic rate (SMR) was also measured three
1671 times for each individual at each temperature, during the inactive (nocturnal) phase of the diel
1672 cycle (measurements took place between 22:00 and 04:00). From bottom to top, horizontal
1673 lines represent the 25th percentile (Q1), the median and the 75th percentile (Q3) of each group.
1674 Vertical lines represent the minimum (Q1 – interquartile range) and maximum (Q3 +
1675 interquartile range) values. Dots represents outliers. See Appendix S2 for further details.

1676

1677 **Fig. 5.** Mean daily variation in body temperature in six asp vipers (*Vipera aspis*) (solid blue
1678 line) shows a close match with minimum shelter temperatures measured using biomimetic

1679 models ($N = 3$; solid black line) over the course of the night. Mean surface temperatures ($N =$
1680 3 biomimetic models; solid yellow line) often exceeded the preferred body temperature of *V.*
1681 *aspis* (mean \pm SD $T_{\text{pref}} = 30.63 \pm 4.22$, dashed black line; Lориoux *et al.*, 2013), highlighting
1682 the ability of this species to thermoregulate efficiently during the day while being more
1683 thermally passive in their shelter over the night. Periods of heatwaves (as defined by Météo
1684 France) are shaded in light grey (hot; T_{max} 30–35 °C) and dark grey (extremely hot; $T_{\text{max}} > 35$
1685 °C). Note that this classification was made at a regional level, leading to some mismatches
1686 with our data set.

1687

1688 **Fig. 6.** Relationship between nocturnal minimum environmental temperature recorded in a
1689 shelter and mean asp viper (*Vipera aspis*) nocturnal body temperature. Nocturnal
1690 temperatures were recorded from 22:00 to 08:00. Data are plotted separately for three
1691 different categories of day according to Météo France classification: normal (maximum air
1692 temperature in the shade < 30 °C; blue), hot (30–35 °C; yellow), and very hot (> 35 °C; red).
1693 Solid lines represent the estimated slope and shaded regions the 95% confidence intervals.
1694 The black dashed line is $y = x$.

1695

1696 **Fig. 7.** Daily net energy gain (NEG_d) predicted by our energy budget model for different
1697 thermoregulation behaviours (thermoconformer *versus* thermoregulator), ecological
1698 behaviours (diurnal *versus* nocturnal) and default metabolic rates at 20 °C (DMR_{20}). For each
1699 increment of daily minimum nocturnal temperature tested (0–30 °C), a daily temperature
1700 cycle was created (see Fig. S3). NEG was then calculated hourly for each temperature cycle,
1701 before being integrated over 24 h to obtain one NEG_d value for each minimum nocturnal
1702 temperature. Scenario 1 represents a thermoconforming ectotherm with no time constraints
1703 on activity. Scenario 2 represents a thermoconforming ectotherm with strictly diurnal

1704 foraging activity. Scenario 3 represents a thermoregulator (preferred temperature $T_{\text{pref}} = 30$
1705 °C) with a 24 h active phase bounded by voluntary thermal limits (18 – 40 °C). Scenario 4
1706 represents a perfect thermoregulator ($T_{\text{pref}} = 30$ °C), bounded by voluntary thermal limits and
1707 with a strict diurnal activity phase. Scenario 5 represents a perfect thermoregulator ($T_{\text{pref}} = 30$
1708 °C) with a nocturnal activity phase, bounded by voluntary thermal limits (15 – 35 °C). The
1709 different colours represent curves for different DMR_{20} values. DMR_{20} is expressed as a
1710 percentage of the daily maximum energy intake, and can be interpreted as a proxy for animal
1711 size, with larger animals having a lower metabolic rate. Circles show the optimum minimum
1712 nocturnal temperature ($T_{\text{N, opt}}$) and represent a tipping point between positive and negative
1713 effects of nocturnal temperature on daily net energy gain. Pictograms indicate the ecological
1714 and thermoregulatory characteristics of the simulated ectotherms.

1715
1716 **Fig. 8.** Plot of effect sizes (Cohen's d) for the effects of warmer nocturnal temperatures (T_{N})
1717 on phenotypic traits of the common lizard (*Zootoca vivipara*). Correlative studies are shown
1718 in orange and experimental studies in grey. Stars indicate significance level (***, $P < 0.001$;
1719 **, $P < 0.01$; *, $P < 0.05$). Cohen's d and associated 95% confidence intervals were estimated
1720 using the t_to_d function in R (*effectsize* package; Ben-Shachar *et al.*, 2020) for all traits
1721 other than the heating rates variables, for which non-linear mixed effect models were used
1722 (*lme.dscore* function in *EMAtools* R package; Kleiman, 2022) and confidence intervals could
1723 not be calculated. BC, body condition; CORT, corticosterone; LM, litter mass; LS, litter size;
1724 OXY, oxygen metabolites; ROM, non-enzymatic antioxidant capacity; SVL, snout–vent
1725 length; TL, telomere length; T_{pref} , preferred body temperature. ‘Levels’ indicates measures
1726 from comparative studies. ‘Change’ indicates measures implying an experimental design
1727 where levels were compared before and after treatments. List of publications: a. Dupoué *et al.*
1728 (2017b); b. Dupoué *et al.* (in preparation); c. Bruschi *et al.* (2023); d. Rutschmann *et al.*

1729 (2021); e. Dupoué *et al.* (2018); f. Rutschmann *et al.* (2020); g. Dupoué *et al.* (2017c); h.

1730 Dupoué *et al.* (2020); i. Rozen-Rechels *et al.* (2021).

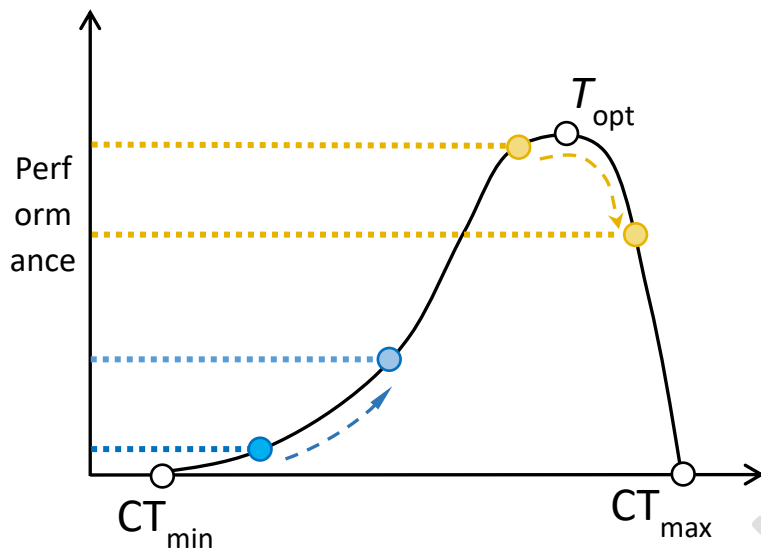
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1733 **Figure 1**

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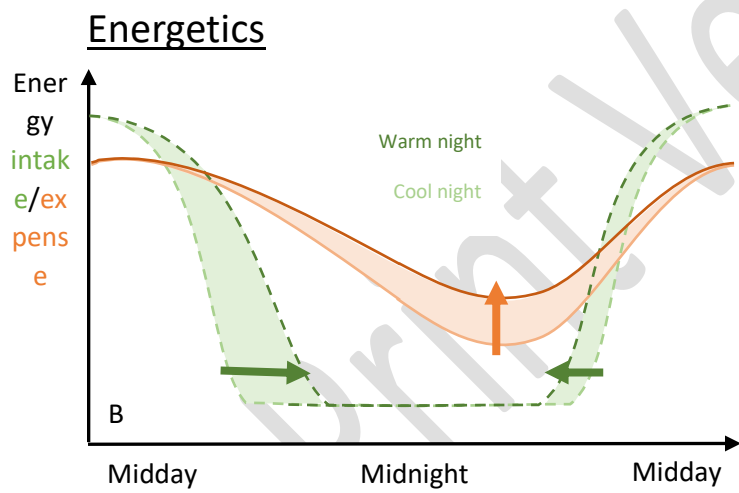
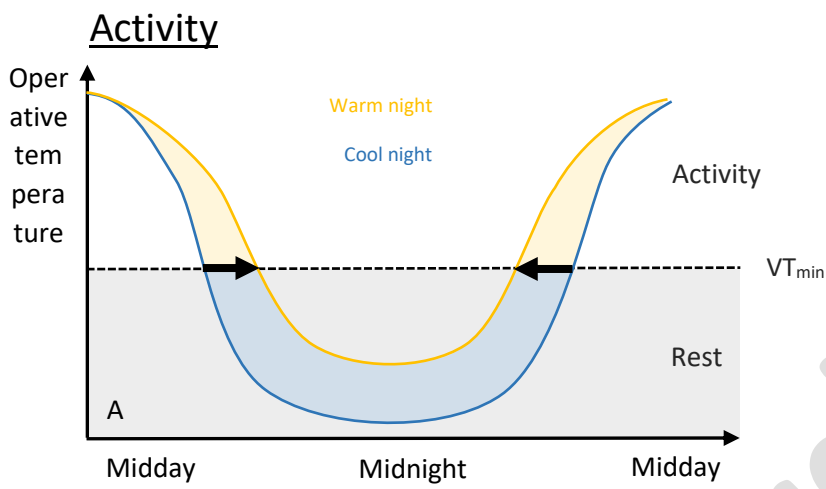
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1736 **Figure 2**

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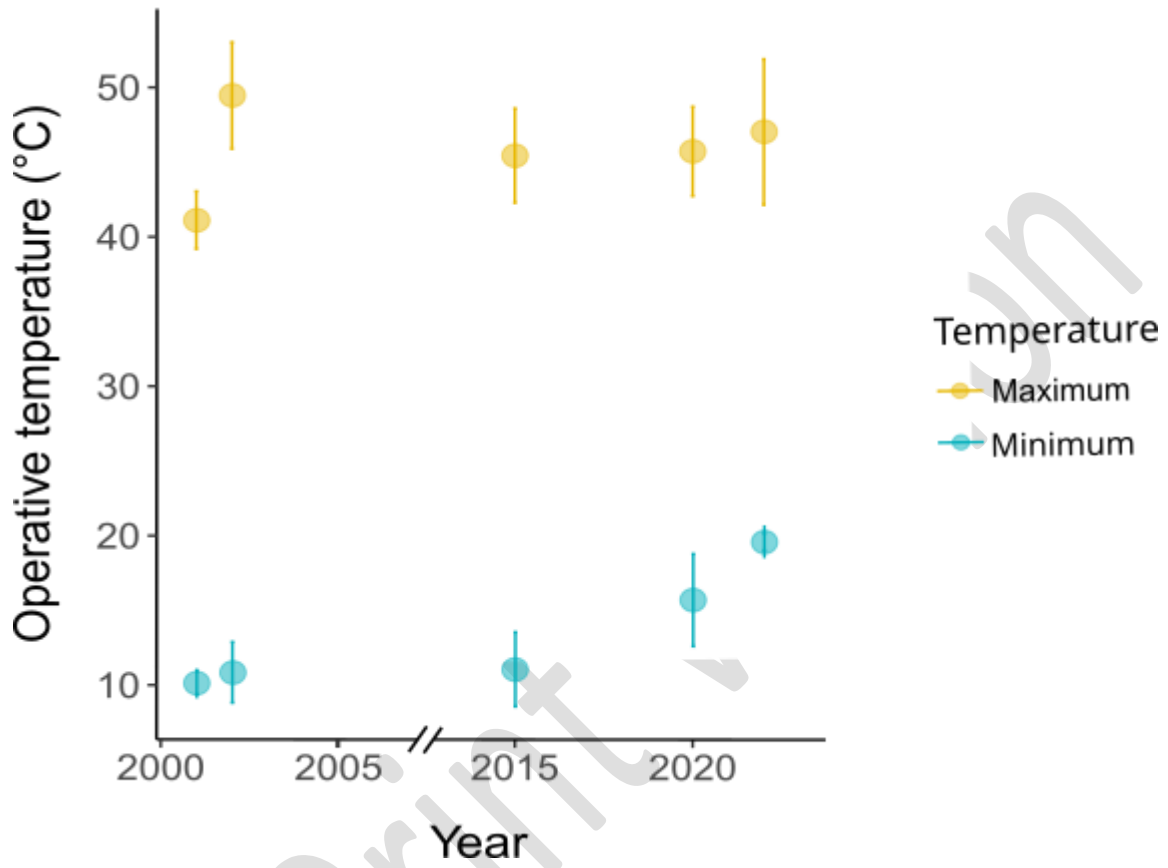
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1741 **Figure 3**

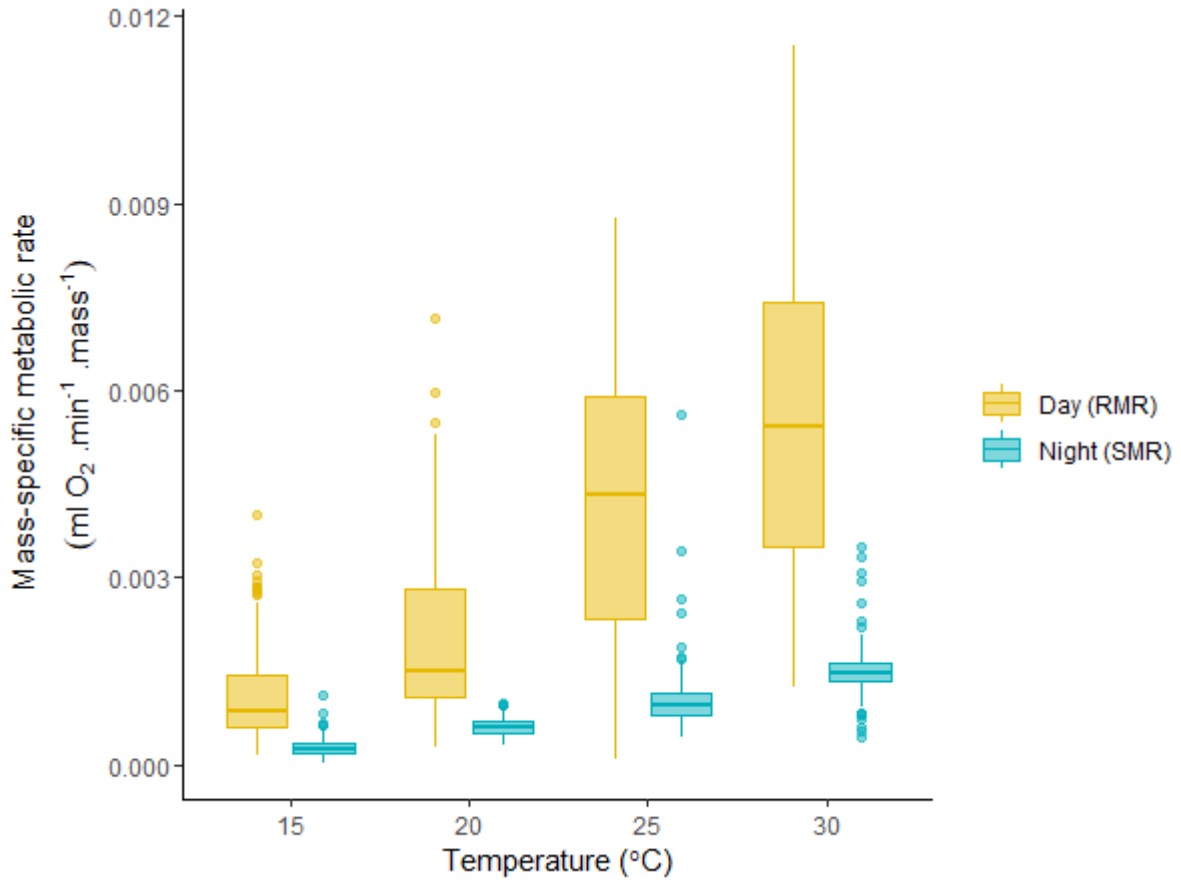


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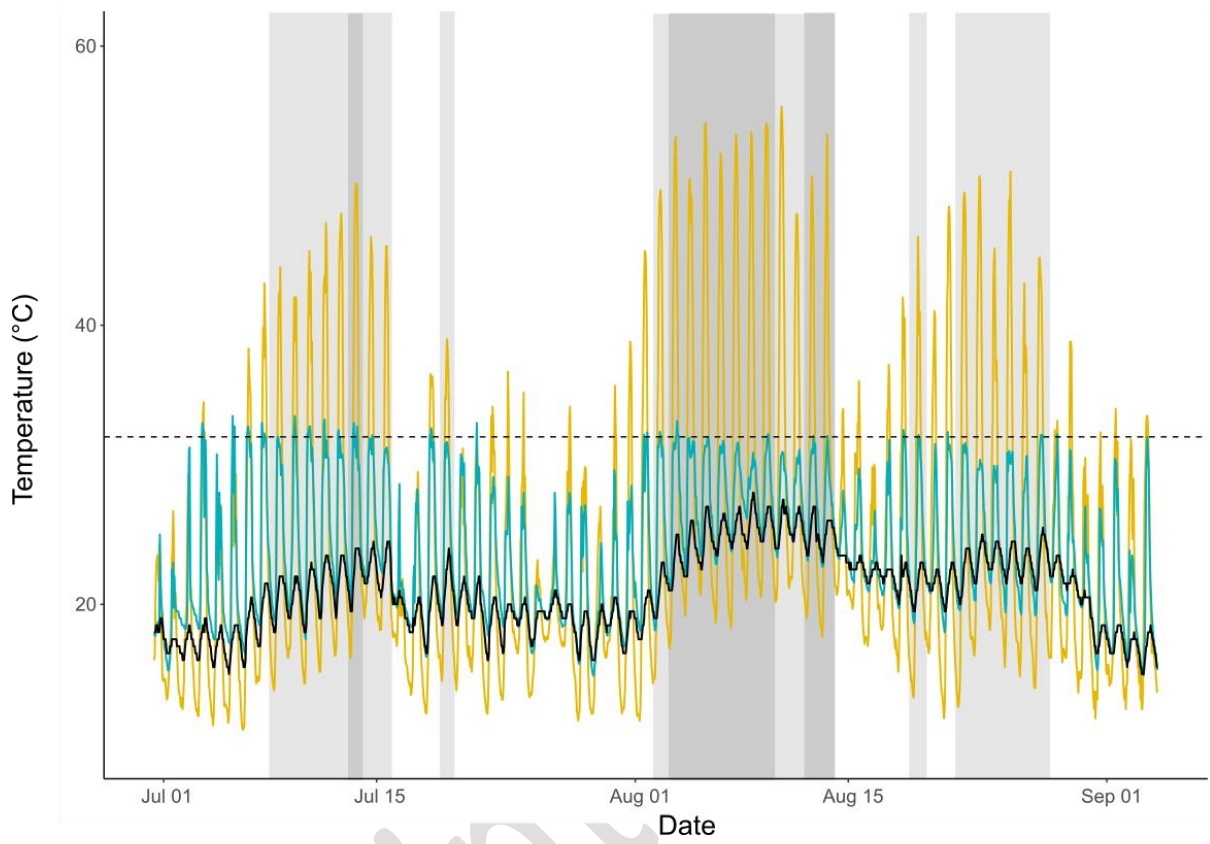
1745 **Figure 4**



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1748 **Figure 5**

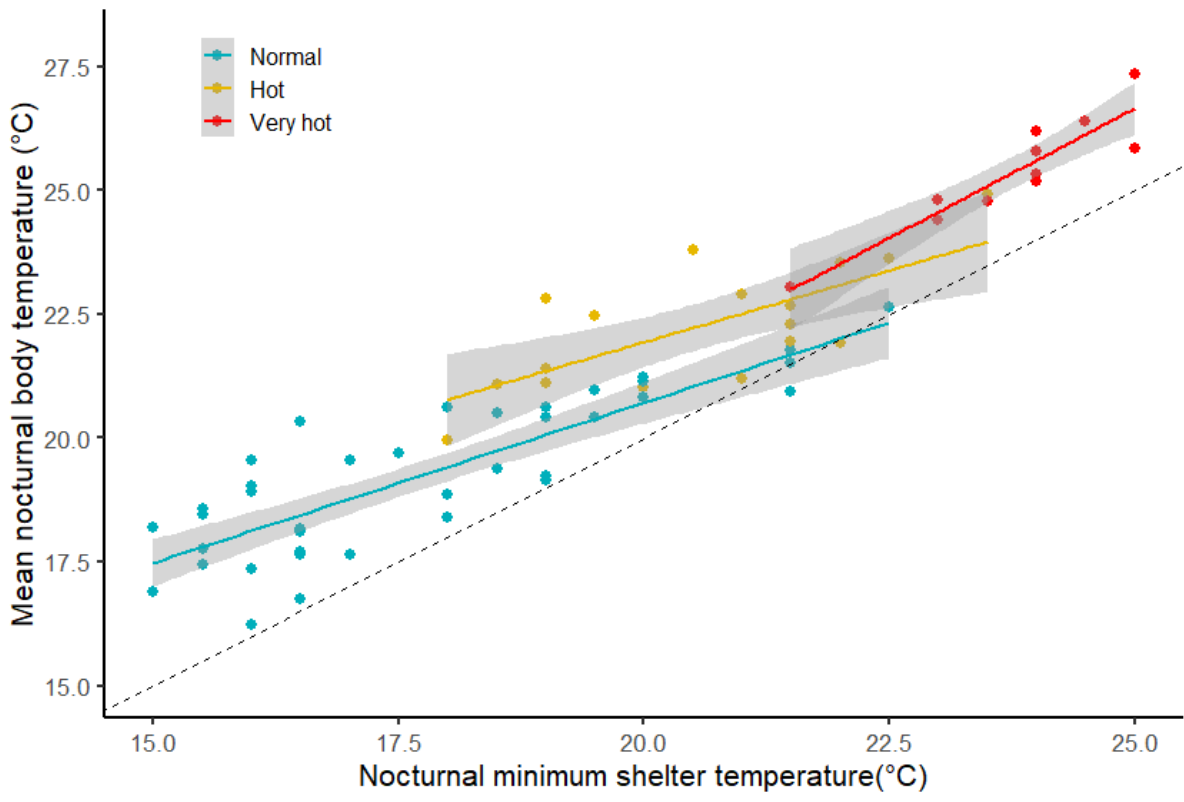


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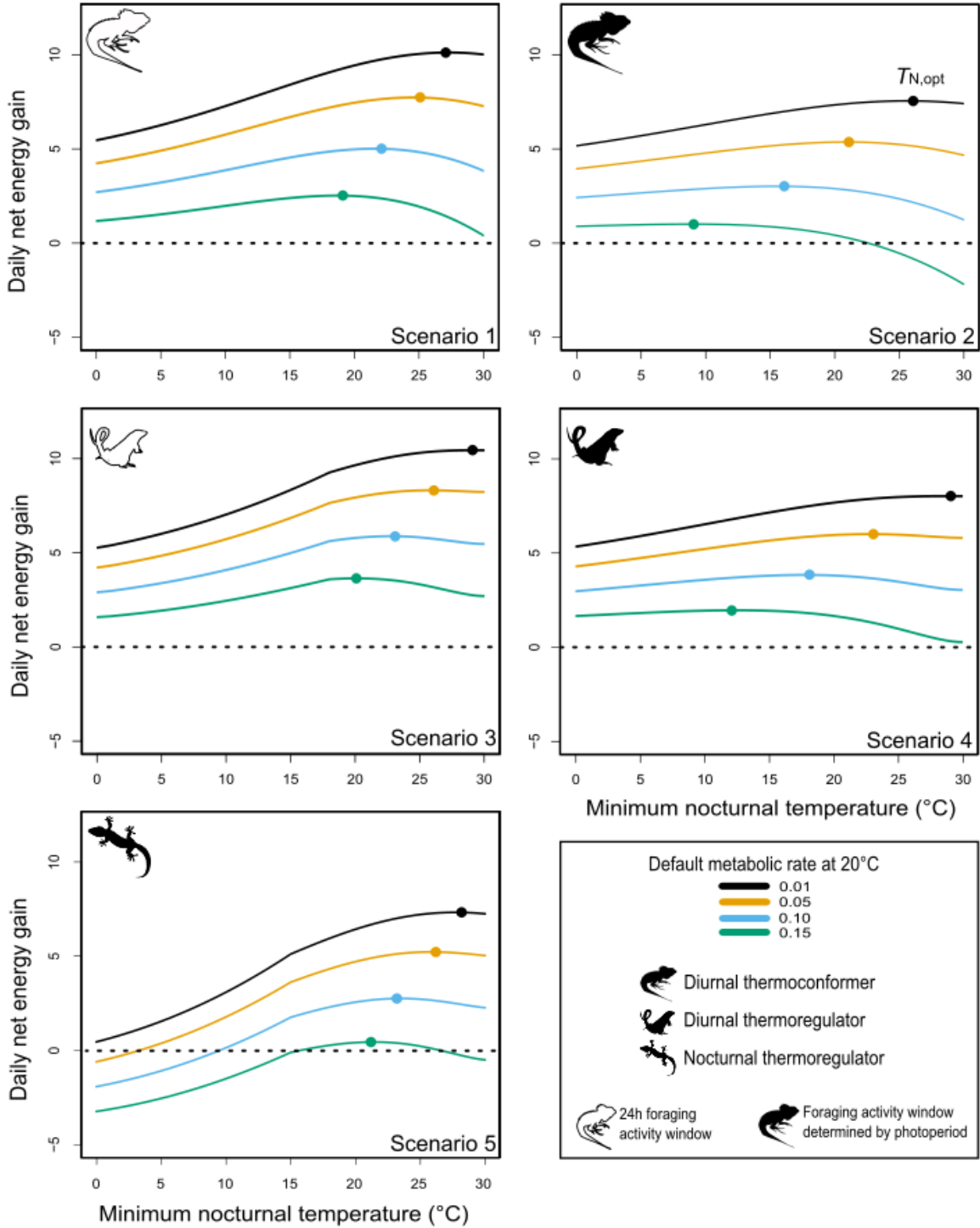
1751 **Figure 6**



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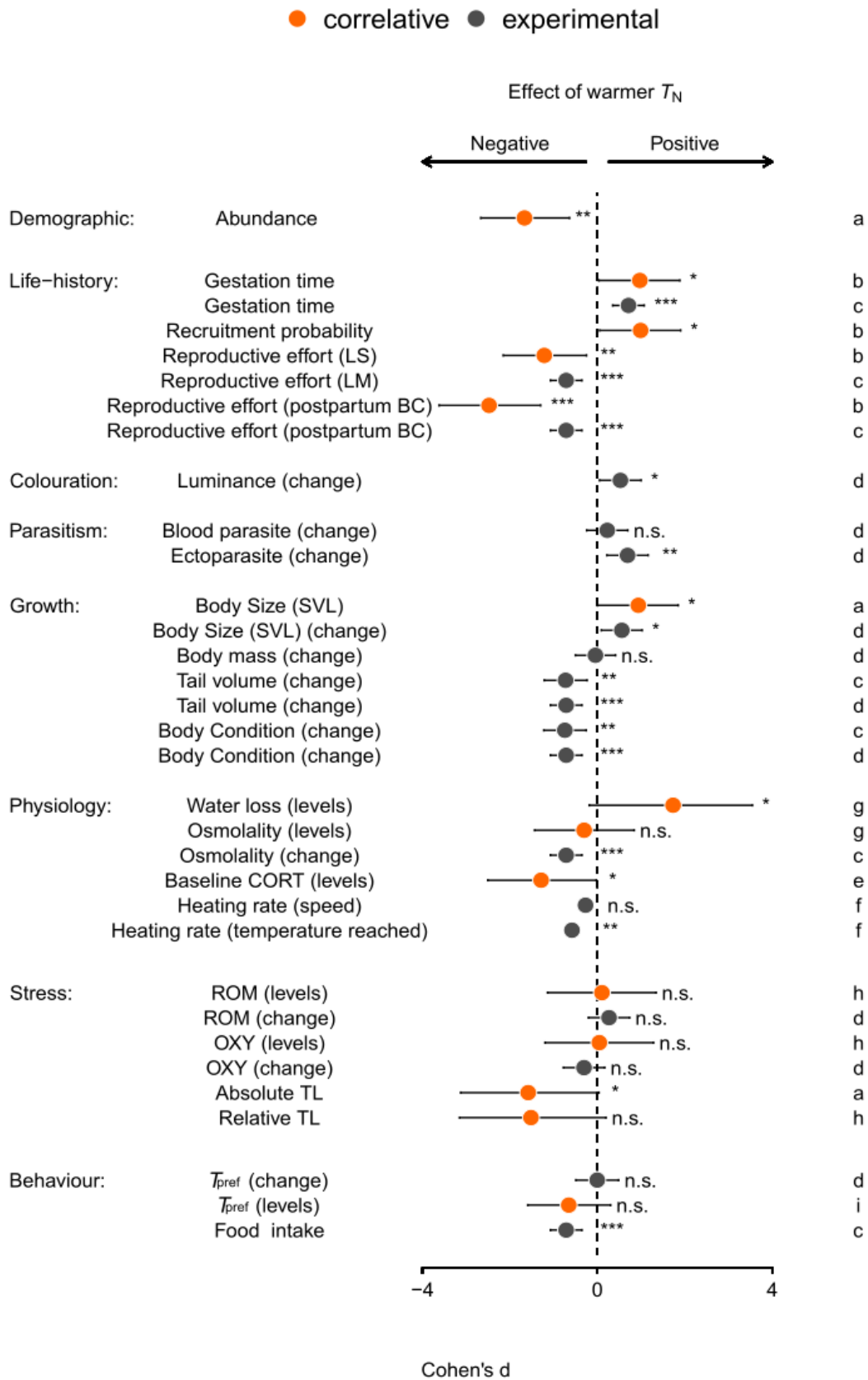
1754 **Figure 7**



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1757 **Figure 8**



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1761 Table 1. Summary of the scenarios tested using our energy balance model. AR, attack rate;
1762 IR, ingestion rate; MR, metabolic rate. All rates (AR, IR and MR) were dependent on
1763 temperature. Depending on the scenario, AR was either positive throughout the 24 h diel
1764 cycle, only diurnal (positive from 07:00 to 20:00), only nocturnal (positive from 20:00 to
1765 07:00) or constrained by a temperature window (e.g. positive when $T \geq 18$ °C and $T \leq 40$ °C).
1766 See Section IV.2 and Appendix S4 for detailed description of each scenario.

1767

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

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1771 **ECOLOGICAL RESPONSES OF SQUAMATE REPTILES TO NOCTURNAL**

1772 **WARMING - Supporting Information**

1773

1774

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1815

1816 Appendix S5. Empirical analysis of energy balance

Appendix S1. Saguaro National Park legacy operative environmental temperature data

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1818

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1820 (1) Study system

1821 D.B. Miles measured operative environmental temperatures (T_e s) at Saguaro National Park (SNP,
 1822 Arizona, USA). T_e s represent the body temperature of an inactive ectotherm in a given microhabitat
 1823 and were originally recorded to estimate the thermal quality of the habitat exploited by the diurnal
 1824 ornate tree lizard (*Urosaurus ornatus*). At SNP, these lizards are arboreal and occupy mesquite
 1825 (*Prosopis velutina*) and paloverde (*Parkinsonia aculeata*) trees. In mid-late spring (~25 May – 15
 1826 June) 2001, 2002, 2015, 2020 and 2022, 2–4 biomimetic lizard-shaped models made of polyvinyl
 1827 chloride (PVC) were placed on the same trees used by lizards for a period of 5–15 days. The sensors
 1828 within these models were programmed to record T_e every 5 min over a 24-h period.

1829 (2) Statistical analyses

1830 Each year, and for each biomimetic logger, we extracted the minimum and maximum temperatures
 1831 recorded each day. We then calculated the mean daily minimum and mean daily maximum T_e
 1832 among loggers to obtain a single value for each day. We used a linear model to investigate whether
 1833 T_e changed significantly over the study period. In the model, we also included an interaction term
 1834 between time of day (i.e. minimum or maximum temperature) and year (as a continuous factor). The
 1835 interaction term was statistically significant: minimum T_e increased faster than maximum T_e in SNP
 1836 over the period 2001–2022 (see Table S1).

1837 **Table S1.** Results of ANOVA linear model relating mean daily operative environmental temperature
 1838 (T_e) to study year, time of the day (i.e. minimum or maximum T_e) and their interaction term.

Explanatory variables	Df	Mean Sq.	F value	P
Year	1	51.9	4.18	0.04
Time of day	1	18464.9	1488.78	<0.005
Year × Time of day	1	111.1	8.89	<0.005
Residuals	63	12.4	–	–

1839 Although we were interested in the trend in temperature changes, note that the difference over the
 1840 study period was 5.56 °C for maximum T_e and 9.37 °C for minimum T_e . The absolute change in
 1841 minimum and maximum T_e over the period 2001–2022 was estimated as the difference between the
 1842 median values obtained for the minimum and maximum T_e recorded in 2022 and 2001.

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1845 Appendix S2. Diurnal and nocturnal metabolic rates of *Podarcis* 1846 *muralis*

1847

1848 **(1) Study species**

1849 The wall lizard (*Podarcis muralis*; Laurenti 1768) is a small heliothermic and strictly diurnal squamate
1850 widespread in Central Europe. Males ($N = 65$) were captured by C. Perry and A. Rutschmann
1851 between April 8 and 17 2022 using the lasso method (Blomberg & Shine, 2006) at three sites, all
1852 located within a 10 km radius of the Station d'Ecologie Théorique et Expérimentale (SETE, Moulis,
1853 France 42°57'26.8" N, 1°05'08.3" E; 436 m ASL). Immediately after capture, we measured body mass
1854 (mean \pm S.D.: 7.17 ± 0.81 g) and snout–vent length (SVL = 69.09 ± 2.69 mm). Lizards were
1855 transported to temperature-controlled environment chambers located in the SETE where they were
1856 marked using a cautery pen with a unique identification number on their ventral scales (Vervust &
1857 Van Damme, 2009). For logistic reasons, lizards were acclimated in pairs in plastic enclosures ($56 \times$
1858 39×28 cm). Each enclosure contained a thin layer of wood straw as a substrate, a water supply,
1859 paving stones used as thermoregulation platforms ($15 \times 15 \times 6$ cm) and two plastic refuges for
1860 sheltering. Every second day, lizards were fed *ad libitum* with mealworms (*Tenebrio* sp. larvae) and
1861 crickets (*Acheta domestica*). Water was provided *ad libitum*. Terraria were misted with a water
1862 sprayer every second day in the morning (08:00). An ultraviolet lamp provided light for 12 h per day
1863 (07:00–19:00). Each tank was heated with an incandescent heat lamp (42 W) for 6 h per day at 1 h
1864 intervals. This provided a diurnal thermal gradient ranging from 24 to 36 °C, a range that includes
1865 the preferred body temperature (T_{pref}) for thermoregulation in this species ($T_{\text{pref}} = 32.9$ °C)
1866 (Bodensteiner *et al.*, 2021). During the night, the lamp was switched off, with nocturnal air
1867 temperature (T_{N}) controlled at 17 °C in the environmental chambers.

1868 **(2) Experimental design**

1869 Forty-five days after capture, we measured both diurnal and nocturnal metabolic rate (MR). For each
1870 individual, six measurements were made at each of four different body temperatures (15, 20, 25, 30
1871 °C), which includes the range of body temperatures over which MR increases exponentially (C. Perry,
1872 personal observations). Following Andrews & Pough (1985), for each body temperature resting MR
1873 (RMR) was measured three times during the active phase of the day (10:00–16:00), while standard

1874 MR (SMR) was measured three times during the resting phase of the day (22:00–04:00). Prior to the
1875 experiment, lizards were randomly assigned to a group of 5–7 individuals (10 groups in total) and
1876 each group was randomly assigned to one of the four temperatures. Both diurnal and nocturnal MR
1877 were measured for the given temperature, and three groups were tested, within a single 24-h diel
1878 cycle. Before being tested again at a different randomly chosen temperature, lizards were allowed to
1879 rest for at least 24 h. The experiment lasted 13 days and nights in total.

1880 **(3) Measurement of metabolic rates**

1881 Thirty minutes prior to MR measurements, lizards were individually placed in a black canvas sock (10
1882 cm × 4 cm), within one of the eight 75 ml opaque plastic metabolic chambers of an incubator
1883 (Aqualytic Incubator TC 140 G, Germany). After this acclimation period, chambers were closed for
1884 three sessions of 15 min each to measure oxygen consumption (PreSens© OXT-4 SMA system)
1885 (Warkentin *et al.*, 2007). Between each session, chambers were opened for 15 min to allow
1886 replacement of oxygen. One of the eight metabolic chambers, which was always the same, remained
1887 empty to serve as a control. Individual MRs were then obtained as the slope (β) of the oxygen
1888 consumption curve as a function of time. To calibrate MR (Warkentin *et al.*, 2007), each β value was
1889 corrected by the average slope (β_{control}) recorded within the control chamber at each temperature
1890 (Andrews & Pough, 1985). Then, MR was estimated as:

$$\text{MR} = \frac{(V_{\text{chamber}} - V_{\text{id}}) * \%O_2 * (\beta - \beta_{\text{control}})}{100} \quad (\text{S1})$$

1891 where V_{chamber} is chamber volume, V_{id} is individual volume (approximated as individual mass), and
1892 $\%O_2$ is the initial proportion of oxygen in the chamber. RMR and SMR were further adjusted by
1893 individual mass following Brown *et al.* (2004) to give mass-specific metabolic rates:

$$\text{MR}_m = \frac{\text{MR}}{\text{Mass}^\alpha} \quad (\text{S2})$$

1894 with α estimated as the slope coefficient of the linear regression between mass and metabolic rate
1895 (0.74 for RMR and 0.91 for SMR).

1896 **(4) Statistical analyses**

1897 All statistical comparisons were performed in R software version 4.2.3. We used a linear mixed-
1898 effects model to test whether the reaction norm (i.e. temperature dependence of MR) varied
1899 significantly between day (RMR) and night (SMR) measurements. In the model, we also included an
1900 interaction term between the time of the day (i.e. SMR *versus* RMR) and temperature. We included

1901 individual as a random effect to control for repeated measures. The interaction term was significant,
1902 with RMR increasing faster with temperature than SMR.

1903 **Table S2.** Results of ANOVA linear model relating metabolic rate to the time of the day [i.e. whether
1904 standard metabolic rate (night) or resting metabolic rate (day) was measured], temperature and
1905 their interaction term.

Explanatory variables	Numerator DF	Denominator DF	F value	P
(Intercept)	1	1534	812.6	<0.005
Time of day	1	1534	1418.6	<0.005
Temperature	1	1534	1678.4	<0.005
Interaction (Temperature × Time of day)	1	1534	482.7	<0.005

1906

1907 We also analysed the variance between temperatures in each metabolic rate group using the
1908 *leveneTest* function in R (Fox, 2016). The variance in MR was significantly different between SMR and
1909 RMR across all temperatures ($F_{7,1594} = 221.4, P < 0.005$). A graphical representation of the data (see
1910 Fig. 4 in the main article) confirms that variance increased with temperature, especially for RMR.

1911

1912 **Appendix S3. Summer heatwave and nocturnal warming: a case**
1913 **study in a diurnal snake**

1914 **(1) Thermoregulation under semi-natural conditions**

1915 To examine the influence of weather conditions on thermoregulation, in late spring 2003 six non-
1916 pregnant adult female asp vipers (*Vipera aspis*) of similar mass and size (mean \pm SD SVL = 49.5 \pm 4.5
1917 cm; body mass = 88.8 \pm 25.6 g) were captured in the wild in western France by M. Guillon. and O.
1918 Lourdais. Vipers were housed in an 80 m² outdoor enclosure at the CEBC-CNRS study site in France
1919 (46°8'48"N; 0°25'31"E), located in the geographic range of *V. aspis*. The enclosure provided a mosaic
1920 of diverse vegetation, basking sites, shade, rocky shelters, and underground refuges, that mimicked
1921 the natural habitat of this species. We implanted temperature loggers (Ibutton @Maxim dallas) into
1922 the body cavity following a previously described protocol (Lourdais *et al.*, 2013). Body temperature
1923 (T_b) was measured every hour of the 24-h diel cycle, from July 1 to September 4. Simultaneously, we
1924 measured T_e every hour in six biomimetic models (copper tubes filled with water) designed to match
1925 the biophysical properties (shape, size and reflective properties) of the study species. We placed the
1926 models into two contrasting microhabitats: on the ground in the open ($N = 3$) and in underground
1927 shelter ($N = 3$) to record the range of T_e . Each day was classified as very hot (>35 °C), hot (maximum
1928 air temperature in the shade 30–35 °C), or normal (<30 °C) according to the French national
1929 meteorological agency (Météo France) classification for the study area (Laadi *et al.*, 2012). Because
1930 behavioural activity occurs only during the day in this species, we distinguished between the
1931 daytime activity period (from 09:00 to 21:00) and the nocturnal resting period (22:00 to 08:00).

1932 **(2) Statistical analyses**

1933 All statistical comparisons were performed in R software version 4.2.3. For each hour, we averaged
1934 data collected for body temperatures ($N = 6$ individuals) and microhabitat T_e ($N = 3$ replicates per
1935 category). We used a linear model to examine the relationship between minimal nocturnal
1936 environmental temperature in the shelter ($T_{N\text{ shelter}}$) and maximal environmental temperatures ($T_{D\text{ open}}$)
1937 recorded in the open during the previous day (see Table S3).

1938 **Table S3.** Results of a linear model relating daily nocturnal shelter environmental minimum
1939 temperature ($T_{N\text{ shelter}}$) to the maximum environmental temperature in the open ($T_{D\text{ open}}$) during the
1940 previous day.

1941

Explanatory variables	df	Sum Sq	Mean Sq	F value	P
-----------------------	----	--------	---------	---------	---

$T_{D\ open}$	1	310.89	310.89	87.61	< 0.005
residuals	64	227.1	3.54		

1942

1943 We used a second linear model to examine variation in mean nocturnal body temperature ($T_{b\ night}$)
 1944 (i.e. averaged across the period 22:00–8:00) with conditions in the previous day. The model included
 1945 the previous day type as a factor (i.e. very hot, hot or normal), $T_{N\ shelter}$ as a covariate and their
 1946 interaction term (see Table S4).

1947 **Table S4.** Results of ANOVA linear model relating mean nocturnal body temperature to the previous
 1948 day type (normal, hot, very hot), the nocturnal shelter minimum temperature ($T_{N\ shelter}$), and their
 1949 interaction term.

1950

Explanatory variable	df	Sum Sq	Mean Sq	F value	P
Previous day type	2	350.8	175.41	256.95	< 0.005
$T_{N\ shelter}$	1	97.83	87.33	127.92	< 0.005
Interaction (Previous day type \times $T_{N\ shelter}$)	2	1.76	0.88	1.28	0.28
Residuals	60	40.96	0.68		

1951

1952

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1954

1955

Appendix S4. Bioenergetic modelling of energy balance

1956

(1) List of abbreviations

α	Conversion efficiency of food to energy parameter
AR_T	Temperature-dependent food attack rate
b_{AR} / b_{IR}	Linear parameter for attack rate and intake rate
DMR_{20}	Default metabolic rate at 20 °C
E_a	Activation energy parameter
$FR_{R,T}$	Functional response (the energy derived from food consumption and assimilation)
h	Handling time
IR_T	Temperature-dependent food ingestion rate
k_b	Boltzmann constant
K_{AR} / K_{IR}	Scaling parameter for attack rate / intake rate
MR_T	Temperature-dependent metabolic rate (energy expenditure)
NEG_d	Daily net energy gain
NEG_h	Hourly net energy gain
$NEG_{R,T}$	Temperature- and resource-dependent instantaneous net energy gain
R	Resource (food) density
q_{AR} / q_{IR}	Quadratic parameter for attack rate and intake rate
T	Temperature
T_A	Arrhenius temperature
T_D	Diurnal air temperature
T_e	Operative environmental temperature
T_N	Nocturnal air temperature
$T_{N,opt}$	Optimal nocturnal air temperature
T_{opt}	Optimal body temperature
T_{pref}	Preferred body temperature
TPC	thermal preference curve
VT_{min}	Voluntary minimum temperature
VT_{max}	Voluntary maximum temperature

1957

(2) Context

1958

(a) Net energy gain model

1959

We extended the energy balance model of Huey & Kingsolver (2019) to characterise the net energy intake of an ectothermic predator at different nocturnal environmental temperatures (T_N s). The model assumes that net energy gain (NEG) depends on a positive input (from food consumption and assimilation) and a negative output (from energy expenditure associated with basal metabolism and body maintenance).

1960

1961

1962

1963

$$NEG_{R,T} = FR_{R,T} * \alpha - MR_T \quad (S3)$$

1964

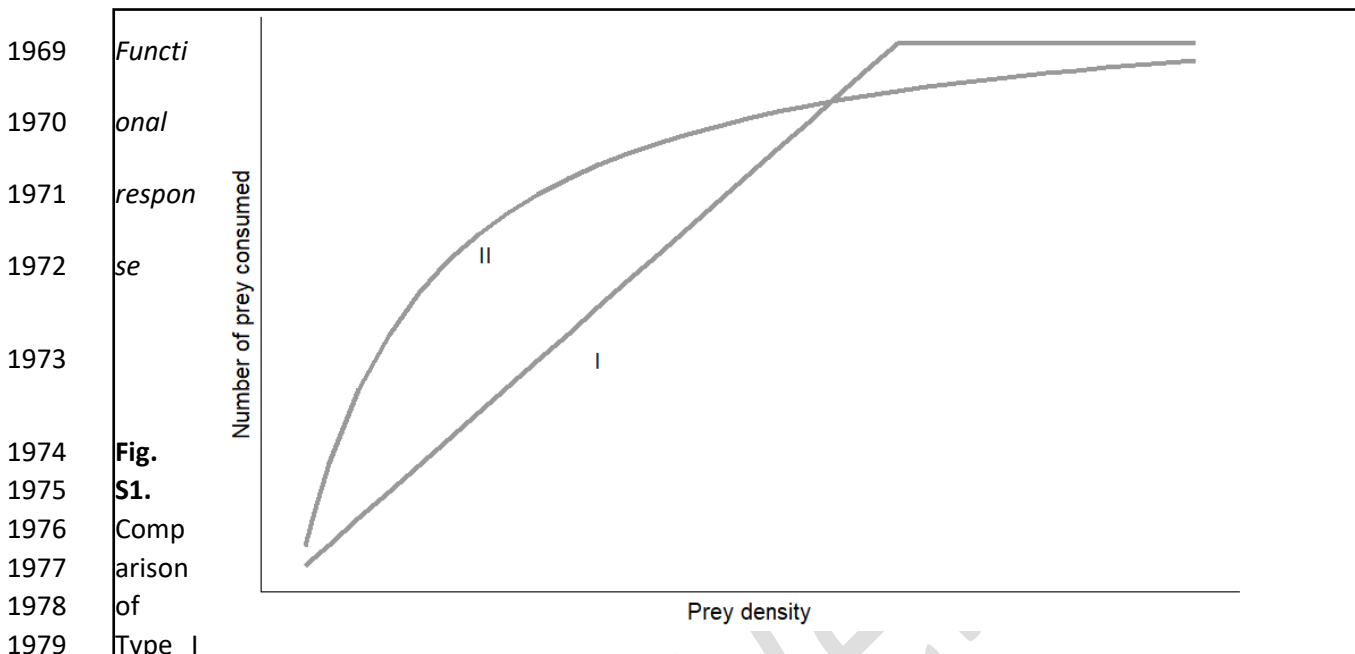
Where NEG and the functional response **FR** depend on resource density (**R**) and temperature (**T**)

1965

and the metabolic rate **MR** depends on temperature alone. The conversion efficiency of food to

1966 energy (α) was set to 69% in all simulations (Levy *et al.*, 2017) and assumed to be independent of
 1967 temperature.

1968 (b)



1980 functional response (as used in Huey & Kingsolver, 2019) with a Type II functional response (as used
 1981 in our model).

1982 Rather than assuming a Type I functional response as in Huey & Kingsolver (2019) where food intake
 1983 increases linearly with prey density up to a saturation point, we used a Type II functional response
 1984 that assumes a decelerating intake rate with food density (Fig. S1). In the Type II functional
 1985 response, intake rate depends on both attack rate (AR ; the rate at which prey is encountered and
 1986 attacked) and an ingestion rate (IR ; the rate at which prey is ingested). Varying AR conveniently
 1987 allowed us to separate a diurnal ($AR > 0$) and nocturnal ($AR = 0$) phase for food acquisition (i.e.
 1988 foraging). The Type II functional response is given by equation S4:

$$FR_{R,T} = \frac{AR_T * R}{1 + AR_T * \frac{R}{IR_T}} \quad (S4)$$

1989 where food intake depends on food density R (arbitrarily set to $R = 2$ in all cases), attack rate AR
 1990 (which determines food intake at low food density) and ingestion rate IR . IR was replaced in our
 1991 equations by the handling time (h ; inversely proportional to IR) which represents the time spent
 1992 handling, eating and digesting prey and therefore determines food intake at high food density:

$$FR_{R,T} = \frac{AR_T * R}{1 + AR_T * h_T * R} \quad (S5)$$

1993 The temperature dependence of AR and IR were modelled using Arrhenius-like equations (see
 1994 Englund *et al.*, 2011).

1995 (c) Attack and intake rates

1996 We scaled all parameters of the **AR** and **IR** equations to have a unimodal relationship with
 1997 body temperature and a maximum of 1 at an optimal body temperature T_{opt} (here, scaled
 1998 such that $T_{opt} = 30\text{ }^{\circ}\text{C}$). AR_T and IR_T were estimated as follows:

$$AR_T = K_{AR} * \exp(b_{AR} * T_A + (q_{AR} * T_A)^2) \quad (S6)$$

$$IR_T = K_{IR} * \exp(b_{IR} * T_A + (q_{IR} * T_A)^2) \quad (S7)$$

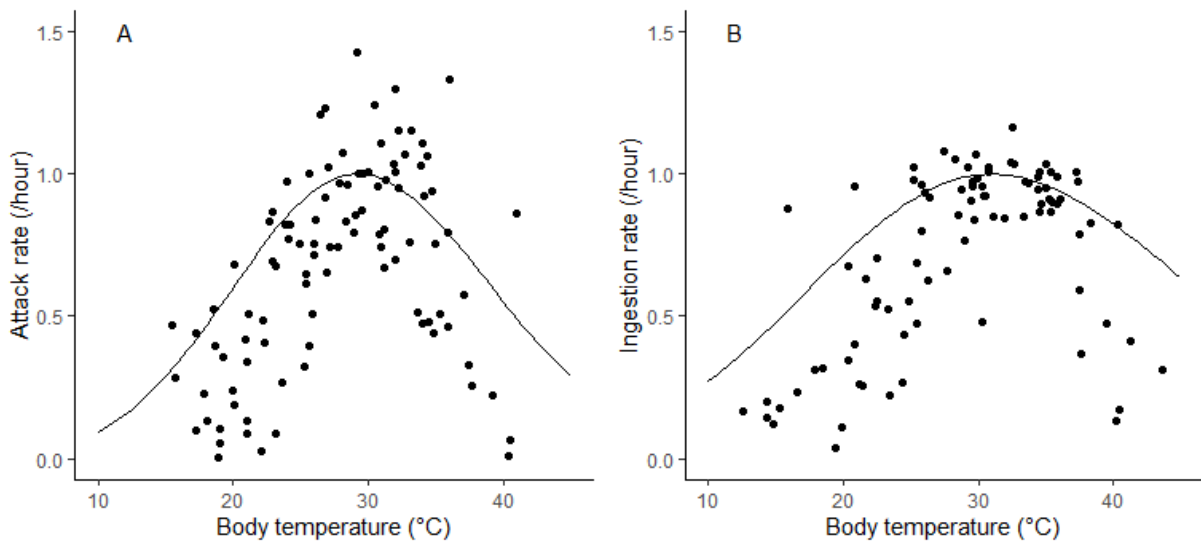
1999 where K_{AR} and K_{IR} are scaling parameters, b and q are the linear and quadratic
 2000 equation, and T_A is Arrhenius temperature. K_{AR} and K_{IR} (1.679^{-220} and 2.957^{-103} respectively)
 2001 were calculated as:

$$K_{AR} = \frac{1}{\max AR} \text{ and } K_{IR} = \frac{1}{\max IR} \quad (S8)$$

2002 Arrhenius temperatures (T_A) were calculated using the Boltzmann constant ($k_b = 8.617 * 10^{-05}$
 2003 $eV.K^{-1}$) and body temperature (T) in degrees Kelvin ($293.5\text{ }^{\circ}\text{K}$ or $20\text{ }^{\circ}\text{C}$) following:

$$T_A = \frac{-1}{k_b * T} \quad (S9)$$

2004



2005

2006

2007 **Fig. S2.** Estimation of parameters b and q for attack rate **AR** (A) and ingestion rate **IR** (B). Data are
 2008 modified from Englund *et al.* (2011) to match an optimal temperature for **AR** and **IR** of $30\text{ }^{\circ}\text{C}$.

2009

2010

2011 Finally, the parameters b and q were estimated using empirical data presented by Englund *et al.*
 2012 (2011) for diverse ectotherms (Fig. S2). We obtained parameters b (i.e. linear slope) and q (i.e.
 2013 quadratic slope) by fitting a non-linear model to the log-transformed raw data of this meta-analysis
 2014 (*lm* function in R; Fig. S2). Note that for both **AR** and **IR**, body temperature data from Englund *et al.*
 2015 (2011) were shifted from T_{opt} of $25\text{ }^{\circ}\text{C}$ to higher values (by adding $5\text{ }^{\circ}\text{C}$ to every body temperature

2016 recorded) in order to match the T_{opt} of 30 °C used in our model. This adjustment corresponds with
2017 the thermal characteristics of a ‘standard’ lizard and allowed better visualization of T_N effects.

2018

2019 (d) *Metabolic rate*

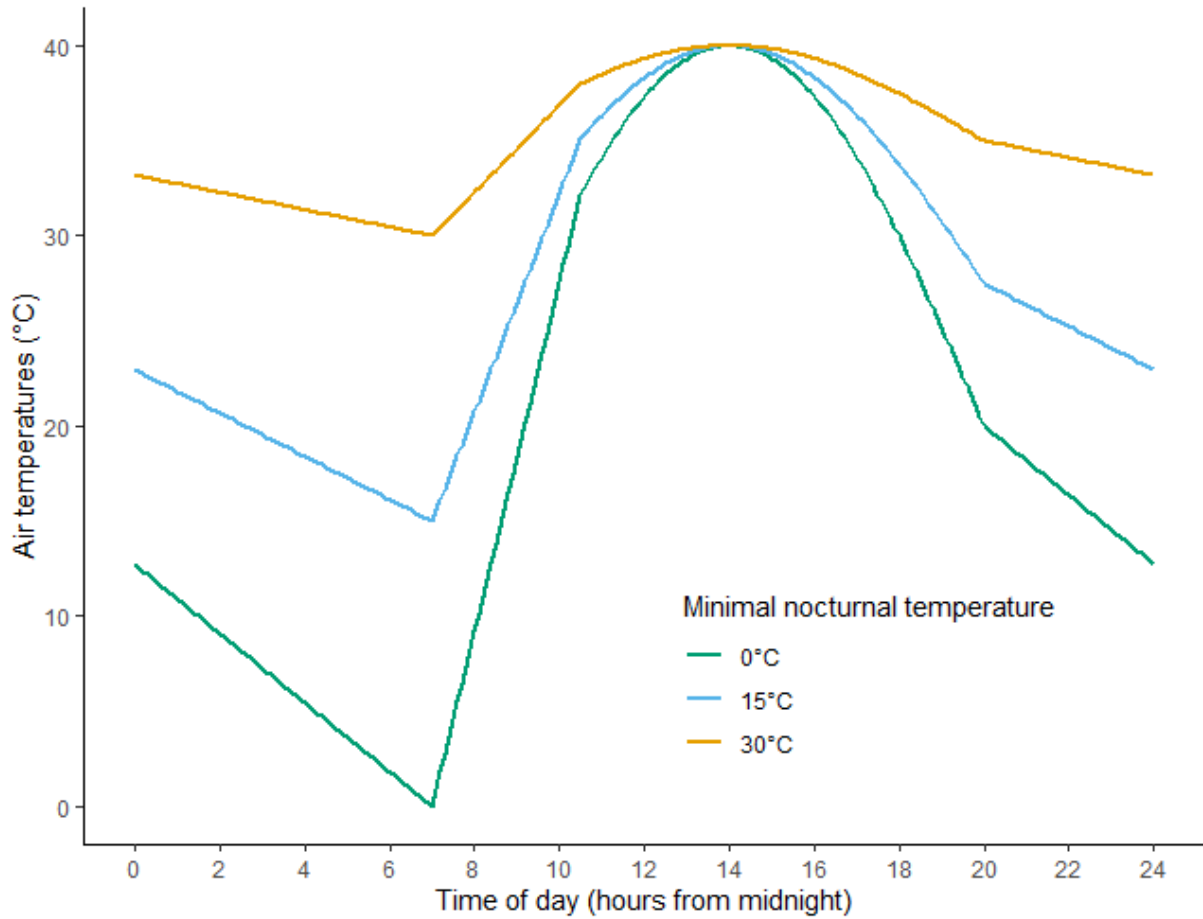
2020 The temperature-dependent metabolic rate (MR_T) represents the energy output of the
2021 model. It was set to a standard value at 20 °C (293.15 °K) and assumed to increase
2022 exponentially with the inverse of body temperature (in °K) according to the following
2023 equation:

$$MR_T = DMR_{20} * \exp\left(E_a * \frac{T - T_0}{k_b * T * T_0}\right) \quad (S10)$$

2024 where DMR_{20} is the default metabolic rate for a maximum energy intake of 1 at 20 °C; E_a (electron-
2025 volt, eV) is the activation energy parameter (set at 0.64 according to Fussmann *et al.*, 2014), T is
2026 body temperature (in °K) and T_0 is the reference temperature (293.15 °K). In our simulations, DMR_{20}
2027 was set to 1, 5, 10 or 15% of the maximum energy intake at 20 °C to explore the impact of changes in
2028 T_N on different organism types (i.e. larger organisms are expected to have a lower mass-specific MR
2029 than smaller ones or species with a fast life history are assumed to have a higher mass-specific MR
2030 than species with a slow life history).

2031 (e) *Daily temperature cycles*

2032 Air temperature was modelled using an asymmetric 24-h periodic function that was built to
2033 match the shape of diurnal cycles recorded during the 2003 heatwave study described in
2034 Section III.3 of main article. Mathematical equations describing this cycle were adapted
2035 from the Parton–Logan function (Parton & Logan, 1981; McMunn & Pepi, 2022) and use a
2036 combination of linear and sine-like functions to simulate a realistic temperature cycle during
2037 a sunny day (Fig. S3). From sunrise at 07:00, the temperature increases linearly from its
2038 minimum until it reaches mean daily temperature at 10:00. From there until sunset (20:00),
2039 it follows a sine-like function, reaching the diurnal peak temperature at 14:00 (40 °C), before
2040 decreasing. Overnight (21:00 to 07:00), the air temperature decreases linearly to reach a
2041 minimal value at sunrise. Because our focus was on nocturnal warming, we held maximum
2042 diurnal temperature constant across simulations (40 °C), while minimum nocturnal
2043 temperature was varied from 0 to 30 °C (Fig. S3). See Section 3.c.iv below for R code.



2044

2045 **Fig. S3.** Daily temperature cycles used in our model based on the Parton–Logan function (Parton &
 2046 Logan, 1981; McMunn & Pepi, 2022). The model uses a combination of linear and sine-like functions
 2047 to simulate a realistic temperature cycle during a sunny day. Atmospheric temperatures increase
 2048 linearly from 07:00 to reach mean daily temperature at 10:00, after which it follows a sine-like
 2049 function, reaching a peak day temperature of 40 °C at 14:00 and then decreasing until 20:00.
 2050 Overnight (20:00 to 07:00), atmospheric temperature decreases linearly to reach once again a
 2051 minimum value at 07:00.

2052

2053

2054 *(f) Daily energy acquisition and expenses*

2055 For each hour of the day, we characterised air temperature using the asymmetric 24-h
 2056 periodic function described above. We used these air temperatures to calculate hourly **AR**,
 2057 **IR** and **MR** (see below for R code) and then calculated hourly net energy gain (**NEG_h**). The
 2058 daily net energy gain (**NEG_d**) was estimated as the sum of **NEG_h** values:

$$\text{NEG}_d = \sum_{i=1}^{24} \text{NEG}_h \quad (\text{S11})$$

2059 We computed NEG_d for different scenarios of thermoregulation behaviours (see Section IV.2 in the
2060 main article), for different minimal nocturnal temperatures ($T_{N,min}$) and for different values of
2061 default metabolic rate (DMR_{20}).

2062 **(3) R code of the bioenergetic model**

2063 *(a) Libraries*

```
2064 library(dplyr)
2065 library(ggplot2)
2066 library(gridExtra)
2067 library(lattice)
2068 library(plotly)
```

2069 *(b) Parameters and default values*

```
2070 alpha <- 0.69 # Conversion efficiency
2071 b_a <- -26.37628 # Linear slope for AR
2072 b_a_N <- -19.94401 # Linear slope for AR (nocturnal species)
2073 b_i <- -12.37742 # Linear slope for IR
2074 c <- 8 # Sinusoidal period parameter
2075 Ea <- 0.64 # Energy activation rate for metabolic expenditure
2076 HA_max <- 20 # Maximal time for activity (Scenario 2 & 4)
2077 HA_min <- 7 # Minimal time for activity (Scenario 2 & 4)
2078 Hmax <- 20 # Time of sunset
2079 Hmin <- 7 # Time of sunrise
2080 k_a <- 1.679279e-220 # Standardizing parameter for AR
2081 k_a_N <- 1.382221e-167 # Standardizing parameter for AR (Nocturnal sp.)
2082 k_b <- 8.6173303e-05 # Boltzmann's constant (eV.K-1)
2083 k_i <- 2.957385e-103 # Standardizing parameter for intake rate
2084 M_met <- 0.1 # Default metabolic expenditure at 20°C (set to
2085 # 10% of maximum intake with default parameters)
2086 pi <- 3.14159265359
2087 q_a <- -0.3436951 # Quadratic slope for AR
2088 q_A_N <- -0.2588205 # Quadratic slope for AR (Nocturnal species)
2089 q_i <- -0.1622324 # Quadratic slope for IR
2090 R <- 2 # Resource rate
2091 Tpref <- 30 # Preferred body temperature; Default value
2092 Tref <- 20 # Standard temperature for metabolic expenditure
2093 VTmax_D <- 40 # Voluntary thermal limit (upper)
2094 VTmin_D <- 18 # Voluntary thermal limit (lower)
2095 VTmax_N <- 30 # Voluntary thermal limit (upper)
2096 VTmin_N <- 15 # Voluntary thermal limit (lower)
```

2097 *(c) Basic functions*

2098 *(i) Arrhenius equation for MR*

2099 Returns **MR** according to environmental temperature.

2100 *Parameters*

```
2101 t # Temperature (in °C)
2102 k0 # Normalizing parameter (k_a or k_i)
```



```

2103 Ea      # Energy activation rate for metabolic expenditure
2104 Tref     # Standard temperature for metabolic expenditure

```

2105 *Function*

```

2106 Arrhenius_function=function(t,k0,Ea,Tref){
2107   T=t+273.15      # Convert °C to °K
2108   T0=Tref+273.15 # Convert standard temperature in °K
2109   k0*exp(Ea*(T-T0)/(k_b*T*T0)) # Standard Arrhenius equation with
2110   }               # a normalizing temperature

```

2111 (ii) Functional response (Type II):

2112 *Parameters*

```

2113 r      # Resource density
2114 a      # Attack rate
2115 h      # Handling rate (inverse of Intake rate)

```

2116 *Function*

```

2117 FR_function=function(r,a,h){a*r/(1+a*h*r)}

```

2118 (iii) Temperature dependence of functional response parameters:

2119 *Parameters*

```

2120 t      # Temperature (in °C)
2121 k0     # Normalizing parameter (k_a or k_i)
2122 b      # Linear slope for AR and IR
2123 q      # Quadratic slope for AR and IR

```

2124 *Function*

```

2125 Temperature_function=function(t,k0,b,q){
2126   T=t+273.15      # Convert °C in °K
2127   Arrhenius_Temp=-1/(k_b*T) # Convert °K in Arrhenius temperature
2128   k0*exp(b*Arrhenius_Temp+q*Arrhenius_Temp^2)}

```

2129 (iv) Temperature cycle function

2130 *Parameters*

```

2131 hour    # Hour of the day
2132 Tmin    # Minimum temperature of the day (Varying from 0 to 30°)
2133 Tmax    # Maximum temperature of the day (40°C)
2134 Hmin    # Time of sunrise (07h00)
2135 Hmax    # Time of sunset (20h00)
2136 c       # Sinusoidal period parameter (8)

```

2137 *Function*

```

2138 Temperature_cycle <- function(hour, Tmin,Tmax,c,Hmin,Hmax){
2139   Tr <- (Tmax-Tmin)/2      # Temperature range
2140   Tm <- (Tmin+Tmax)/2     # Mean temperature
2141   Tcx <- (Tr*sin(2*pi/24*(Hmax-c)))+Tm # Hmax temperature
2142   Tcn <- Tmin             # Hmin temperature
2143   Hourx <- c+12-6        # Warmest hour of the day
2144   Hm <- (Hourx+Hmin)/2   # Hour for mean temperature
2145   coefn <- (Tcn-Tcx)/((24+Hmin)-Hmax) # Slope coef. for the
2146   # nocturnal linear function
2147   coefd <- ((Tr*sin(2*pi/24*(Hm-c))+Tm)-Tcn)/(Hm-Hmin) # Slope coef. for the
2148   # diurnal linear function
2149
2150   ifelse(hour<=Hmin, (Tcx + coefn*((24-Hmax)+hour)),

```

```

2151   ifelse(hour<=Hm, (Tcn+coefd*(hour-Hmin)),
2152   ifelse(hour>=Hmax, (Tcx+ coefn*(hour-Hmax)),
2153   (Tr*sin(2*pi/24*(hour-c))+Tm))))}

```

2154 *Example plot*

2155 Example of daily temperature cycle with a $T_{N,min}$ of 0, 15 and 30 °C at 07:00 and a T_{max} of
 2156 40 °C at 14:00. Days start at 07:00 and end at 20:00. R code is provided for $T_{N,min} = 0$ °C.

```

2157   x_range=c(0,24)
2158   y_range=c(0,40)
2159   x_lab=c("Time of day (hours from midnight)")
2160   y_lab=c("Temperature (°C)")
2161   curve(Temperature_cycle(x,0,40,8,7,20),
2162         xlim=x_range,
2163         ylim=y_range,
2164         xlab=x_lab,
2165         ylab=y_lab,
2166         col="blue",
2167         axes=FALSE)
2168   axis(side=1, at = seq(0,24,2))
2169   axis(side=2, at = seq(0,40,10))

```

2170 (v) Testing the influence of nocturnal temperature and DMR_{20}

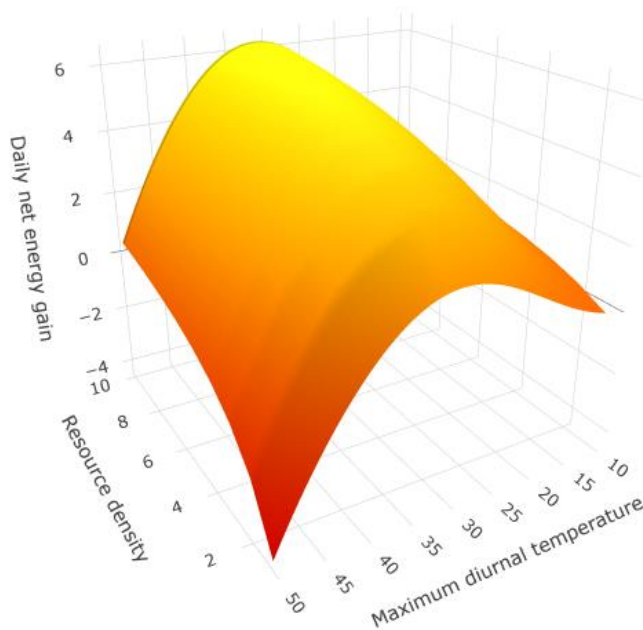
2171 In all scenarios, we evaluated the response of the NEG_d to varying minimum T_N ranging
 2172 from 0 °C to 30 °C. We also modified the value of $DMR_{20} = 0.01, 0.05, 0.1,$ and 0.15
 2173 (Andrews & Pough, 1985) to explore the effects of nocturnal thermal conditions on species
 2174 with low, moderate or high resting metabolic rates. For the sake of simplicity, we provide
 2175 below the code for one level of DMR_{20} (= 0.1). To explore other parameter combinations,
 2176 users can modify values for M_{met} . Results for the different DMR_{20} values are provided in Fig.
 2177 7 of the main article.

2178 (4) Scenarios

2179 (a) Scenario 0. Model validation

2180 Scenario 0 was designed to validate our model by confirming results from Huey & Kingsolver (2019).
 2181 We modelled a thermoconforming ectotherm (i.e. an animal that spends no time or metabolic
 2182 energy on the regulation of body temperature) in an environment with variation in resource density
 2183 (varying from 1 to 10) and maximum TD (10–50 °C). Minimum T_N was fixed to 5 °C and DMR_{20} to 0.1.
 2184 As in Huey & Kingsolver (2019), the model highlights that reduced resource levels in warmer
 2185 environments trigger a ‘metabolic meltdown’ (i.e. declining energy intake paired with increased
 2186 energetic expenditure and a reduced activity opportunity due to warmer diurnal maximum
 2187 temperatures in the middle of the day) (Fig. S4). Details of the energy balance function are provided
 2188 in Scenario 1. Only parameterisation for $T_{N,min}, T_{D,max}, DMR_{20}$ and R changed.

2189



2190

2191 **Fig. S4.** Daily net energy gain rate (NEG_d) at different maximum diurnal temperatures ($T_{D,max}$) and
 2192 resource density (R). Minimum T_N ($T_{N,min}$) is fixed to 5°C. DMR_{20} is fixed to 0.1. Yellow colours
 2193 represent high values of NEG_d . Red colours represent low values of NEG_d .

2194 *(b) Scenario 1. Thermoconformer with 24-h foraging activity*

2195 In Scenario 1, we modelled a thermoconforming ectotherm with an activity window of 24 h.
 2196 This allowed us to investigate effects of minimum T_N , in the absence of time partitioning of
 2197 activity and behavioural control of body temperature.

2198 *Attack rate*

2199 **AR** is positive over the entire 24-h cycle and depends only on environmental temperature.

2200 **AR** is calculated hourly with the *Attack_function_TC1_H* function, and is then integrated
 2201 over the entire day using the *Attack_function_TC1_24* function.

2202 *Parameters*

```

2203 x          # Hour of the day
2204 Tmin       # Minimum temperature of the day (e.g., Varying from 0 to 30°C)
2205 Tmax       # Maximum temperature of the day (e.g., 40°C)
2206 Hmin       # Time of sunrise (e.g., 07:00)
2207 Hmax       # Time of sunset (e.g., 20:00)
2208 c          # Sinusoidal parameter (e.g., 8)
2209 k_a        # Normalizing parameter for AR
2210 b_a        # Linear slope for AR: -26.37628
2211 q_a        # Quadratic slope for AR: -0.3436951
  
```

2212 *Hourly attack rate:*
 2213 Attack_function_TC1_H=**function**(x,Tmin,Tmax,c,Hmin,Hmax){
 2214 Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_a,b_a,q_a)}

2215 *Daily attack rate:*
 2216 Attack_function_TC1_24= Vectorize(**function**(Tmin,Tmax,c,Hmin,Hmax){
 2217 integrate(**function**(x)
 2218 Attack_function_TC1_H(x,Tmin,Tmax,c,Hmin,Hmax), 0, 24)\$value/24})

2219 *Ingestion rate*

2220 **IR** is positive over the entire 24-h cycle and depends only on environmental temperature. **IR**
 2221 is calculated hourly with the *Ingestion_function_TC1_H* function, and is then integrated
 2222 over the entire day using the *Ingestion_function_TC1_24* function.

2223 *Parameters*

2224 k_i # Normalizing parameter for IR
 2225 b_i # Linear slope for IR
 2226 q_i # Quadratic slope for IR

2227 *Hourly intake rate:*
 2228 Ingestion_function_TC1_H=**function**(x,Tmin,Tmax,c,Hmin,Hmax){
 2229 Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_i,b_i,q_i)}

2230 *Daily mean intake rate:*
 2231 Ingestion_function_TC1_24= Vectorize(**function**(Tmin,Tmax,c,Hmin,Hmax){
 2232 integrate(**function**(x)
 2233 Ingestion_function_TC1_H(x,Tmin,Tmax,c,Hmin,Hmax), 0, 24)\$value/24})

2234 *Metabolic expenditure*

2235 **MR** is positive over the entire 24-h cycle and depends only on environmental temperature.
 2236 **MR** is calculated hourly with the *Metabolism_function_TC1_H* function, and is then
 2237 integrated over the entire day using the *Metabolism_function_TC1_24* function.

2238 M_met # Default metabolic expenditure at 20°C
 2239 Tref # Standard temperature for metabolic expenditure
 2240 Ea # Energy activation rate for metabolic expenditure

2241 *Hourly MR*

2242 Metabolism_function_TC1_H=**function**(x,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
 2243 Arrhenius_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),M_met,Ea,Tref)}

2244 *Daily MR*

2245 Metabolism_function_TC1_24= Vectorize(**function**(Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
 2246 integrate(**function**(x)
 2247 Metabolism_function_TC1_H(x,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref),0, 24)\$value})

2248 *Energy balance*

2249 NEG_d is calculated using the difference between daily energy acquisition and expenditure. It
2250 therefore includes the calculation of daily mean FR, which uses daily mean AR and daily
2251 mean IR.

2252 *Parameters*

```
2253 alpha # Resource conversion efficiency
2254 ar_max # Maximum attack rate
2255 hr_max # Maximum handling time rate
```

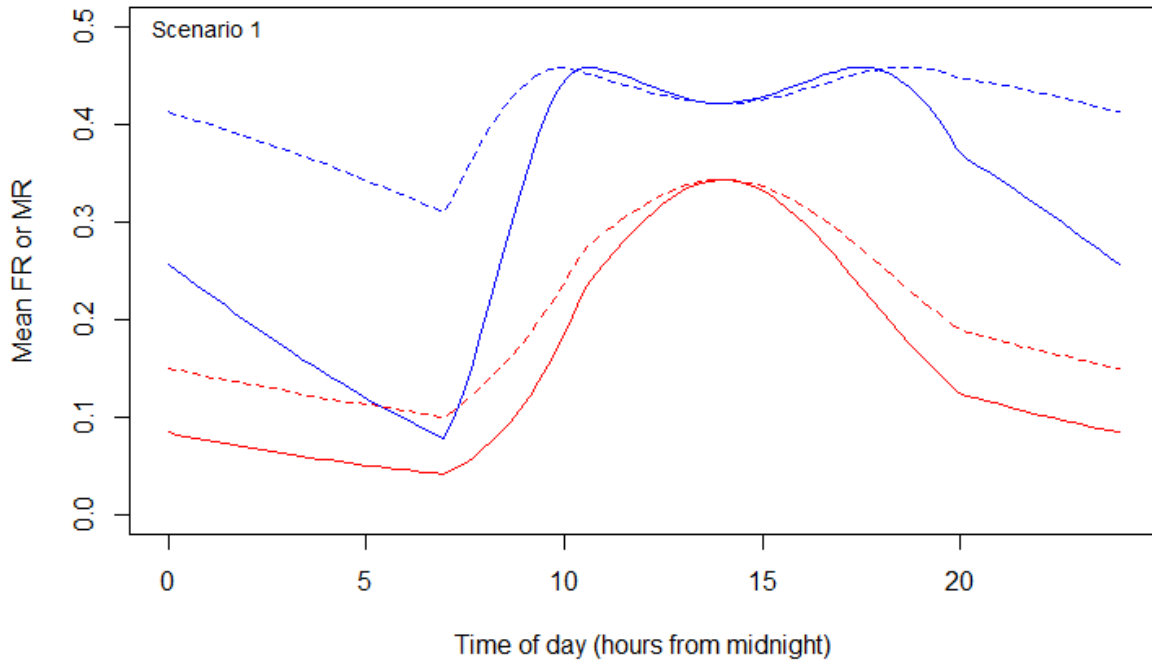
2256 *Daily MR*

```
2257 Energy_balance_TC1_24=
2258 function(r,Tmin,Tmax,c,Hmin,Hmax,alpha,ar_max,hr_max,M_met,Tref){
2259 24*FR_function(R,
2260 ar_max*Attack_function_TC1_24(Tmin,Tmax,c,Hmin,Hmax),
2261 hr_max/Ingestion_function_TC1_24(Tmin,Tmax,c,Hmin,Hmax))*alpha -
2262 Metabolism_function_TC1_24(Tmin,Tmax,c,Hmin,Hmax,M_met,Tref)}
```

2263 *Plot: energetic inputs (FR) and outputs (MR) over a 24-hour cycle*

```
2264 x_range <- c(0,24)
2265 y_range <- c(0,0.5)
2266 curve(Metabolism_function_TC1_H(x,10,35,8,7,20,0.1,20), col="red",
2267 xlab="Time of day (hours from midnight)",
2268 ylab = "Mean FR or MR",
2269 xlim=x_range,ylim=y_range)
2270 curve(FR_function(2,1*Attack_function_TC1_H(x,10,35,8,7,20),
2271 1/Ingestion_function_TC1_H(x,10,35,8,7,20))*0.69,add=TRUE,col="blue")
2272 curve(Metabolism_function_TC1_H(x,20,35,8,7,20,0.1,20),col="red",add=TRUE,lty=2)
2273 curve(FR_function(2,1*Attack_function_TC1_H(x,20,35,8,7,20),
2274 1/Ingestion_function_TC1_H(x,20,35,8,7,20))*0.69,add=TRUE,col="blue",lty=2)
2275 text(2,0.5,label="Scenario 1", cex=0.9)
```

2276



2277

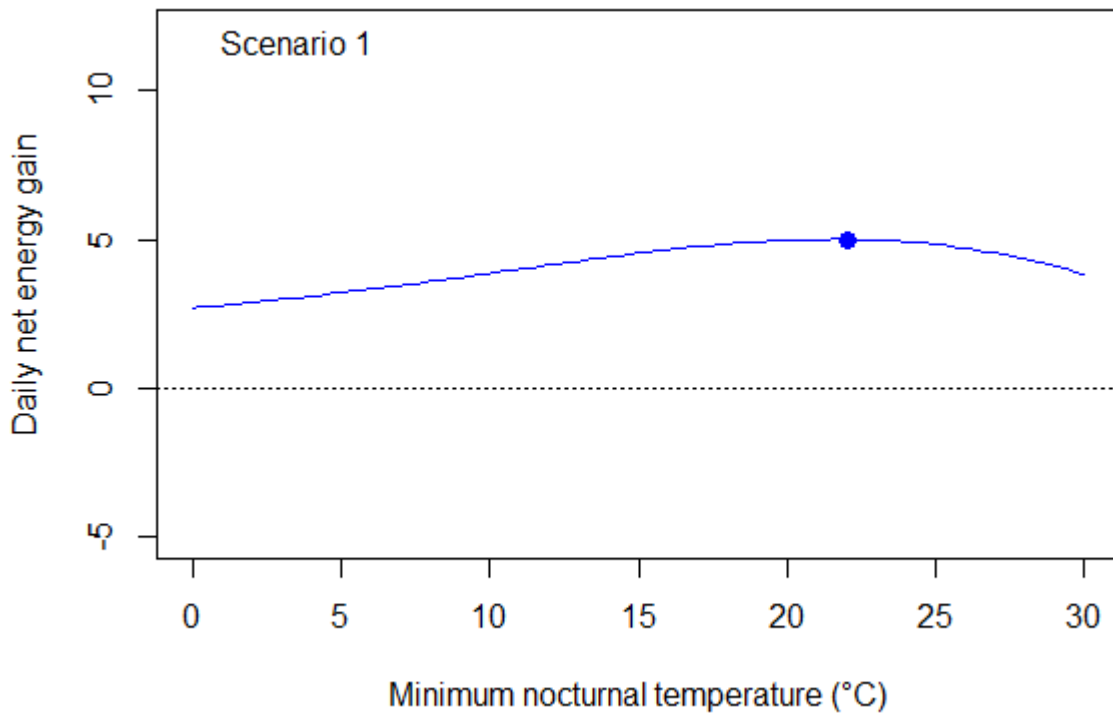
2278 **Fig. S5.** Metabolic rate (MR) (in red) and function rate (FR) (in blue) are represented for Scenario 1
 2279 for a minimum T_N of 10 °C (solid lines) or 20 °C (broken lines) for each hour.

2280 *Plot: Energy balance vs $T_{N,min}$*

```

2281 # Plot  $NEG_d$  over a range of nocturnal temperature (i.e., 0 to 30°C)
2282 x_range=c(0,30)
2283 y_range=c(-5,12)
2284 x_lab=c("Minimum nocturnal temperature (°C)")
2285 y_lab=c("Daily net energy gain")
2286 curve(Energy_balance_TC1_24(r=2,
2287           Tmin=x,Tmax=35,c=8,Hmin=7,Hmax=20,
2288           alpha=0.69,ar_max=1,hr_max=1,
2289           M_met=0.1,Tref=20),
2290       xlim=x_range,ylim=y_range,xlab=x_lab,ylab=y_lab,col='blue')
2291 abline(0,0,lty=3)
2292 legend(-1,12.5,legend="Scenario 1",bty="n")
2293
2294
2295 # Add optimal nocturnal temperature for NEG
2296 Sc1_0.1 <- (Energy_balance_TC1_24(r=2,
2297           Tmin=seq(0,30),Tmax=35,c=8,Hmin=7,Hmax=20,
2298           alpha=0.69,ar_max=1,hr_max=1,
2299           M_met=0.1,Tref=20))
2300 Sc1_0.1 <- cbind(seq(0,30,1),Sc1_0.1)
2301 colnames(Sc1_0.1) <- c("Tmin","NEG")
2302 Sc1_0.1.x <- Sc1_0.1[which(Sc1_0.1[, 'NEG'] == max(Sc1_0.1[, 'NEG'])),1]
2303 Sc1_0.1.y <- Sc1_0.1[which(Sc1_0.1[, 'NEG'] == max(Sc1_0.1[, 'NEG'])),2]
2304 points(Sc1_0.1.x,Sc1_0.1.y,col='blue',pch=16,cex=1.2)

```



2305

2306 **Fig. S6.** Daily net energy gain (NEG_d) for Scenario 1 at different minimum nocturnal temperatures
 2307 ($T_{N,min}$) and with a default metabolic rate (DMR_{20}) of 0.1. The circle represents the tipping point
 2308 between positive and negative effects of nocturnal temperature increase on NEG_d .

2309 (c) Scenario 2. Thermoconformer with diurnal foraging activity

2310 In Scenario 2, we extended the model to represent a thermoconforming ectotherm, with an
 2311 activity cycle based on photoperiod: the organism was active during the day and inactive at
 2312 night. To make this tractable without explicitly modelling the kinematics of gut passage time
 2313 and food assimilation (Levy *et al.*, 2017), we assumed that foraging behaviour (i.e. AR) was
 2314 only possible between 07:00 and 20:00 (AR, IR & MR all >0), while IR and MR were
 2315 calculated for the entire 24-h cycle (AR = 0 while IR & MR >0).

2316 *Attack rate*

2317 HA_min # Minimum hour for activity (AR>0)
 2318 HA_max # Maximum hour for activity (AR<0)

```

2319 Attack_function_TC2_H=function(x,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max){
2320   ifelse(x<HA_min,0,
2321   ifelse(x>HA_max,0,
2322   Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_a,b_a,q_a))))}
2323
2324 Attack_function_TC2_24= Vectorize(function(Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max){
2325   integrate(function(x)
2326
```

```

2327   Attack_function_TC2_H(x,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max), 0,
2328 24)$value/24})

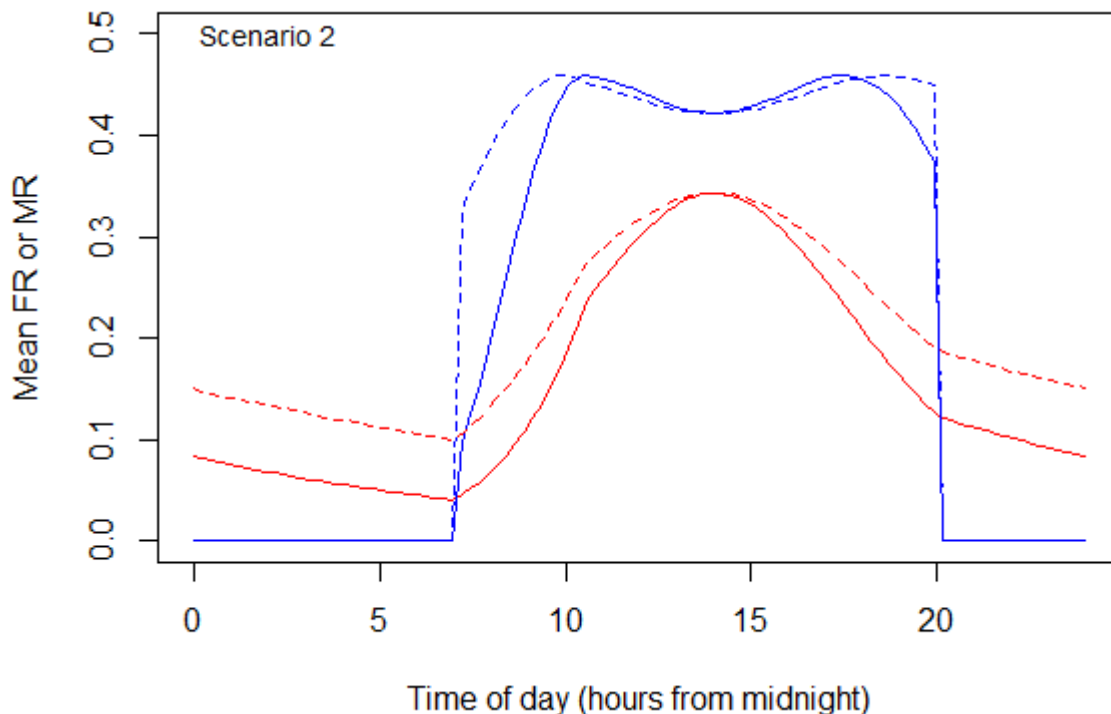
2329   Intake rate
2330 Ingestion_function_TC2_H=function(x,Tmin,Tmax,c,Hmin,Hmax){
2331   Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_i,b_i,q_i)}
2332
2333 Ingestion_function_TC2_24= Vectorize(function(Tmin,Tmax,c,Hmin,Hmax) {
2334   integrate(function(x)
2335   Ingestion_function_TC2_H(x,Tmin,Tmax,c,Hmin,Hmax), 0, 24)$value/24})

2336   Metabolic expenditure
2337 Metabolism_function_TC2_H=function(x,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2338   Arrhenius_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),M_met,Ea,Tref)}
2339
2340 Metabolism_function_TC2_24= Vectorize(function(Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2341   integrate(function(x)
2342   Metabolism_function_TC2_H(x,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref),0,24)$value})

2343   Energy balance
2344 Energy_balance_TC2_24=
2345   function(r,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max,alpha,ar_max,hr_max,M_met,Tref){
2346   24*FR_function(r,
2347
2348   a=ar_max*(Attack_function_TC2_24(Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max)),
2349   h=hr_max/Ingestion_function_TC2_24(Tmin,Tmax,c,Hmin,Hmax))*alpha -
2350   Metabolism_function_TC2_24(Tmin,Tmax,c,Hmin,Hmax,M_met,Tref)}

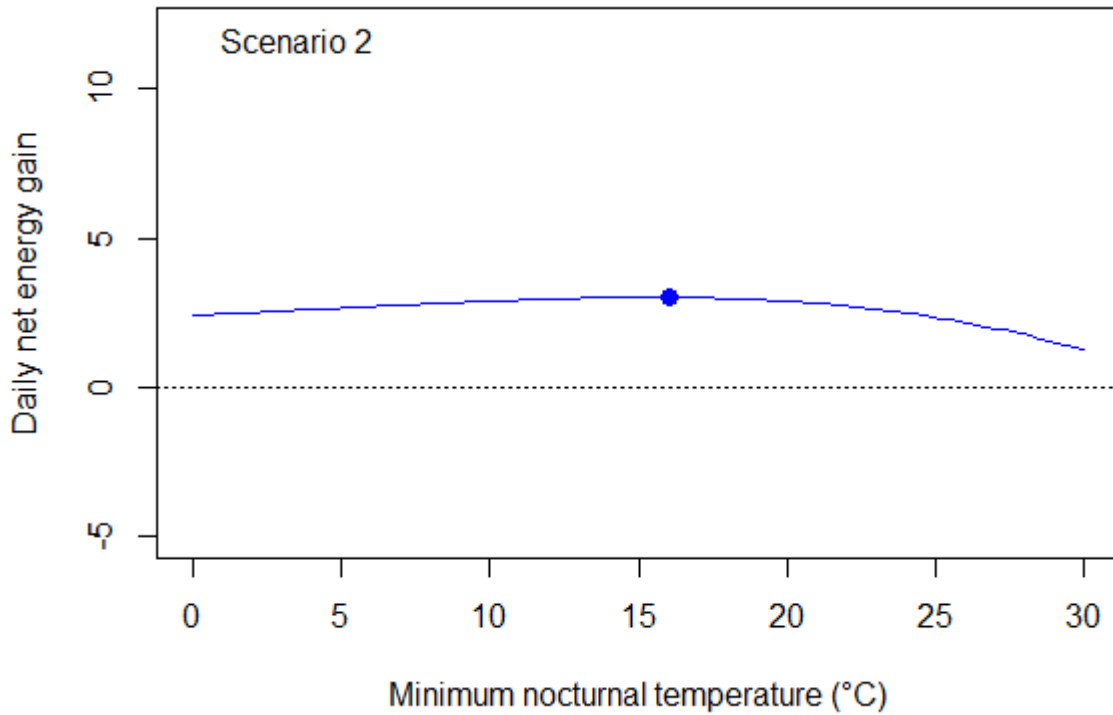
2351   Plot: energetic inputs (FR) and outputs (MR) over the day

```



2352 **Fig. S7.** Metabolic rate (MR) (in red) and function rate (FR) (in blue) are represented for Scenario 2
2353 for a minimum T_N of 10 °C (solid lines) or 20 °C (broken lines) for each hour.

2354 *Plot: Energy balance vs $T_{N,min}$*



2355

2356 **Fig. S8.** Daily net energy gain (NEG_d) for Scenario 2 at different minimum nocturnal temperatures
 2357 ($T_{N,min}$) and with a default metabolic rate (DMR_{20}) of 0.1. The circle represents the tipping point
 2358 between positive and negative effects of nocturnal temperature increase on NEG_d .

2359 (d) Scenario 3. Thermoregulator with 24-h foraging activity

2360 In Scenario 3, we modelled a perfectly thermoregulating ectotherm (i.e. an animal that
 2361 maintains body temperature within a range of optimal temperatures for performance) for
 2362 which the activity window was limited only by environmental temperature. This scenario
 2363 represents the case of an ectothermic predator able to extend its foraging activity over part
 2364 of the night when T_{NS} are suitable. Here, we assumed that AR is limited by a lower (18 °C)
 2365 and upper (40 °C) threshold corresponding to typical minimum (VT_{min}) and maximum (VT_{max})
 2366 voluntary temperatures for foraging in terrestrial lizards (Rozen-Rechels *et al.*, 2020).
 2367 Moreover, because the organism is able to thermoregulate, we assumed that individuals
 2368 could maintain a body temperature of 30 °C matching T_{opt} for foraging whenever
 2369 environmental temperatures were within the thermal range 18–40 °C.

2370 *Attack rate*

2371 T_{pref} # Preferred temperature for activity
 2372 VT_{min_D} # Minimum temperature for activity
 2373 VT_{max_D} # Maximum temperature for activity

```
2374 Attack_function_TR1_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,VTmin_D,VTmax_D){
2375   ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<VTmin_D,0,
2376     ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)>VTmax_D,0,
2377       ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
```

```

2379 Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_a,b_a,q_a),
2380 Temperature_function(Tpref,k_a,b_a,q_a))))}
2381
2382 Attack_function_TR1_24= Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,
2383 Hmax,VTmin_D,VTmax_D){
2384 integrate(function(x)
2385 Attack_function_TR1_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,VTmin_D,VTmax_D),
2386 0,24)$value/24})

```

2387 *Intake rate*

```

2388 Ingestion_function_TR1_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax){
2389 ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2390
2391 Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_i,b_i,q_i),
2392 Temperature_function(Tpref,k_i,b_i,q_i))}
2393
2394 Ingestion_function_TR1_24= Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax) {
2395 integrate(function(x)
2396 Ingestion_function_TR1_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax), 0, 24)$value/24})

```

2397 *Metabolic expenditure*

```

2398 Metabolism_function_TR1_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2399 ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2400
2401 Arrhenius_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),M_met,Ea,Tref),
2402 Arrhenius_function(Tpref,M_met,Ea,Tref))}
2403
2404 Metabolism_function_TR1_24=
2405 Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2406 integrate(function(x)
2407 Metabolism_function_TR1_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref),
2408 0, 24)$value})

```

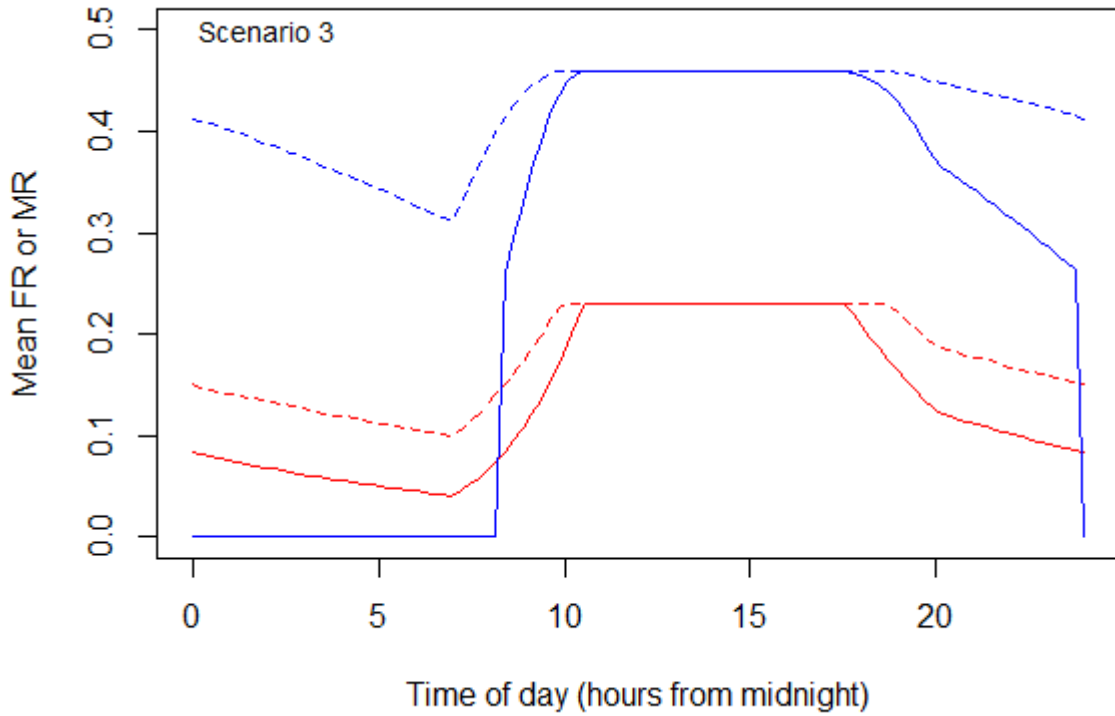
2409 *Energy balance*

```

2410 Energy_balance_TR1_24=
2411
2412 function(r,Tpref,Tmin,Tmax,c,alpha,ar_max,hr_max,Hmin,Hmax,VTmin_D,VTmax_D,HA_min,H
2413 A_max,M_met,Tref){
2414 24*FR_function(r,
2415
2416 a=ar_max*(Attack_function_TR1_24(Tpref,Tmin,Tmax,c,Hmin,Hmax,VTmin_D,VTmax_D)),
2417 h=(hr_max/Ingestion_function_TR1_24(Tpref,Tmin,Tmax,c,Hmin,Hmax))*
2418 alpha - Metabolism_function_TR1_24(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref)}

```

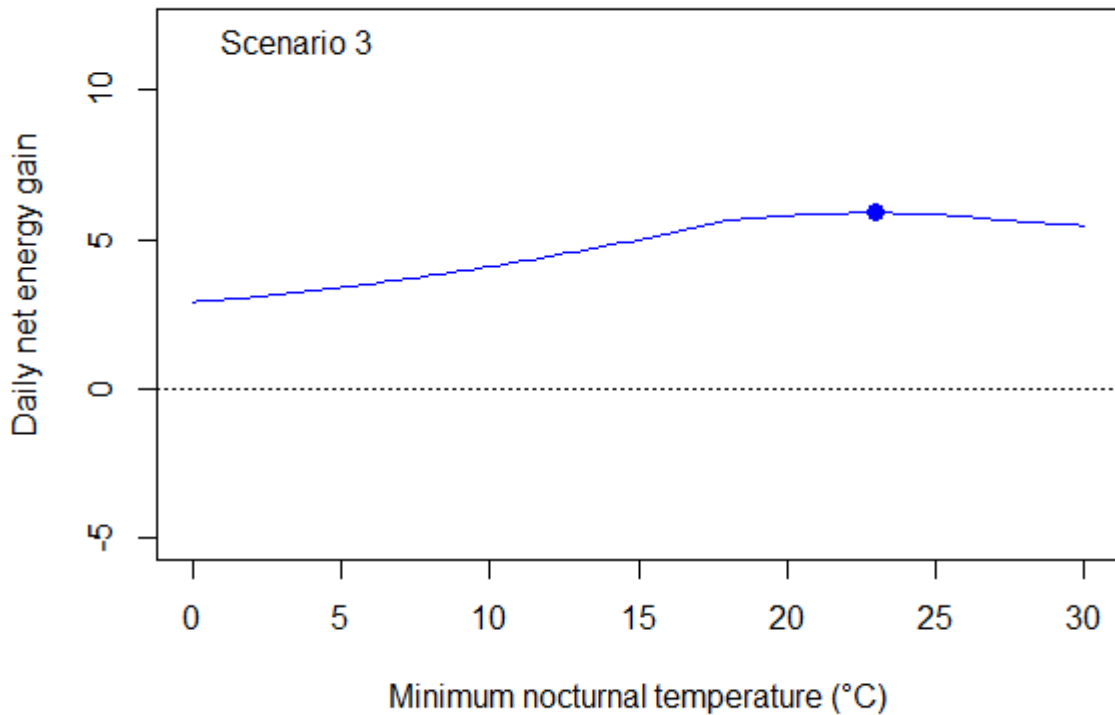
2419 *Plot: energetic inputs (FR) and outputs (MR) over the day*



2420

2421 **Fig. S9.** Metabolic rate (MR) (in red) and function rate (FR) (in blue) are represented for Scenario 3
2422 for a minimum T_N of 10 °C (solid lines) or 20 °C (broken lines) for each hour.

2423 *Plot: Energy balance vs T_{min}*



2424

2425 **Fig. S10.** Daily net energy gain (NEG_d) for Scenario 3 at different minimum nocturnal temperatures
 2426 ($T_{N,min}$) and with a default metabolic rate (DMR_{20}) of 0.1. The circle represents the tipping point
 2427 between positive and negative effects of nocturnal temperature increase on NEG_d .

2428 *(e) Scenario 4. Thermoregulator with diurnal foraging activity*

2429 Scenario 4 modelled a perfect thermoregulator with an activity window strictly delimited by
 2430 photoperiod. As in Scenario 2, **AR** is limited by daylight, while **IR** and **MR** were dependent
 2431 only on body temperature. In this scenario, body temperature during daytime was set to 30
 2432 °C whenever environmental temperatures exceeded the 30 °C threshold (i.e. efficient
 2433 behavioural thermoregulation).

2434 *Attack rate*

```
2435 Attack_function_TR2_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max){
2436   ifelse(x<HA_min,0,
2437     ifelse(x>HA_max,0,
2438       ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2439         Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_a,b_a,q_a),
2440         Temperature_function(Tpref,k_a,b_a,q_a))))})
2441
2442
2443 Attack_function_TR2_24=
2444 Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max){integrate(function(x
2445 )
2446   Attack_function_TR2_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max), 0,
2447 24)$value/24
2448 })})
```

2449 *Intake Rate*

```
2450 Ingestion_function_TR2_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax){
2451   ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2452     Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_i,b_i,q_i),
2453     Temperature_function(Tpref,k_i,b_i,q_i))}
2454
2455 Ingestion_function_TR2_24= Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax) {
2456   integrate(function(x) Ingestion_function_TR2_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax),
2457     0, 24)$value/24})
```

2459 *Metabolic rate*

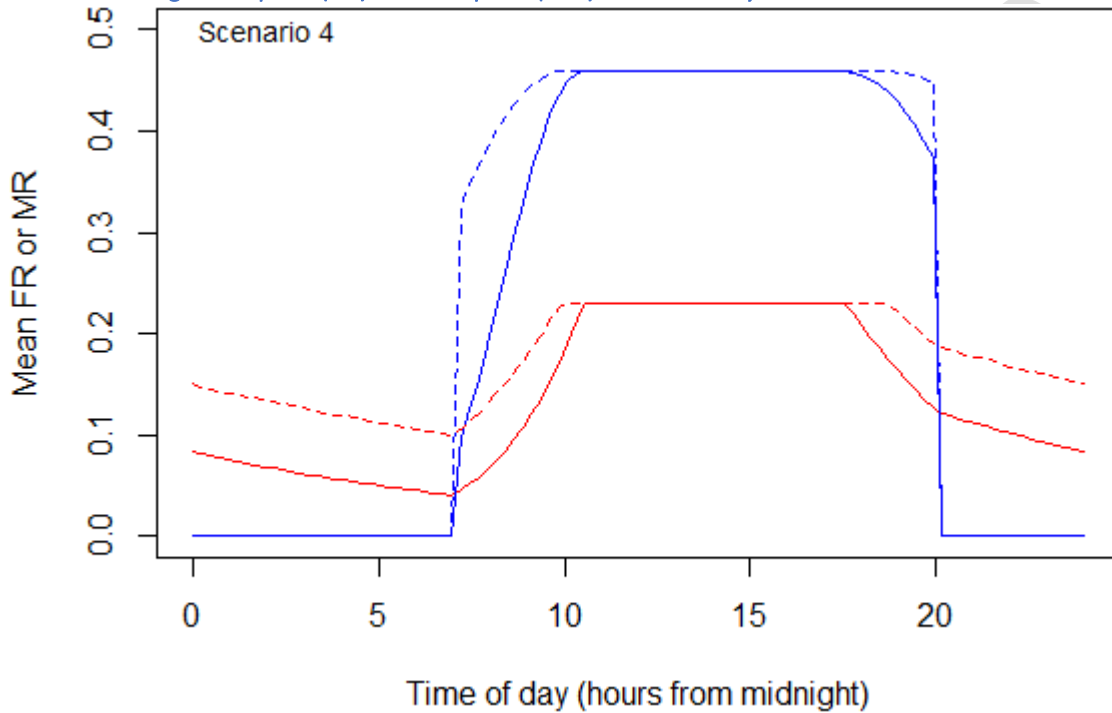
```
2460 Metabolism_function_TR2_H=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2461   ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2462     Arrhenius_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),M_met,Ea,Tref),
2463     Arrhenius_function(Tpref,M_met,Ea,Tref))}
2464
2465 Metabolism_function_TR2_24=
2466 Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2467   integrate(function(x)
2468     Metabolism_function_TR2_H(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref),
2469     0, 24)$value})
```

```

2471 Energy balance
2472 Energy_balance_TR2_24=
2473
2474 function(r,Tpref,Tmin,Tmax,c,alpha,ar_max,hr_max,Hmin,Hmax,HA_min,HA_max,M_met,Tref)
2475 {
2476     24*FR_function(r,
2477
2478     a=ar_max*(Attack_function_TR2_24(Tpref,Tmin,Tmax,c,Hmin,Hmax,HA_min,HA_max)),
2479     h=hr_max/Ingestion_function_TR2_24(Tpref,Tmin,Tmax,c,Hmin,Hmax))*
2480     alpha -
2481     Metabolism_function_TR2_24(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref)}

```

2482 *Plot: energetic inputs (FR) and outputs (MR) over the day*

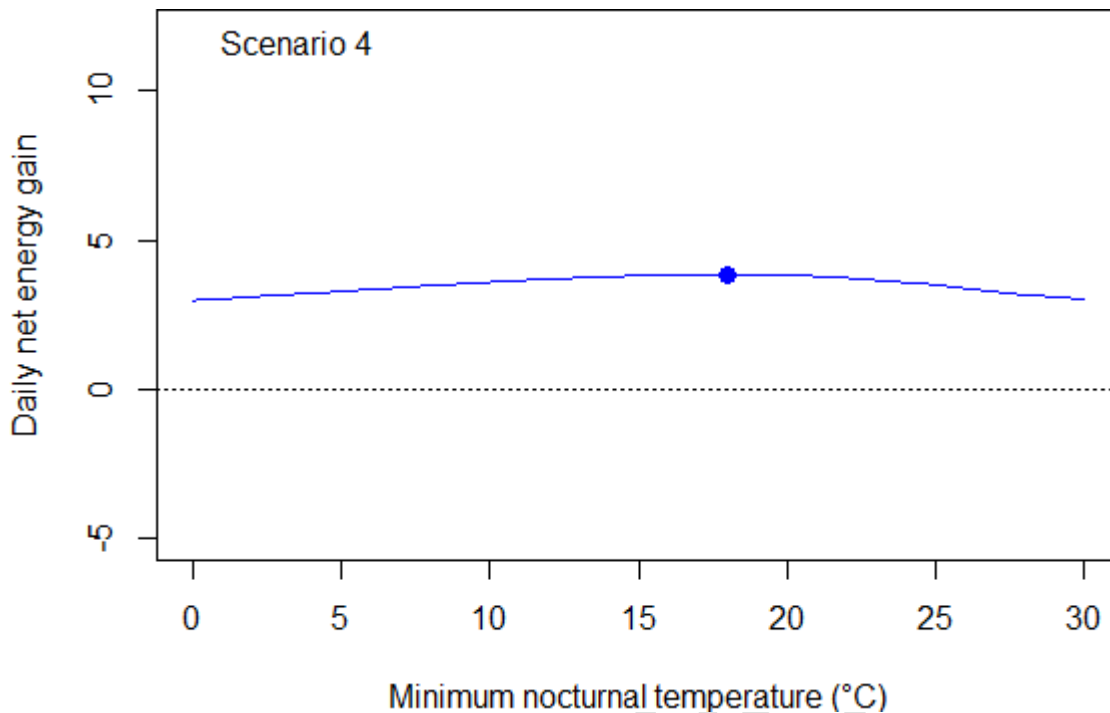


2483

2484 **Fig. S11.** Metabolic rate (MR) (in red) and function rate (FR) (in blue) are represented for Scenario 4
2485 for a minimum T_N of 10 °C (solid lines) or 20 °C (broken lines) for each hour.

2486

Plot: Energy balance vs Tmin



2487

Minimum nocturnal temperature (°C)

2488 **Fig. S12.** Daily net energy gain (NEG_d) for Scenario 4 at different minimum nocturnal temperatures2489 ($T_{N,min}$) and with a default metabolic rate (DMR_{20}) of 0.1. The circle represents the tipping point2490 between positive and negative effects of nocturnal temperature increase on NEG_d .

2491 (f) Scenario 5. Thermoregulator with nocturnal foraging activity

2492 Scenario 5 illustrates the case of a nocturnal thermoregulator with a foraging activity

2493 window delimited by photoperiod. Here, AR is positive only at night (20:00 to 07:00)2494 and depends on body temperature. IR and MR depend only on body temperature. We

2495 assume that the nocturnal thermoregulator selects refugia to maintain a diurnal body

2496 temperature close to 30 °C (T_{pref}), whenever diurnal environmental temperatures2497 exceeded 30 °C [i.e. efficient behavioural thermoregulation; see Chukwuka *et al.* (2021)

2498 for an example], i.e. is a perfect thermoregulator. At night, foraging activity is delimited

2499 by the voluntary thermal limits for activity (VT_{min} and VT_{max}) arbitrarily fixed at 15 °C

2500 and 35 °C. Outside this range, individuals do not forage.

2501 *Attack rate*

```

2502 Attack_function_N=function(x,VTmin,VTmax,Tmin,Tmax,c,Hmin,Hmax){
2503   ifelse(x<Hmin | x>Hmax,
2504     ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax) >= VTmin &
2505       Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax) <= VTmax,
2506         Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),
2507           k_a, b_a, q_a),
2508         0),
2509     0)}
2510

```

2510

```

2511 Attack_function_N_24= Vectorize(function(VTmin,VTmax,Tmin,Tmax,c,Hmin,Hmax) {
2512     integrate(function(x) Attack_function_N(x,VTmin,VTmax,Tmin,Tmax,c,Hmin,Hmax),
2513         0,24)$value/24})

```

2514 *Intake Rate*

```

2515 Ingestion_function_N=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax){
2516     ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<=Tpref,
2517
2518     Temperature_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),k_i,b_i,q_i),
2519     Temperature_function(Tpref,k_i,b_i,q_i))}
2520
2521 Ingestion_function_N_24= Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax) {
2522     integrate(function(x) Ingestion_function_N(x,Tpref,Tmin,Tmax,c,Hmin,Hmax),
2523         0, 24)$value/24})

```

2524 *Metabolic rate*

```

2525 Metabolism_function_N=function(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2526     ifelse(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax)<Tpref,
2527
2528     Arrhenius_function(Temperature_cycle(x,Tmin,Tmax,c,Hmin,Hmax),M_met,Ea,Tref),
2529     Arrhenius_function(Tpref,M_met,Ea,Tref))}
2530
2531 Metabolism_function_N_24=
2532     Vectorize(function(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref){
2533     integrate(function(x)
2534     Metabolism_function_N(x,Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref),
2535     0, 24)$value})

```

2536 *Energy balance*

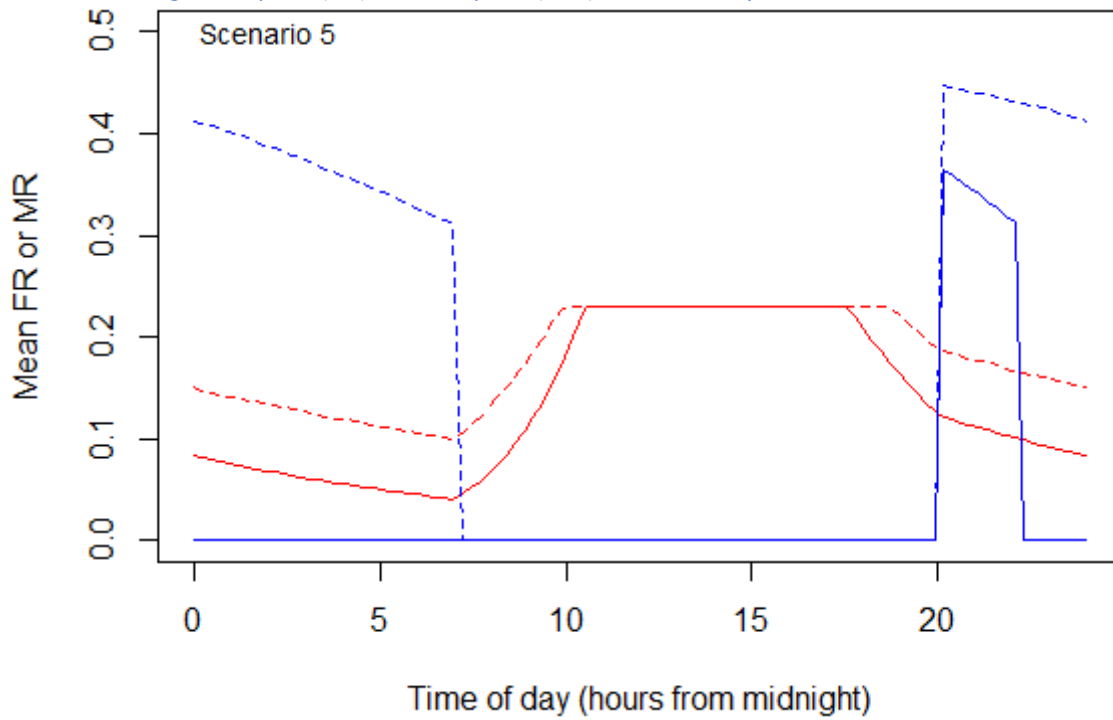
```

2537 Energy_balance_N_24=
2538
2539 function(r,VTmin,VTmax,Tpref,Tmin,Tmax,c,alpha,ar_max,hr_max,Hmin,Hmax,M_met,Tref)
2540 {
2541     24*FR_function(r,
2542     a=ar_max*(Attack_function_N_24(VTmin,VTmax,Tmin,Tmax,c,Hmin,Hmax)),
2543     h=hr_max/Ingestion_function_N_24(Tpref,Tmin,Tmax,c,Hmin,Hmax))*
2544     alpha - Metabolism_function_N_24(Tpref,Tmin,Tmax,c,Hmin,Hmax,M_met,Tref)}

```

2545

Plot: energetic inputs (FR) and outputs (MR) over the day

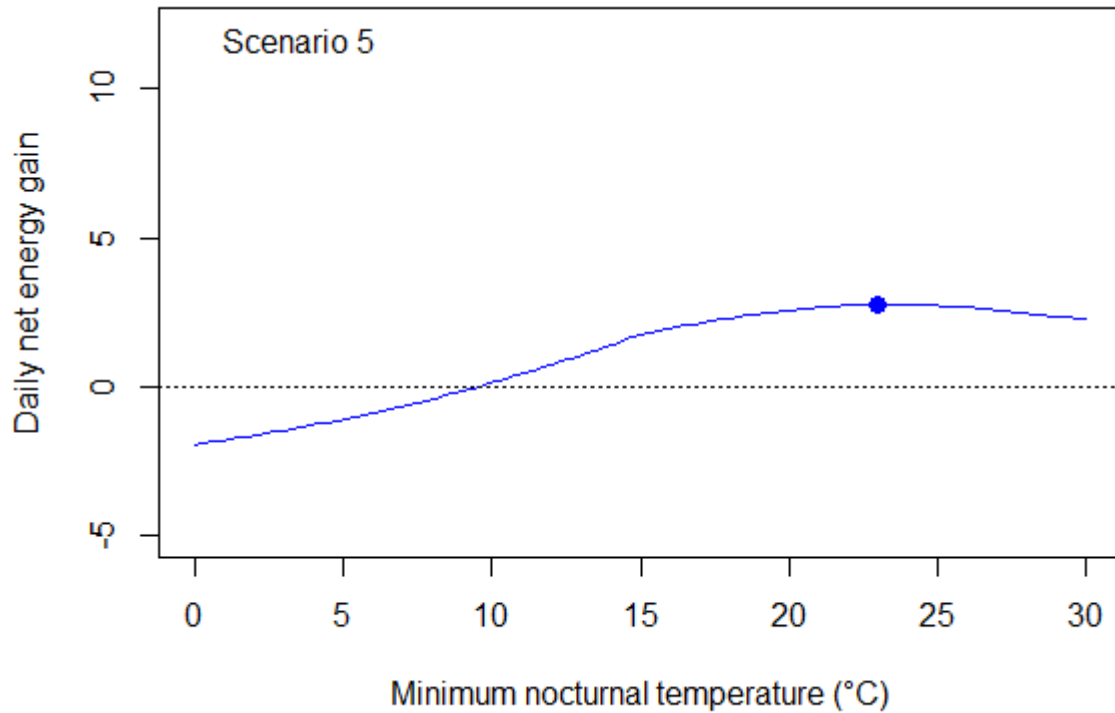


2546

2547

2548

Fig. S13. Metabolic rate (MR) (in red) and function rate (FR) (in blue) are represented for Scenario 5 for a minimum T_N of 10 °C (solid lines) or 20 °C (broken lines) for each hour.



2549
2550

Plot: Energy balance vs Tmin

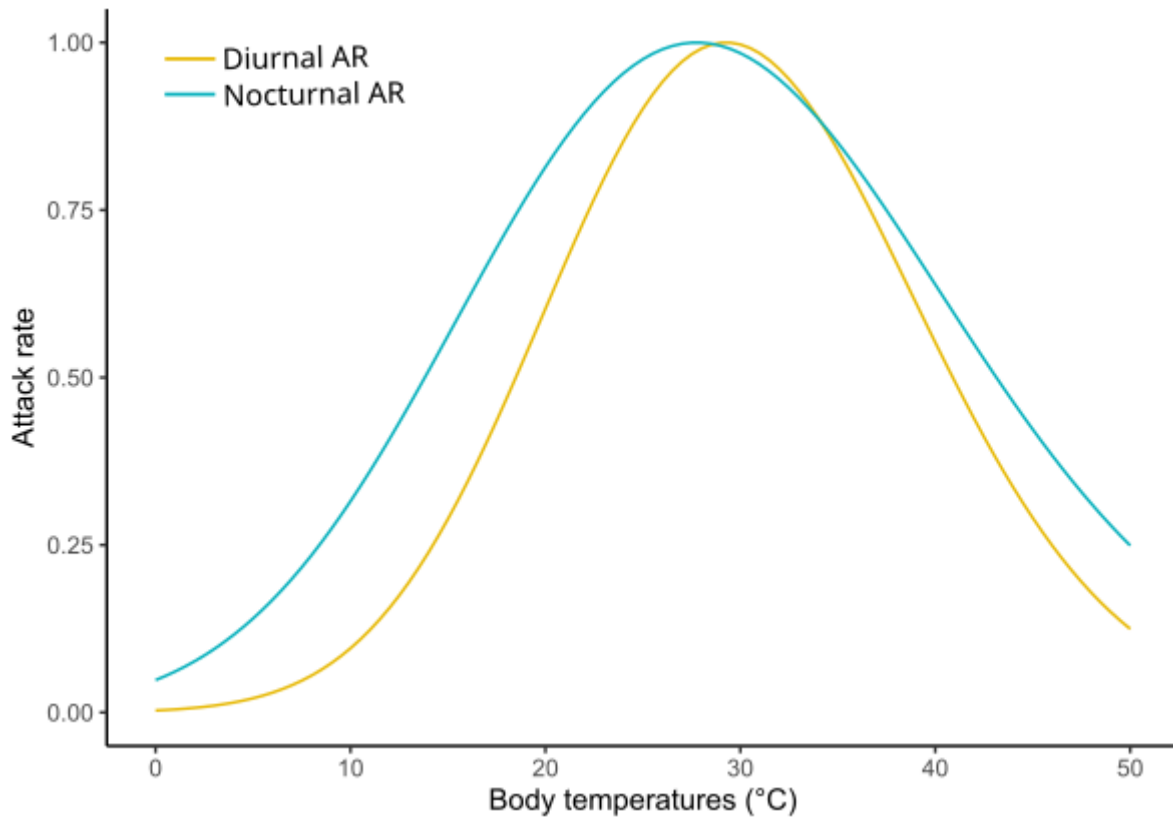
2551 **Fig. S14.** Daily net energy gain (NEG_d) for Scenario 5 at different minimum nocturnal temperatures
2552 ($T_{N,min}$) and with a default metabolic rate (DMR_{20}) of 0.1. The circle represents the tipping point
2553 between positive and negative effects of nocturnal temperature increase on NEG_d .

2554

2555 *(g) Effects of efficient AR at low temperature*

2556 For many nocturnal ectotherms, the efficiency of locomotion is higher at lower
2557 temperatures and the thermal performance curve (TPC) for locomotion plateaus at
2558 lower temperatures than in closely related diurnal ectotherms, which may represent a
2559 thermal adaptation to nocturnal life. This thermal adaptation can greatly improve AR
2560 efficiency at night (Dayananda *et al.*, 2020; Ibarngüengoytía *et al.*, 2007).

2561 To evaluate the effect of higher efficiency, we simulated this scenario by modifying
2562 parameters b and q of the default AR function (see Fig. S15). The consequence of this
2563 change was that T_{opt} for nocturnal AR was slightly lower (decreased from 30 °C to 27 °C)
2564 than in diurnal species.



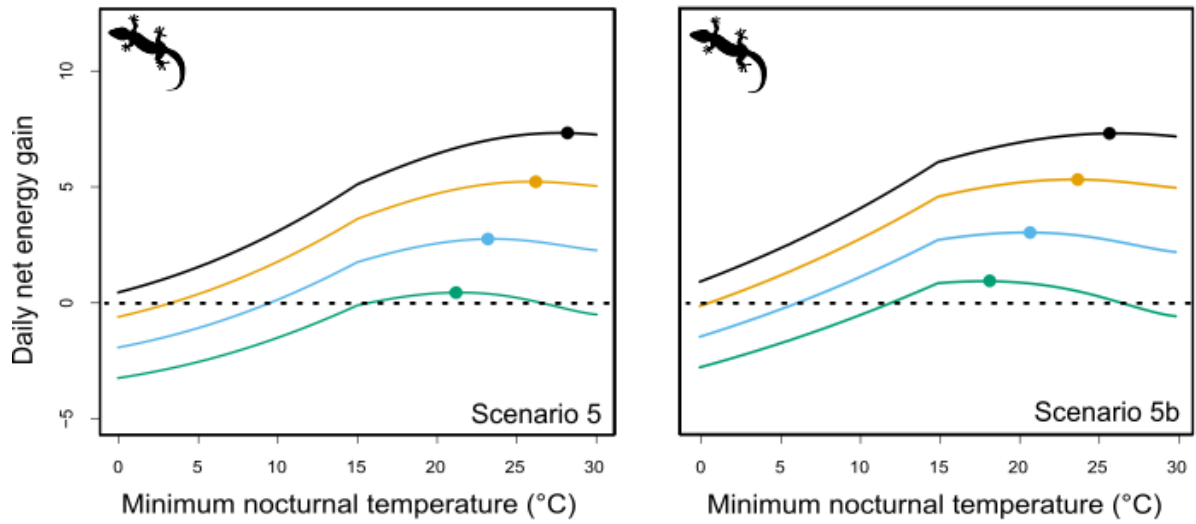
2565

2566

2567 **Fig. S15.** Comparison of different attack rates (AR) functions for a diurnal (yellow) and nocturnal
 2568 (blue) ectotherm.

2569

2570 Fig. S16 shows the difference in NEG_d for a nocturnal species using a modified AR that better
 2571 represents the physiology of a nocturnal species (left panel) and for a nocturnal species with an AR
 2572 similar to that used for the diurnal species of Scenarios 1–4 (right panel). As expected, the adjusted
 2573 AR increased NEG_d but caused a more rapid decline above $T_{N,opt}$. To enhance comparisons between
 2574 Scenarios 1–4 and Scenario 5, we made the deliberate choice to work with a diurnal AR for the
 2575 nocturnal species. Note that with a modified AR (i.e. nocturnal AR; Scenario 5b in Fig. S16), NEG_d are
 2576 slightly higher. However, conclusions provided in the main manuscript for the nocturnal species
 2577 remain unchanged.



2578

2579 **Fig. S16.** Comparison of NEG_d for different attack rates (AR) functions. In scenario 5, AR is
 2580 parameterized to match the AR used for previous scenarios (Scenarios 1–4), to facilitate comparison.

2581 In Scenario 5b, AR is modified to better represent the AR of a nocturnal species (see Fig. S15).

2582 Coloured lines represent different DMR_{20} values (black = 0.01; yellow = 0.05; blue = 0.1; green =

2583 0.15). Solid dots represent $T_{N,opt}$.

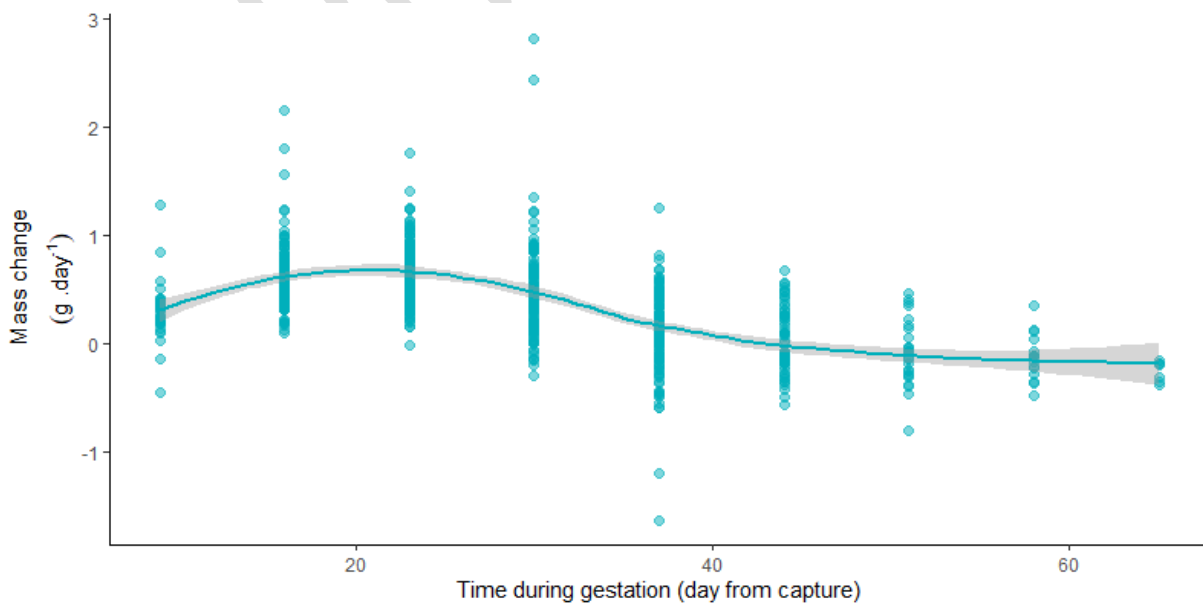
2584

2585

2586 Appendix S5. Empirical analysis of energy balance

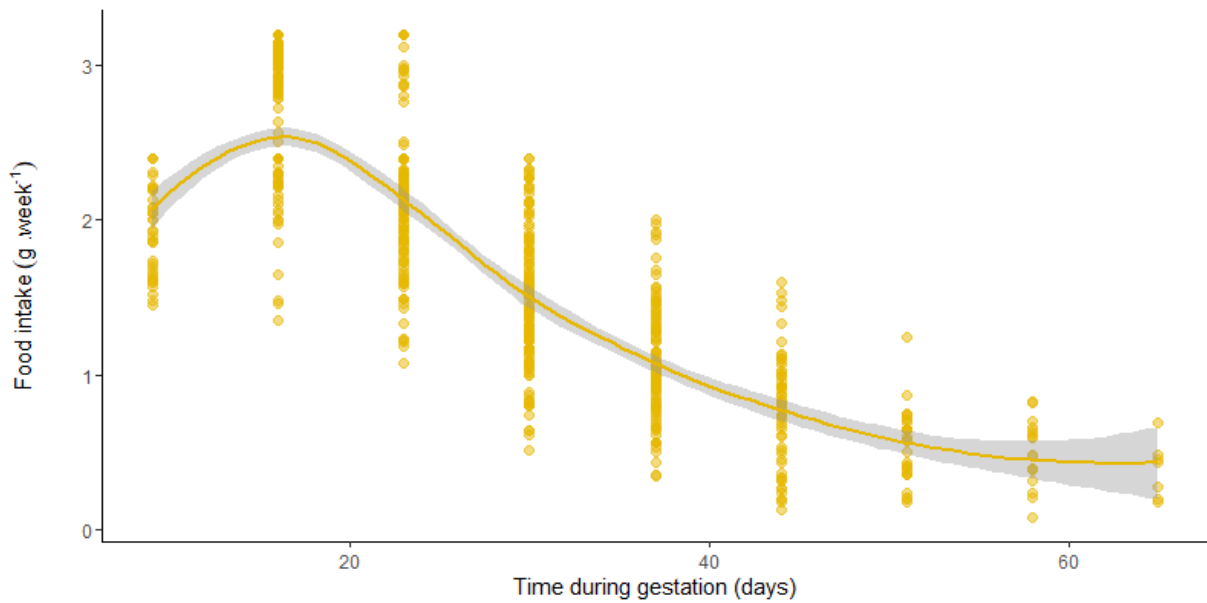
2587 We used unpublished data from the experiment described in Bruschi *et al.* (2023) to analyse the
2588 effects of diurnal and nocturnal temperatures on energy balance. Gravid female common lizards
2589 (*Zootoca vivipara*; mean body mass at capture 3–4 g) captured in natural populations in France
2590 during early gestation were raised under controlled laboratory conditions until parturition and
2591 exposed to four combinations of nocturnal and diurnal temperatures (cold and hot treatments) as
2592 well as two levels of humidity over the gestation period [see Bruschi *et al.* (2023) for details]. We
2593 analysed records of weekly food intake (total mass of crickets consumed) and weekly mass change
2594 (total body mass change) for 131 females measured during gestation (633 observations, ~5 weekly
2595 measurements per female). Over most of the gestation period (40–60 days), body mass increased
2596 non-linearly with time, before plateauing (and sometimes decreasing) close to parturition (Fig. S17).
2597 We observed an average mass increase of +1.8 g during gestation. A similar pattern can be observed
2598 for food intake, with females ceasing to feed when close to parturition (Fig. S18).

2599 We first estimated a conversion factor of 0.31 between weekly food intake (g food/week) and food
2600 intake (g/week) using a linear regression. We then estimated the efficiency of energy
2601 transformation. To do this, we analysed the (normally distributed) residuals from the previous linear
2602 regression throughout gestation and according to the experimental treatments. Gestation time was
2603 included as a non-linear factor (time²) and estimated as the number of days from the start of the
2604 experiment. Experimental treatments (day temperature, night temperature and humidity; described
2605 in Bruschi *et al.*, 2023) were implemented as additive and interactive effects. Female identity was
2606 included as a random effect to control for repeated measures and allow for individual variation in
2607 the intercept. We used manual backward selection to remove non-significant interactions until the
2608 best model was obtained (significance threshold $P < 0.05$) (Table S5). See also Section IV.4 of the
2609 main article.



2610

Fig. S17. Records of female common lizard (*Zootoca vivipara*) body mass change over the gestation period. Mass increased in the early stages of pregnancy (positive change) before stabilizing (mass change ≈ 0).



2611

2612

2613

2614

2615 **Table S5.** Results of ANOVA linear mixed-effect model relating the efficiency of energy
 2616 transformation to time [both as a linear effect (time) and a non-linear effect (time²)], and to diurnal
 2617 and nocturnal temperatures. Significant interaction terms are also reported.

	Numerator DF	Denominator DF	F value	P
Intercept	1	498	17.33	<0.005
Time	1	498	25.18	<0.005
Time ²	1	498	28.08	<0.005
Diurnal temperature	1	128	3.66	0.058
Nocturnal temperature	1	128	4.05	0.046
Time × Diurnal temperature	1	498	12.18	<0.005
Time ² × Diurnal temperature	1	498	22.84	<0.005

2618

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