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RESEARCH ARTICLE

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Intense nocturnal warming alters growth strategies, colouration and parasite load in a diurnal lizard

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Abstract

1. In the past decades, nocturnal temperatures have been playing a disproportionate role in the global warming of the planet. Yet, they remain a neglected factor in studies assessing the impact of global warming on natural populations.
2. Here, we question whether an intense augmentation of nocturnal temperatures is beneficial or deleterious to ectotherms. Physiological performance is influenced by thermal conditions in ectotherms and an increase in temperature by only 2°C is sufficient to induce a disproportionate increase in metabolic expenditure. Warmer nights may expand ectotherms' species thermal niche and open new opportunities for prolonged activities and improve foraging efficiency. However, increased activity may also have deleterious effects on energy balance if exposure to warmer nights reduces resting periods and elevates resting metabolic rate.
3. We assessed whether warmer nights affected an individual's growth, dorsal skin colouration, thermoregulation behaviour, oxidative stress status and parasite load by exposing yearling common lizards (*Zootoca vivipara*) from four populations to either ambient or high nocturnal temperatures for approximately 5 weeks.
4. Warmer nocturnal temperatures increased the prevalence of ectoparasitic infestation and altered allocation of resources towards structural growth rather than storage. We found no change in markers for oxidative stress. The thermal treatment did not influence thermal preferences, but influenced dorsal skin brightness and luminance, in line with a predicted acclimation response in colder environments to enhance heat gain from solar radiation.
5. Altogether, our results highlight the importance of considering nocturnal warming as an independent factor affecting ectotherms' life history in the context of global climate change.

KEYWORDS
colouration change, ectotherms, energetic balance, nocturnal temperatures, oxidative stress

1 | INTRODUCTION

Mean air temperature has been increasing in the past decades and is expected to continue increasing through 2,100 (Allen et al., 2018). Yet, while most climate change studies have focused on the role of diurnal temperatures (T_D), historical records suggest that climate warming is driven by a faster increase of nocturnal temperatures (T_N) than diurnal temperatures in most parts of the globe (Vose et al., 2005). Reasons underlying this asymmetry remain under debate, but include changes in global cloudiness, precipitation, soil moisture or in the thickness of the planetary boundary layer (Davy et al., 2017 and references therein). The escalation of T_N influences multiple aspects of terrestrial ecosystems' functioning (Gaston, 2019; Speights et al., 2017) by affecting vegetation maturation (Mu et al., 2015) and structure (Alward et al., 1999), microbial activity (Palareti et al., 2016), community composition and food web dynamics (Barton & Schmitz, 2018; Ma et al., 2020; Miller et al., 2017).

At present, little is known about the ecophysiological consequences of nocturnal warming on terrestrial animals. Most studies exploring the impacts of global warming are daytime-biased and focus on average warming, ignoring consideration of nocturnal ecology (Gaston, 2019). As a consequence, the daily partitioning of global warming effects between diurnal and nocturnal components has received scant attention, with the very notable exception of several studies emphasising insects. For example, Kingsolver et al. (2015) demonstrated that an experimental increase in ambient temperature of 5°C during the night or day results in differential growth effects for tobacco hornworms (*Manduca sexta*). Other studies have suggested that a change in nocturnal temperatures should alter multiple traits in insects including metabolic expenditure, growth rates and developmental time (Colinet et al., 2015; Zhao et al., 2014).

Physiological processes and behavioural activity of ectothermic species are directly influenced by the temperature of their environment (Seebacher & Franklin, 2005). For such species, the relationship between metabolism, performance or behavioural activity and body temperature often follows a right-skewed bell-shaped curve (Figure 1A): the trait value gradually increases from the critical thermal minimum (CT_{min}) up to the maximal performance at the thermal optimum (T_{opt}), before experiencing a swift decrease towards the critical thermal maximum (CT_{max}). Due to the shape of this curve, it is commonly assumed that increasing temperatures near CT_{min} may have a lower impact on metabolism, performance or behavioural activity than increasing temperatures beyond T_{opt}, where the slope towards CT_{max} is steeper (Sinclair et al., 2016; Sunday et al., 2014). Yet, in critical traits involved in energy balance such as metabolism, increases in temperature that range between 0.5°C and 2°C have been demonstrated to cause a disproportionate increase in metabolic expenditure (respectively about +3% to about +17%) (Dillon et al., 2010). In diurnal species, the energy balance during daytime depends on individual's activity level and energy intake from foraging. At night, metabolic expenditure declines steadily and depends on ambient temperatures, because nocturnal thermoregulatory behaviour is often limited for diurnal species (Colinet et al., 2015). In this context, a warmer T_N that shifts the thermal conditions away from CT_{min} may thus substantially raise metabolic expenditure (Figure 1B), with different consequences for an individual's energy balance.

Current assessments about the impacts of rising T_N on ectothermic species in the literature are rare but differ regarding the potential costs and benefits (Barton & Schmitz, 2018; Speights et al., 2017). Some studies demonstrate that higher T_N may open new temporal niches by extending an individual's daily activity period (Clarke & Zani, 2012; Ziska, 2014), increasing the number

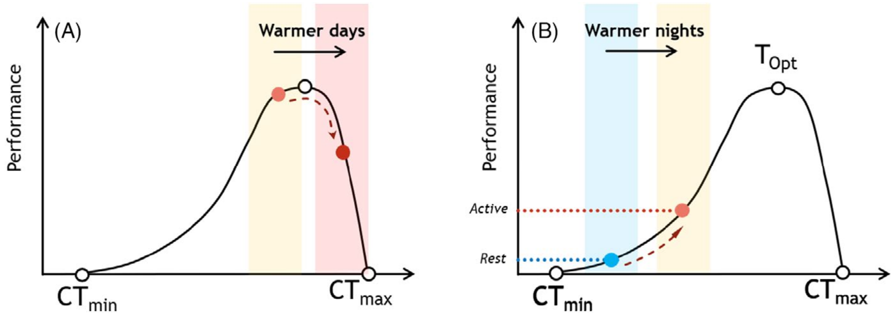

FIGURE 1 Hypothetical impact of an increase in diurnal and nocturnal temperature on individual performance. For ectotherms, the relationship between performance and temperature follows a right-skewed bell-shaped curve (Huey & Slatkin, 1976). (A) Increasing diurnal temperatures are considered a potential threat for ectotherms as they may push individuals from temperatures near T_{opt} (yellow box) towards CT_{max} (red box), therefore reducing performance (red arrow). (B) Nocturnal temperatures are generally low (blue rectangle) and associated with a resting metabolic expenditure. An increase in nocturnal temperatures (yellow rectangle) may increase individual performance (red arrow) by moving body temperatures towards activity levels, reducing optimal resting time and raising energetic costs of rest

of frost-free nights (Andrade et al., 2016) or altering activity towards nighttime in environments where daily temperatures exceed CT_{max} (Lara Resendiz, 2019; Nordberg & Schwarzkopf, 2019). With increasing T_N, individuals may also benefit from an acceleration of development that can lead to earlier onset of reproduction (Speights et al., 2017) or enhanced immediate survival by improving the ability to escape predators (Burraco et al., 2017). However, if exposure to higher T_N is severe and long-lasting, one might also expect several negative effects. First, the short-term advantage provided by an extended period of activity can have long-term costs as the supplementary energy expended overnight could disrupt an individual's energetic (e.g. fat reserve) and physiological (e.g. telomere lengths, oxidative stress) balance, which could decrease life expectancy (Alonso-Alvarez et al., 2006; Burraco et al., 2020; Metcalfe & Monaghan, 2001). Second, high T_N may have an instantaneous negative effect by affecting an individual's rest and recovery time (Bai et al., 2019; Kayser et al., 2014; Ma et al., 2015). For many species, low T_N constitutes a thermal refuge, where individuals recover from diurnal activity (Speights et al., 2017; Zhao et al., 2014). If this period of quiescence is compromised, individuals may not be able to recuperate from their diurnal activity, which may, in turn, have negative effects on their physiology, alter their daily behaviour and, if nocturnal warming is long enough, have negative repercussions on their stress levels and life cycle.

In this study, we investigated the functional responses of the common lizard (*Zootoca vivipara*) to an experimental increase in nocturnal temperatures. In the past decade, this species faced several heat waves in the southern part of the distribution, sometimes leading to extreme T_N. The common lizard is a cold-adapted specialist and recent studies highlighted that functional traits correlate with geographical differences in nocturnal temperatures across its southern range. For example, the nocturnal temperatures of local populations correlate with individual physiological strategies, including heating rate (Rutschmann et al., 2020), baseline corticosterone level (Dupoué et al., 2016) or water balance strategy (Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017). More concerning results point out that warmer nocturnal temperatures also correlate with faster erosion of telomeres early in life and population decline, and therefore with a higher 'stress level' of individuals and populations (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). Yet, a mecanistic understanding of the biological impact of T_N remains lacking. To better assess the consequences of warmer nights, we studied the response of yearling common lizards to an intense increase in nocturnal temperatures. We exposed individuals to two nocturnal thermal treatments over a period of 38 days. A control treatment simulated T_N close to the common lizard's lower limit of activity, whereas lizards in the treatment group experienced an increase in T_N, matching extreme temperatures recorded overnight in natural populations. Both groups experienced similar ambient temperature conditions during the day. We predicted that warmer T_N should increase metabolic expenditure and individual growth rate, which may trigger a trade-off with other physiological and metabolic functions. To test this prediction, we therefore compared several functional traits before and after treatment.

We predicted individuals from the warmer treatment to grow faster as a direct consequence of a higher assimilation rate (Bestion et al., 2015; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). In addition, we expected enhanced growth rates to incur a cost to other morphological traits such as body mass or fat reserve, which may lead to elevated physiological stress (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). To verify this second prediction, we quantified the balance between oxidative damage and antioxidant defences (i.e. oxidative stress) (Costantini, 2014; Metcalfe & Monaghan, 2001; Monaghan et al., 2009). If exposure to warmer nocturnal temperatures induced a stress response, then we also predicted an increased susceptibility to parasitic infestation due to the immunosuppressive effect of stress (Harvell et al., 2002). Finally, we tested whether and how lizards could buffer the physiological costs of increased nocturnal temperatures by selecting cooler body temperatures during the day (Angilletta et al., 2002) and by developing a lighter colouration that reduces heat gain during daytime (thermal melanism hypothesis; Clusella Trullas et al., 2007).

2 | MATERIALS AND METHODS

2.1 | Study species and populations

The common lizard (*Z. vivipara*) is a small-sized species in the family Lacertidae whose distribution encompasses Northern Europe and Asia. In the study populations, lizards emerge in spring from winter hibernation to grow and reproduce over summer. The population structure consists of juveniles (born in the summer), yearlings (non-reproductive 1-year-old individuals) and adults (2-year-old individuals or older). We focused on yearling males, because they exhibit the highest growth rate during the activity season. We sampled individuals from four populations (ca. 20 lizards per populations, total $n = 78$), located in the Massif Central, France (Table 1) and brought them back to the laboratory. Populations were selected based on their similarity in diurnal and nocturnal thermal characteristics. Yet, significant differences existed between populations, notably when comparing extreme temperatures recorded overnight (97.5% upper quantile of the distribution of nocturnal temperatures; see Table 1, Figure 2A,B and Appendix S1). To control for these differences, and detect patterns related to them, population identity was always included in our models as a fixed effect.

2.2 | Thermal conditions

Each lizard was housed individually in a plastic terrarium (11 × 18 × 11cm) containing a cardboard shelter and a substrate of

TABLE 1 Habitat characteristics. Elevation (in m), latitude and longitude of each population sites and average nocturnal (T_N) and diurnal (T_D) temperatures (in °C). Extreme temperatures ($T_{N(EX)}$ and $T_{D(EX)}$) correspond to the 97.5% upper quantile of the temperature distribution recorded in each location

Population	Elevation	T_N	$T_{N(Ex)}$	T_D	$T_{D(Ex)}$	Lat.	Long.
Barnassac	1,527	13.6 ± 4.2	23.1	18.6 ± 7.3	33.6	44°25′40.4″N	3°45′50.1″E
Tour du Viala	1,190	13.1 ± 3.7	23.0	16.9 ± 6.1	30.5	44°20′17.4″N	3°46′4.7″E
Col du Pendu	1,420	12.6 ± 3.1	19.5	17.1 ± 6.1	31.5	44°39′18.3″N	4°01′49.7″E
Bouvier	1,461	12.4 ± 3.7	21.0	18.8 ± 8.7	37.5	44°45′25.6″N	3°31′05.7″E

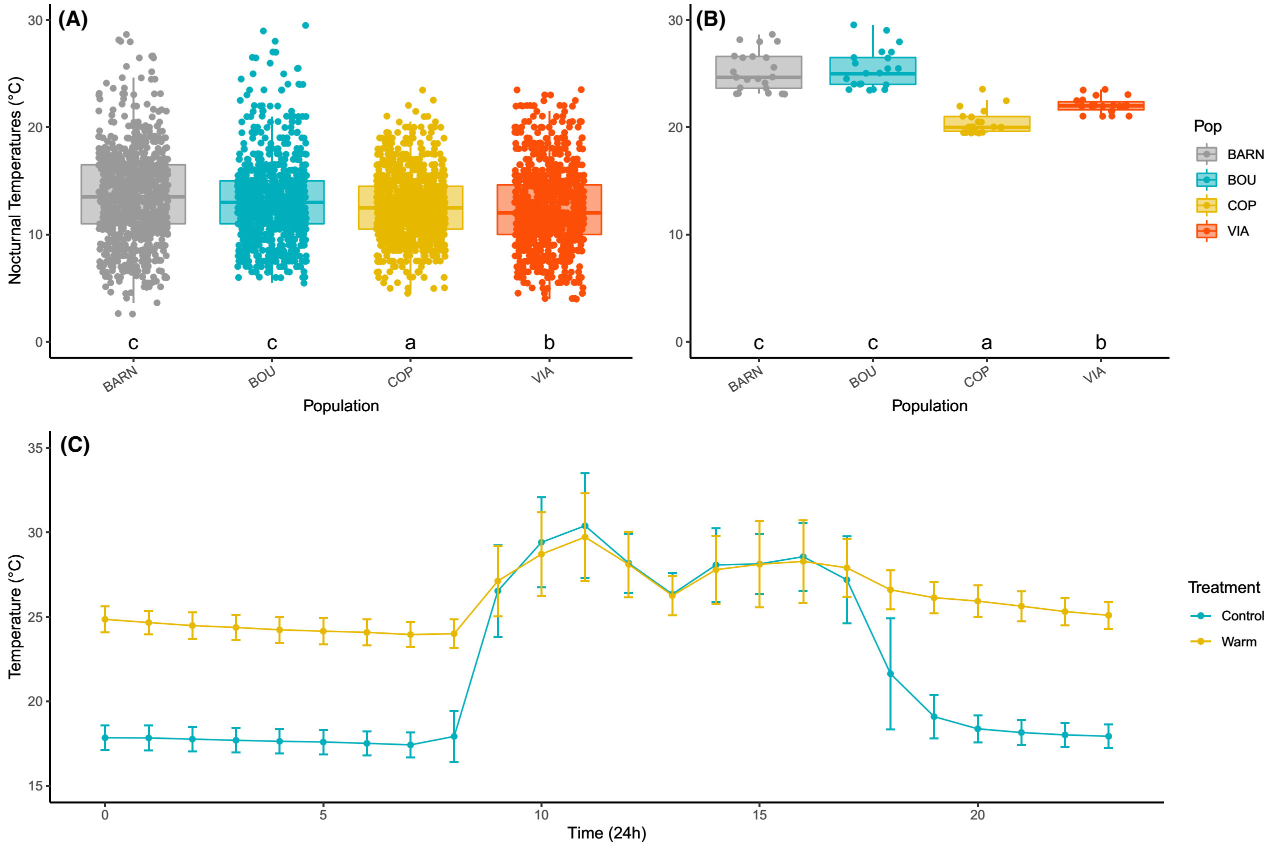

FIGURE 2 Environmental conditions in source populations and daily cycle of temperature in laboratory conditions. Average (A) and extreme (B) nocturnal temperatures recorded overnight in the four sampled populations. Letters indicate significant differences among populations, according to a post-hoc Tukey test. Extreme high temperatures are defined as the 97.5% upper quantile of the distribution of nocturnal temperatures. (C) The differences between the warm (yellow) and the control (blue) nocturnal temperature treatments over a 24-hr day–night cycle. Over the day, lizards from the two thermal treatments were maintained in similar conditions and were allowed to bask under a 25W bulb for 6 hr a day, from 9.00 to 12.00 and from 14.00 to 17.00. The absence of heat during the mid-day time (12.00–14.00) explains the pattern of diurnal temperatures

sterilized soil. Terraria were misted four times a day. Lizards were allowed to bask under a 25W bulb for 6 hr a day. Every second day, lizards were fed live crickets, maggots or mealworms ad libitum. Lizards were randomly divided into two thermal treatments. During the day, all lizards were held in a common room under the same thermal conditions. Every evening between 17:30 and 18:30 hours, lizards in the control group (T_{Nc}) were transferred to a room tracking ambient temperature. Lizards in the warm nocturnal temperature treatment (T_{Nw}) were transferred to a room maintained at higher nocturnal temperatures. Every morning between 8:00 and 8:30 hours, lizards were returned to the main room (See Figure 2C and Appendix S1). All terraria were randomly allocated on the shelves every morning and evening. Note that we matched individuals for size and mass between treatment groups to eliminate potential bias towards heavier or longer individuals in one treatment (See Appendix S2 and Figure S4).

In each treatment, two iButtons (Thermochron©, Maxim Integrated Products, Sunnyvale, CA, USA) were buried in two different terraria to estimate thermal conditions experienced by the lizards. Temperatures were recorded every hour during the experimental period. Temperatures in T_{Nw} were chosen to reflect the extreme nocturnal temperatures recorded in natural populations (Table 1), simulating the potential effect of global warming. Temperatures in T_{Nc} were chosen to be near the lower limit for activity for the common lizard that is around an air temperature of 17–20°C (average temperature in $T_{Nc} = 17.8 \pm 0.7$°C and $T_{Nw} = 24.6 \pm 0.9$°C; $t_{1195.7} = 145.65$, $p < 0.005$) (Rozen-Rechels et al., 2020).

2.3 | Timing of the experiment

All measurements described in the next sections were performed twice, before and after the 5-week (38 days) treatment. For each lizard and for each trait *i*, a differential $\boldsymbol{\Delta}_{\mathbf{i}}$ was calculated as the difference between post- and pre-treatment measurements (e.g. $\boldsymbol{\Delta}_{\mathbf{SVL}}$ = SVL post-treatment − SVL pre-treatment). A period of 38 days was chosen to mirror the typical duration of summer heat waves in the Massif Central region (personal observations). It also covers approximately 25% of the summer activity (May–September) for common lizards and corresponds to a period of rapid growth for young lizards. Thus, this duration was sufficient to detect differences in individual growth rates and observable changes in oxidative balance (Dupoué, Angelier, et al., 2020). Lizards were fasted between the day of capture and the end of the first set of measurements (2 days). Measurements were taken in the following order after capture: (a) ectoparasite removal, (b) morphological measurements, (c) digital scanning for colour analysis, (d) preferred body temperature and (e) blood sampling. All lizards were fed after blood sampling. We fasted lizards for 2 days prior to the second run of measurements. All individuals were released to their site of capture. See Appendix S3 for a timeline of the experimental design.

2.4 | Morphological measurements

We measured snout to vent length (SVL, mean ± *SD* = 40.2 ± 2.5 mm), body length (=SVL + tail length: BL = 93.6 ± 13.4 mm) and body mass (BM = 1.31 ± 0.25 g). We estimated tail's volume (TV = 331.1 ± 76.7 mm^3) as an index of fat reserves (Avery, 1974) and muscular state (see Appendix S4 for more details). We also calculated an index of body condition (BC) as the residuals of a linear regression relating BL and BM (Richard et al., 2012).

2.5 | Colour measurements

Pre- and post-treatment dorsal images of yearlings were obtained with a high-resolution digital scanner (Canon®, CanoScan Lide 110; image size: 2,550 × 2,600 pixels). Each scan was cropped to the area of interest (i.e. dorsal section, see Figure S6) and the background was removed. We analysed two aspects of colour variation with the *colordistance* R package (Weller, 2019), as described in Appendix S5. Briefly, we focused first on the luminance of each dorsal section and calculated the distance between the luminance before and after treatment ($\boldsymbol{\Delta}_{\mathbf{LUM}}$). Second, we estimated the change in colouration by quantifying the variation in colour composition by extracting the predominant colours in all pictures (pre-and post-treatment pictures grouped together; four colours were selected: COL_1 to COL_4; Figure 4A; Figure S8). Then, we evaluated their relative abundance for each individual, before and after the treatment, to calculate four colouration distances (Δ_{COL_1} to Δ_{COL_4}). Colours can be classified from the darker to the lighter one (position on the spectral range) as follows: COL_1 (HEX Code: #41362E), COL_2 (#604B40), COL_3 (#6E5F4C) and COL_4 (#7E7167).

2.6 | Thermoregulatory behaviour

The preferred temperature T_{pref} is defined as the range of body temperatures selected by an ectotherm in a cost-free environment (Angilletta et al., 2002; Hertz et al., 1993). We measured T_{pref} using 10 plastic tracks (120 × 25 × 20 cm) lined with a substrate of sterile soil. In each track, we created a thermal gradient by heating one side with a 60W incandescent bulb (39.4 ± 4.02°C) while the cool side was maintained at ambient temperature (23.7 ± 2.7°C). Two UVB 30W fluorescent lamps positioned over each track provided uniform illumination with white light to avoid a potential effect of a luminance gradient. Thermal gradient tracks were heated at least 45 min prior to each experiment. We assigned a lizard to each track at random and allowed them to thermoregulate for 80 min after 10 min of acclimation. We recorded the back-surface temperature of each lizard as a proxy of body temperature (Rutschmann et al., 2020). Measurements were repeated every 10 min (9 values per individual), with an infrared thermometer (Raytek, Raynger MX2; distance-to-spot ratio is 60:1) and with minimal disturbance. The distance of detection (300 mm) was calibrated between all measures according to the manufacturer's recommendations for a spot diameter of 6 mm.

2.7 | Oxidative status

Oxidative status was assessed using two blood markers. Lizards were bled (60 μl whole blood) from the post-orbital sinus at days 0 and 39. Samples were immediately centrifuged for 5 min at 13,500 rpm to separate plasma and blood cells and kept frozen at −28°C in airtight tubes until analyses. Plasma concentration of reactive oxygen metabolites (ROM) and non-enzymatic antioxidant capacity (OXY) were used as indices of oxidative damage and defences, respectively. We followed a protocol developed for this species (Josserand et al., 2020). ROM concentration was measured with the d-ROMs test (MC003, Diacron International, Italy). This test measures the oxidative capacity of a plasma sample in relation to the activity of organic hydroperoxides (biomolecules damaged by free radicals; Costantini, 2016). The antioxidant capacity of the plasma was assessed with the OXY-absorbent kit (MC435, Diacron International, Italy). This test measures the ability of plasma to buffer an oxidant attack of hypochlorous acid (Costantini et al., 2011). Samples for d-ROMs were read at 540 nm after 75 min of incubation at 37°C. Samples for OXY were read at 540 nm after 10 min of incubation at 37°C. Plates were randomised by population, treatment and timing (pre- versus post-). We measured ROM and OXY using two plates, so we repeated 14 samples to estimate the coefficient of variation both within (intra-plate; ROM: 8.86%, OXY: 1.02%) and between plates (inter-plate; ROM: 9.19%, OXY: 2.05%).

2.8 | Parasite load

Ecto- and endo-parasite loads were estimated for each individual. On the day of capture, all individuals were examined for mites (genus *Ophionyssus*). All parasites were hand removed with tweezers and the lizards were treated with an antiparasitic solution of 0.29% fipronil (Frontline Spray^{TM}). Twenty days later, we checked for the presence of mites to avoid infestation in the laboratory. We took advantage of this opportunity to once again categorize lizards for the presence or absence of ectoparasites (EctoP = 0 or 1). We also took advantage of blood sampling to test for the presence of blood parasites (BloodP, *Karyolysus* spp., RM-P, personal observation) before and after treatment. When individuals were bled, a drop of blood was smeared on a slide whenever blood flow was sufficient. Blood was fixed with 100% methanol for 5 min and stained for 40 min with a 10% solution of Giemsa stain (azur-eosin methylene). BloodP were counted under a Leica Microsystems DMLB microscope at 1,000× magnification. A total of 2,000 blood cells per blood smear were screened following Megía-Palma et al. (2018).

2.9 | Statistics

All statistics were performed using R software (R Core Team, 2020, v. 3.2.0). All differences between post- and pre-treatment measures ($\mathbf{\Delta}$) were analysed using linear models, with the exception of ecto- and blood-parasite loads that were analysed using Generalised Linear Model and Generalised Linear Mixed Model, respectively (see dedicated section).

2.9.1 | Morphology

The difference (Δ_i) for each morphological trait *i* was analysed using a Gaussian linear model. We included temperature treatment and population of origin as fixed effects. The initial value of the morphological trait (i_{initial}) was entered as a covariate. We also included the interaction between treatment and population.

2.9.2 | Colouration

The luminance differential ($\mathbf{\Delta_{LUM}}$) was analysed using a Gaussian linear model, including population of origin, temperature treatment, initial luminance and the interaction between treatment and population as fixed effects. We used four linear models to test whether the four most represented dorsal colours changed during the experimental treatment ($\mathbf{\Delta_{COL\_1}}$ to $\mathbf{\Delta_{COL\_4}}$). Two lizards were discarded from the analyses, because their images revealed moult residuals, affecting their colouration.

2.9.3 | Thermal preferences

We used a linear mixed-effects model to analyse T_{pref}. For each individual, we estimated $\mathbf{\Delta_{Tpref}}$ as the difference between the mean body temperature calculated over the post-experimental run and the mean body temperature calculated over the pre-experimental run. In the fixed part of the model, we included initial T_{pref}, population of origin and experimental treatment. We also included the interaction between the population of origin and treatment. The identity of the experimental arena was added as a random effect to capture the variance between the 10 thermal arenas used repeatedly in the experimental setup.

2.9.4 | Oxidative status

We used a Gaussian linear model to test whether changes in ROMs ($\mathbf{\Delta_{ROM}}$) and in OXY ($\mathbf{\Delta_{OXY}}$) were impacted by the experimental design, the population of origin, the initial values of ROMs (or OXY) and the interaction between the treatment and the population of origin.

2.9.5 | Parasite load

Ectoparasite presence (EctoP) was examined using a generalized linear model (GLM) with a binomial distribution. Initial state of parasitism (presence/absence), population of origin and treatment (and their interaction) were included as predictor variables. Unfortunately, some individuals were more difficult to bleed than others before or after the treatment notably not only because of small body size but also because of individuals' level of hydration, body temperature and person in charge. Yet, despite standardized before blood sampling to avoid any bias, we were not able to collect blood to assess *BloodP* for all individuals (N pre-treatment warm = 25, control = 25; N post-treatment warm = 35, control = 34). Consequently, it was not possible to analyse the difference in *BloodP* load, since some individuals in the post-treatment sample were not included in the pre-treatment sample, and *vice versa*. *BloodP* exhibited an excess number of zeros, so we used a generalized linear mixed model, with a zero-inflated Poisson distribution (GLMMadaptive package; Rizopoulos, 2020). Population, timing (pre-versus post-treatment) and treatment, as well as the interactions between timing and treatment and population and treatment were included as fixed terms in the model. We included individual identity as a random effect.

2.10 | Initial values

We screened for potential differences between experimental groups at the onset of the experiment for all measurements. Except for ROM (1.27 ± 0.41, $p = 0.003$), we found no difference between treatment for initial values (all $p > 0.07$). The difference in ROM was driven by five individuals, all assigned in T_{Nw}, exhibiting extreme high values. These high initial values of ROM were uncorrelated with any of other traits studied here and therefore individuals were retained in our analyses (See Appendix S6 for more information).

3 | RESULTS

Complete summary tables for all traits are available in Appendix S7.

3.1 | Morphology

Δ_{SVL} was positively influenced by the warmer treatment (i.e. higher growth; Figure 3A; 0.59 ± 0.25, $t = 2.38$, $p = 0.02$). In contrast, Δ_{MASS} was not impacted by the experimental treatment (Figure 3B; $p = 0.84$). Change in body condition Δ_{BC} was negatively influenced by warmer nocturnal temperatures (Figure 3C; −0.07 ± 0.02, $t = -3.01$, $p = 0.003$). Finally, Δ_{TAIL} was negatively influenced by T_{Nw} (Figure 3D; −26.6 ± 9.48; $t = -2.8$; $p = 0.006$). All morphological differences were negatively impacted by the initial measurement (all $p < 0.007$). Neither the population of origin (all $p > 0.12$) nor the interaction between treatment and population (all $p > 0.06$) had an effect on morphological differences.

3.2 | Colouration

Δ_{LUM} was significantly higher in T_{Nw} (3.43 ± 1.64; $t = 2.1$; $p = 0.04$) in all but one population (Bouvier), as indicated by the significant interaction between population and treatment (Figure 4B; −5.53 ± 2.25; $t = -2.259$; $p = 0.02$; all other $p > 0.58$). Initial luminance had a negative correlation with Δ_{LUM} (−0.79 ± 0.12; $t = -6.46$; $p < 0.005$). Regarding colouration (Δ_{COL}; Figure 4C), three out of the four dominant colours were significantly affected by T_{Nw}. The proportion of the darkest colour (Δ_{COL_1}; *#41362E*) declined in all populations (−0.14 ± 0.06; $t = -2.34$; $p < 0.02$), except in Bouvier where an opposite and significant difference was observed (0.19 ± 0.03; $t = -2.48$; $p < 0.015$; all other $p > 0.45$). In all populations, the proportion of COL_2 (Δ_{COL_2}; *#604B40*) increased in T_{Nw} (0.02 ± 0.01; $t = 2.07$; $p = 0.04$), and particularly in Col du Pendu (0.03 ± 0.01; $t = 2.1$; $p = 0.03$, all other $p > 0.6$). Δ_{COL_3} (*#6E5F4C*) was unaffected by the treatment (−0.05 ± 0.02, $t = 1.63$, $p = 0.11$) except for Bouvier, where it increased significantly in T_{Nc} (−0.05 ± 0.02, $t = -2.15$, $p = 0.03$). The

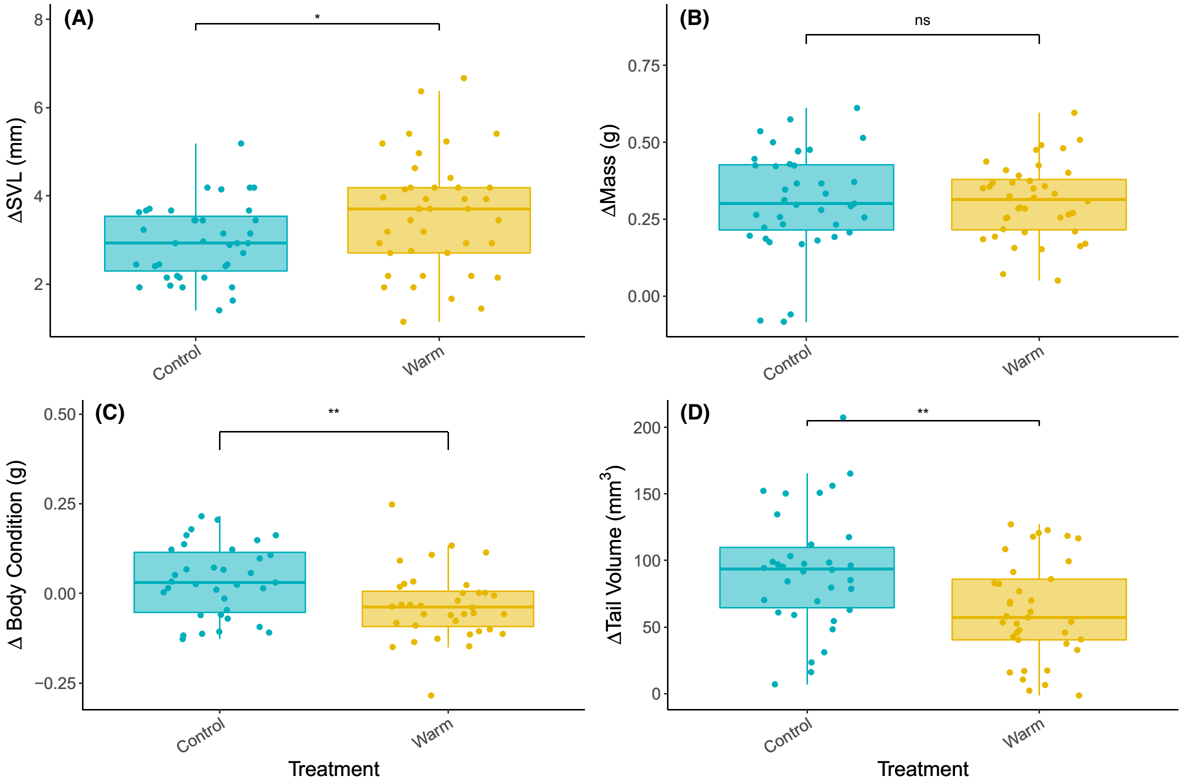

FIGURE 3 Morphology. (A) Yearling growth rate in body size (in mm), (B) body mass difference (in g), (C) body condition (in g) and (D) difference in tail volume (in mm^3) according to temperature treatment (T_{Nc}: pale blue; T_{Nw}: pale yellow). To ease the graphical representation, Δ_{SVL}, Δ_{Mass} and Δ_{Tail} are all corrected for their initial values. As a residual, Δ_{BC} is not corrected

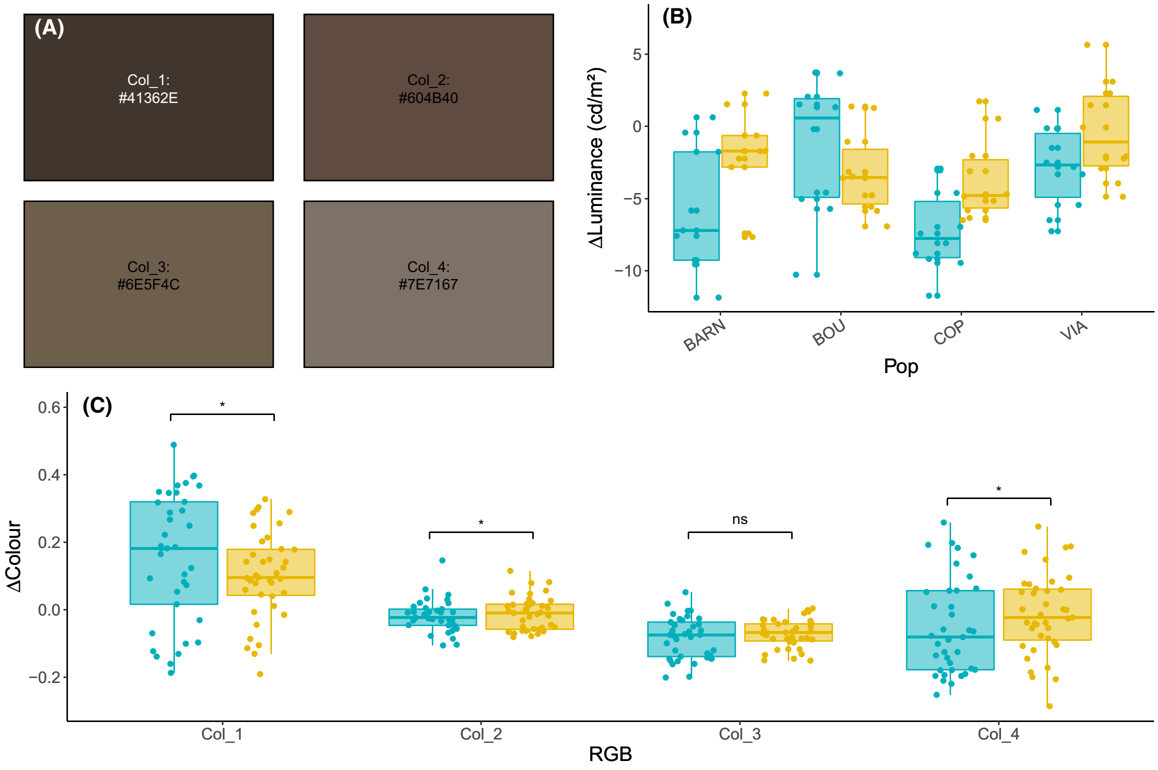

FIGURE 4 Colouration. (A) The four most dominant colours in individual dorsal patterns and their associated HEX code. (B) Dorsal luminance (in cd/m^2) depending on the treatment. (C) Change of the proportion of colours in the dorsal pattern depending on the treatment. To ease the graphical representation, Δ_{COL} and Δ_{LUM} are both corrected for initial values of Col and Lum

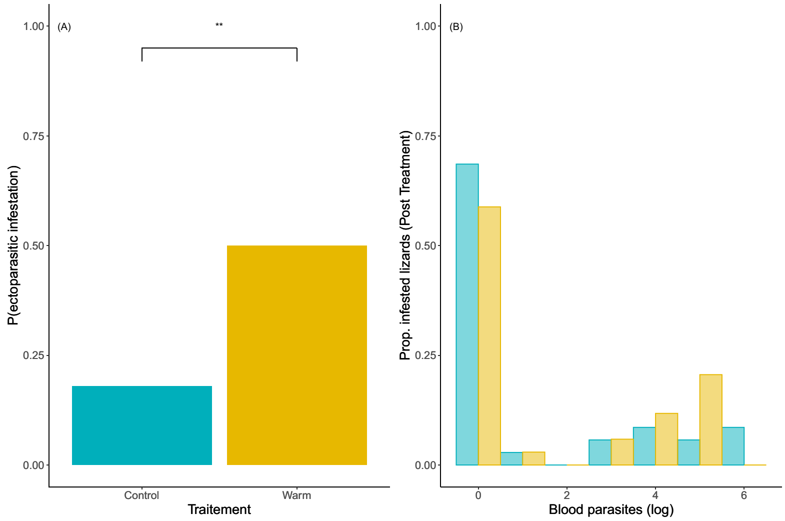

FIGURE 5 Parasite load. (A) Yearlings infestation rate by mites depending on the treatment. (B) Proportion of yearlings infested by blood parasites at the end of the treatment

proportion of COL_4 (*#7E7167*) was positively affected by T_{Nw} for all populations (0.04 ± 0.02; $t = 2.24$; $p = 0.03$). All $\boldsymbol{\Delta}_{\mathbf{COL}}$ were negatively affected by the initial proportion of colouration (all $p < 0.005$).

3.3 | Thermal preferences

We found no effect of nocturnal temperatures on $\boldsymbol{\Delta}\mathbf{T}_{\mathbf{pref}}$ (-0.001 ± 0.19, $t = 0.32$, $p = 0.99$; Figure S10). Yet, on average, individuals favoured warmer temperatures during the second measurement after controlling for a negative correlation with initial T_{pref} (-0.81 ± 0.07, $t = -10.88$, $p < 0.005$). We found no influence of population (all $p > 0.07$).

3.4 | Oxidative status

Both $\boldsymbol{\Delta}_{\mathbf{ROM}}$ and $\boldsymbol{\Delta}_{\mathbf{OXY}}$ were negatively influenced by the initial levels of ROMs and OXY (ROMs: -1.02 ± 0.07, $t = -14.26$, $p < 0.005$; OXY: -1.00 ± 0.02, $t = -59.01$, $p < 0.005$). We did not detect any effect of treatment on $\mathbf{\Delta_{ROM}}$ and $\mathbf{\Delta_{OXY}}$ (See Figure S11; $p > 0.20$), of the population of origin (all $p > 0.14$) nor of the interaction between the population of origin and the treatment (all $p > 0.11$).

3.5 | Parasitic load

Ectoparasitic infestation (***EctoP***) was influenced by the experimental treatment (Figure 5A; 1.63 ± 0.55, $z = 2.97$, $p = 0.003$) but not by the initial presence of ectoparasites ($p = 0.19$). ***EctoP*** did not differ among populations (all $p > 0.30$). Blood parasite load (***BloodP***) did not change due to the treatment (zero-inflation model, interaction between treatment and time: $p = 0.72$). ***BloodP*** also did not differ between treatments (Figure 5B; count model, interaction between treatment and time: $p = 0.84$). Yet, individuals from Bouvier showed a lower rate of infection in T_{Nw} (−1.61 ± 0.68, $z = -2.35$, $p = 0.02$).

4 | DISCUSSION

After 5 weeks of exposure to manipulated, high nocturnal temperatures, without changes in diurnal conditions, we found significant alterations in morphology, colouration and rate of infestation by ectoparasites in yearlings of the common lizard, *Z. vivipara*. We did not detect an effect of treatment on thermal preferences, infection rate by blood parasites or oxidative stress status.

4.1 | Intense nocturnal warming drives allocation of energy towards structural growth rather than storage

In all populations, exposure to high warm nocturnal temperatures had a positive influence on the growth in body length (SVL), with lizards from T_{Nw} growing 20% faster on average compared to controls. These results corroborate similar patterns from previous studies on the same species in which juvenile common lizards exhibited enhanced growth rates in body size when exposed to elevated daily temperatures (Bestion et al., 2015; Chamaille-Jammes et al., 2006). Comparable effects of T_N have also been described for other ectothermic species, with warmer T_N accelerating egg, larval or pupal development in several insect species (Speights & Barton, 2019; Whitney-Johnson et al., 2005; Wu et al., 2012). However, to the best of our knowledge, this study is the first to show that warmer T_N can have a direct, positive effect on a lizard growth rate.

Faster body growth may be attributable to higher energy acquisition or higher allocation towards structural growth during warmer nights or both (Speights et al., 2017). Yet, if not compensated by higher caloric intake, higher energetic expenditure during warmer nights may require rapid functional adjustments, including depletion of energetic reserves (Dillon et al., 2010; Huey & Kingsolver, 2019). Despite lizards having unrestricted access to food and water in captivity, our results indicate that faster growth rate triggered a potential trade-off with other key morphological traits. First, body mass did not differ between treatments. Consequently, yearlings grew faster in T_{Nw} but showed lower post-treatment body condition. In addition, lizards in T_{Nw} had a reduced tail volume compared to controls. Tail volume in lizards is a reliable proxy of reserves available to respond to energetic or hydric stress, by metabolising fat or proteins, respectively (Bateman & Fleming, 2009; Brusch et al., 2018). We therefore hypothesize that the nocturnal treatment initiated two distinct strategies resulting from a plastic allocation of energy towards structural growth versus storage. Individuals from T_{Nw} expended more available energy to compensate for increased metabolic activity, whereas individuals from T_{Nc} built up reserves for future needs.

It is interesting to note here that lizards were fed ad libitum and provided with a constant supply of water. We did not record potential differences in food consumption between treatments; however, recent unpublished data (Brusch et al., pers. comm.) suggest that warmer conditions over night increase food consumption rates in adult female common lizards. This suggests that yearling common lizards were probably eating more in the warm nocturnal treatment group because food was not a limiting factor. All else being equal, the potential food limitation occurring in a natural population should therefore exacerbate the ‘trade-off’ between structural and reserve growth effect mediated by T_N observed in our experiment. In other words, the trade-off should be stronger when food availability becomes a limiting factor and lizards cannot increase their food intake as they could in the laboratory conditions. Ultimately, this mechanism could alter food webs, as already observed in different studies (Speights & Barton, 2019). The potential for warmer temperatures to alter patterns of energy allocation challenges assumptions about the optimal energy budget for common lizards prior to sexual maturation, as modelled in González-Suárez et al. (2011). Their model compared a net allocation scenario and a net production one. In the net allocation model, yearlings first assigned a fixed proportion of energy to reproduction, the remainder being paid to maintenance and growth, respectively. Alternatively, in the net production model, maintenance is paid first, and the remainder is assigned to growth and reproduction, proportionally. In contrast, our results suggest fluctuating allocation rules towards growth, reserves and future reproduction that vary with environmental temperatures, hence a potential a change in the assimilation and allocation rules as well. Further work, also including females, would help to disentangle the effect of T_N on male versus female’ reproduction allocation strategies.

Assessing which pace of life strategy (faster growth with a lower condition versus slower growth with a higher condition) yields a higher life-time fitness advantage is difficult, as differential growth early in life may have important long-term effects (Metcalfe & Monaghan, 2001). There are multiple fitness advantages for early growth and warmer temperatures on current and future reproduction (Horváthová et al., 2013; Sears, 2005). For example, experimental acceleration of growth in juvenile common lizards has been demonstrated to favour rapid sexual maturation and earlier reproduction (Bestion et al., 2015). Furthermore, reproduction is known to be size-dependent in reptiles, with larger females often producing larger clutches or litters (Le Galliard et al., 2004). However, rapid growth early in life may compromise the accumulation of energy reserves (this study), and lead to lower survival of individuals with reduced energy reserves, as well as the ability invest into reproduction later in their life (Bestion et al., 2015; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017).

4.2 | Impacts of a faster growth on oxidative balance and parasitic susceptibility

One option to assess whether effects of accelerated growth are deleterious is to measure individual stress levels, by quantifying their oxidative balance (Costantini, 2014; Salin et al., 2015). Contrary to our prediction, we did not find any changes in oxidative status attributable to the thermal treatment. In fact, oxidative damages showed a slight decrease in both treatments ($\mathbf{\Delta}_{\mathbf{ROM}} = -0.2 \pm 2.2$) while the antioxidant capacity of the plasma increased in both treatments ($\mathbf{\Delta}_{\mathbf{OXY}} = 10.3 \pm 40.7$). One potential explanation is that despite the difference in T_N, general laboratory conditions were benign with respect to the risks of oxidative stress. Common lizard populations characterized by higher T_N exhibit lower levels of oxidative stress in the field, which suggests that warmer environmental conditions may not necessarily challenge oxidative balance regulation in this species (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). Similar reduction of oxidative damage has been observed in the corn snake (*Pantherophis guttatus*) after a simulated heat wave (Stahlschmidt et al., 2017). Yet, faster growth rate is correlated with increased oxidative stress across many species (Metcalfe & Monaghan, 2001; Monaghan et al., 2009; Salin et al., 2015). Here, we found no correlation between individual growth rate and $\mathbf{\Delta}_{\mathbf{ROM}}$ ($r = 0.003$; $t_{71} = 0.03$, $p = 0.97$) or $\mathbf{\Delta}_{\mathbf{OXY}}$ ($r = 0.07$; $t_{71} = 0.62$, $p = 0.53$). A full assessment of whether or not warmer nights induce an increase in cellular stress might require further analyses including multiple markers of oxidative stress (Stier et al., 2017). Moreover, frequent sampling for the signature of oxidative stress and over a longer duration would enhance the ability to characterize the dynamics of oxidative damage over time (Dupoué, Angelier, et al., 2020).

Our results also showed that increased T_N can have immediate effects on susceptibility to parasite infestation. We did not detect any statistical difference between treatments regarding blood parasites. However, we found clear evidence that individuals from T_{Nw} were more vulnerable to an ectoparasitic infestation. The provenance of mites re-infesting individuals is questionable. Even if we hand removed and applied an antiparasitic treatment, it is possible that some mites survived and re-infected individuals during captivity. It is also possible that mites survived the sterilisation of the soil used as substrate in each terrarium. In our study, we did not detect an influence of mites on SVL or body mass (Appendix S7), but we removed parasites from individuals before deleterious effects could become obvious. In wild populations, hematophagous mites are known to influence common lizards' mass and/or survival (Sorci & Clobert, 1995) and could represent a serious burden for infected yearlings. It is difficult, however, to determine whether the increased parasitic infestation in the warmer nocturnal treatment is the result of a weakened immune response, a consequence of an extended period of activity of lizards, or the by-product of a favourable environment for ectoparasite reproduction.

4.3 | Behavioural and colour adjustment to warmer nocturnal temperatures

Behavioural adjustments during the daytime may alleviate physiological costs of higher T_N. For example, lizards acclimated to warmer T_N may adopt diurnal thermoregulation strategies to reduce body temperatures and minimize levels of activity. Yet, contrary to our expectations, diurnal T_{pref} was not altered by the treatment. Instead, average T_{pref} was higher at the end of the experiment in both treatments ($\mathbf{\Delta}_{\mathbf{bT}} = 2.09°\text{C} \pm 2.45$), suggesting acclimation of thermal preference by lizards to general laboratory conditions (Pintor et al., 2016) or to seasonality (post-hibernation versus mid-summer conditions) (Díaz et al., 2006). It is also possible that the differences in elevation between capture sites and laboratory facilities (585 m a.s.l.) contributed to this pattern (mean elevation difference = 814 ± 146 m) (Megía-Palma et al., 2020). The absence of differences between treatments is consistent with previous comparative studies that demonstrated a relative insensitivity of T_{pref} to variation in thermal conditions in the common lizard (Gvoždík, 2002). Yet, we cannot disregard that other behavioural strategies may be used by lizards during the activity period to buffer effects of warmer T_N. For example, lizards may change their basking effort, shift the timing of their daily activity (Rozen-Rechels et al., 2020) or alter the exploitation of different micro-habitats (Gvoždík, 2002) to compensate for physiological effects of changes in T_N.

Behaviour is the main strategy that ectotherms use for short-term regulation of body temperature, and the common lizard is often described as an active thermoregulator (Rozen-Rechels et al., 2020). Yet, other mechanisms may also mitigate the effects of extreme thermal environments such as the production of heat shock proteins, changes in critical thermal limits and basal metabolic rate or the modulation of body shape and colouration (Gilbert & Miles, 2019; Rutschmann et al., 2020; Seebacher & Franklin, 2005). In our study system, lizards experienced changes in dorsal colour depending on the treatment: yearlings shifted towards lower luminance and darker colours in T_{Nc} in all populations with the exception of Bouvier. In contrast, lizards in T_{Nw} exhibited a higher luminance and lighter colours on their dorsum. According to the thermal melanism hypothesis, lighter-coloured individuals should be favoured in environments where the risk of overheating risks is high since they will not absorb solar radiation and heat as fast as darker individuals (Clusella Trullas et al., 2007; Geen & Johnston, 2014). Heat gain due to radiation is close to null during over-night, but warmer T_N could increase sensitivity to diurnal heat stress (Speights et al., 2017) and be a criterion of developmental plasticity affecting skin darkness. That is, lizards from the warmer treatment may adjust colouration towards a lighter dorsal colouration to diminish skin solar absorbance and mitigate the consequences of heat stress in a warmer environment. In any case, our results illustrate that T_N may represent a relevant driver triggering a plastic adjustment of body colouration.

5 | CONCLUSIONS

Recent evidence suggests that warmer nocturnal temperatures can advance the timing of reproduction and increase the quality of the offspring as demonstrated in the long-lived, viviparous Otago gecko *Woodworthia* sp. (Moore et al., 2020). Other studies have shown an augmentation of T_N of 6°C increased the probability of a second clutch in the common side-blotched lizard *Uta stansburiana* (Clarke & Zani, 2012). These studies corroborate our results and support the current paradigm: ectotherms can rapidly acclimate to warmer T_N and use them to improve energy intake and expand their thermal niche over part of the night or in different seasons (Lara Resendiz, 2019; Ziska, 2014). Yet, our work, as well as previous findings (Speights et al., 2017; Zhao et al., 2014), also suggests that one cannot ignore the potential costs of nocturnal warming, especially when warming is intense (our results) and when diurnal temperatures are already high (Monasterio et al., 2013; Zhao et al., 2014). Long-term experimental studies, monitoring changes in an individuals' life-history traits are necessary to resolve under which conditions warmer nights are detrimental to ectotherms. The extent to which T_N will affect common lizard populations and other ectotherms species therefore remains an open question.

Our results also show minor, but interesting differences in the responses of lizards among different populations. Indeed, lizards from Bouvier were the only individuals to change towards darker colours and exhibit a lower rate of blood parasite infections in the warmer treatment. Both were unexpected results. Despite an initial choice of populations based on their similar climate conditions, a closer examination of the weather data revealed that extreme overnight temperatures during the summer are significantly higher in Bouvier and Barnassac than in Col du Pendu and Tour du Viala. Whether the high temperatures at night in Bouvier, or other environmental differences not quantified such as the risk of predation or grazing, have selected for lizards with contrasted responses to extreme T_N is difficult to assess without complementary analyses. We encourage future studies to incorporate the effects of nocturnal temperatures in experimental designs (Gaston, 2019; Speights et al., 2018), but we also stress the importance of using multi-population comparison approaches to obtain a comprehensive perspective on the responses of species to climate change (Barton, 2017).

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AUTHORS' CONTRIBUTIONS

A.R., A.D., S.M. and J.-F.L.G. designed the study; A.R., C.L., M.B., D.B.M. and J.C. conducted the field work; A.R. and C.L. performed the experiments; D.R.-R. and P.B. designed the thermal preference experiment; M.R. and R.M.-P., respectively, analysed the plasma samples for oxidative status and blood parasites prevalence; A.R. analysed all data with the help of D.R.-R. (thermal data) and A.B. (colouration data) and drafted the manuscript with A.D. All authors interpreted the results, provided editorial advices and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The dataset is available online on the Dryad database https://doi.org/10.5061/dryad.79cnp5hvm (Rutschmann et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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