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RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

How melanism affects the sensitivity of lizards to climate change

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Abstract

1. The impact of climate change on global biodiversity is firmly established, but the differential effect of climate change on populations within the same species is rarely considered. In ectotherms, melanism (i.e. darker integument due to heavier deposition of melanin) can significantly influence thermoregulation, as dark individuals generally heat more and faster than bright ones. Therefore, darker ectotherms might be more susceptible to climate change.

2. Using the colour-polyphenic lizard *Karusasaurus polyzonus* (Squamata: Cordylidae), we hypothesized that, under future climatic projections, darker populations will decrease their activity time more than brighter ones due to their greater potential for overheating.

3. To test this, we mechanistically modelled the body temperatures of 56 individuals from five differently coloured populations under present and future climate conditions. We first measured morphological traits and integumentary reflectance from live animals, and then collected physiological data from the literature. We used a biophysical model to compute activity time of individual lizards as proxy for their viability, and thereby predict how different populations will cope with future climate conditions.

4. Contrary to our expectations, we found that all populations will increase activity time and, specifically, that darker populations will become relatively more active than bright ones. This suggests that darker populations of *K. polyzonus* may benefit from global warming.

Sebastian Mader and Jonathan Goldenberg contributed equally to this work.

5. Our study emphasizes the importance of accounting for variation between populations when studying responses to climate change, as we must consider these variations to develop efficient and specific conservation strategies.

1 | INTRODUCTION

Global biodiversity is under threat as ecosystems are compromised and extinction risks increase due to anthropogenic climate change (Lawler et al., 2009; Maclean & Wilson, 2011; Urban, 2015; Warren et al., 2011). This risk of extinction is directly connected to species' range contractions and thereby local population extinctions (extirpations; Ceballos et al., 2017; Thomas et al., 2004), as species are unable to track shifting suitable climates and/or are unable to adapt to the changes occurring in their current range. Despite the urgent need to understand the underlying mechanisms, the proximate causes of climate change-induced extirpations are surprisingly unclear (Cahill et al., 2013; Spence & Tingley, 2020). Where identified, they have been mostly revealed to be species-specific interactions of abiotic and biotic factors (Cahill et al., 2013). Without disentangling these factors and examining their specific effects, it is not possible to fully understand how climate change will affect species' viability and to detect populations at risk.

Ectotherms might be particularly vulnerable to climatic changes because they depend on the surrounding environment for thermoregulation (Buckley et al., 2012). Indeed, basic physiological functions such as locomotion, growth and reproduction are directly linked to body temperature (Huey & Kingsolver, 1989; Huey & Stevenson, 1979). Among a multitude of biophysical attributes influencing thermoregulation (e.g. Olalla-Tárraga & Rodríguez, 2007; Seebacher & Franklin, 2005; Stevenson, 1985), reflectance of solar radiation regulated by skin darkness plays a major role. This is referred to as the thermal melanism hypothesis (TMH; for a review, see Clusella-Trullas, van Wyk, et al., 2007). The TMH states that dark individuals are, compared to bright individuals, advantaged in cold environments because of faster heating rates and higher steady-state body temperatures (Gates, 1980; Lusis, 1961; Norris, 1967; Watt, 1968). By contrast, brighter individuals are likely advantaged under warm conditions, where heat stress is prevalent over cold stress, as they reflect more radiation away from the body.

Clusella-Trullas et al. (2009) found that melanism has a small but positive effect on both heating rate and steady-state body temperature of lizards. Although other studies suggested that melanism only plays a minor role in thermoregulation relative to, for example, body mass or behaviour (Crisp et al., 1979; Stevenson, 1985), melanin-rich integuments might compensate for slower heating rates in larger organisms (Azócar et al., 2015). A field study detected no difference in body temperature between melanistic and non-melanistic individuals, but found that melanistic ones occupied more shaded, and therefore cooler, microhabitats (Muri et al., 2015). Hence, melanism in colder environments might allow individuals to exploit other habitats where, for example, competition or predation is lower (Muri et al., 2015). Furthermore, in multiple lizard species, melanism is correlated with lower solar radiation and, to some extent, lower air temperature (Azócar et al., 2015; Clusella-Trullas et al., 2008; Janse van Rensburg et al., 2009). Overall, this raises the question of whether climate change, specifically climate warming, will differently affect dark and light individuals, at both the population and species level (Moore et al., 2021).

Roulin (2014) suggested that melanistic organisms might be favoured under climate change due to the protective properties of melanin against UV radiation (Bornman et al., 2019; Brenner & Hearing, 2008). By contrast, the increased heating caused by melanism might be disadvantageous (Clusella-Trullas & Nielsen, 2020). In insects, many butterfly and dragonfly populations have become brighter (higher reflectance), potentially due to warming temperatures (e.g. MacLean et al., 2019; Zeuss et al., 2014). Similarly, the frequency of melanistic individuals declined in two beetle species (Brakefield & De Jong, 2011; Zvereva et al., 2019). However, to the best of our knowledge, no previous work has explicitly tested potential interactive effects between melanism and future climate projections on squamates.

Here, we examine the effect of climate change on activity patterns of differently coloured populations of the Karoo girdled lizard *Karusasaurus polyzonus* (Smith, 1838) (Figure 1), a species widely distributed across South Africa encompassing different environmental regimes, and displays no sexual dichromatism and limited sexual size dimorphism (Bates et al., 2014). This allows us to specifically study the interaction of melanization with changing climate. We hypothesized that activity time would decline for all populations under future climatic projections due to increasing maladaptation to the predicted warmer climatic conditions (Angilletta, 2009). Furthermore, due to their current southernmost distribution in South Africa, and thus limited migration opportunities to colder environments, we predicted that darker individuals will be more severely impacted than their non-melanistic counterparts due to the likely stronger heating effect of darker integuments.
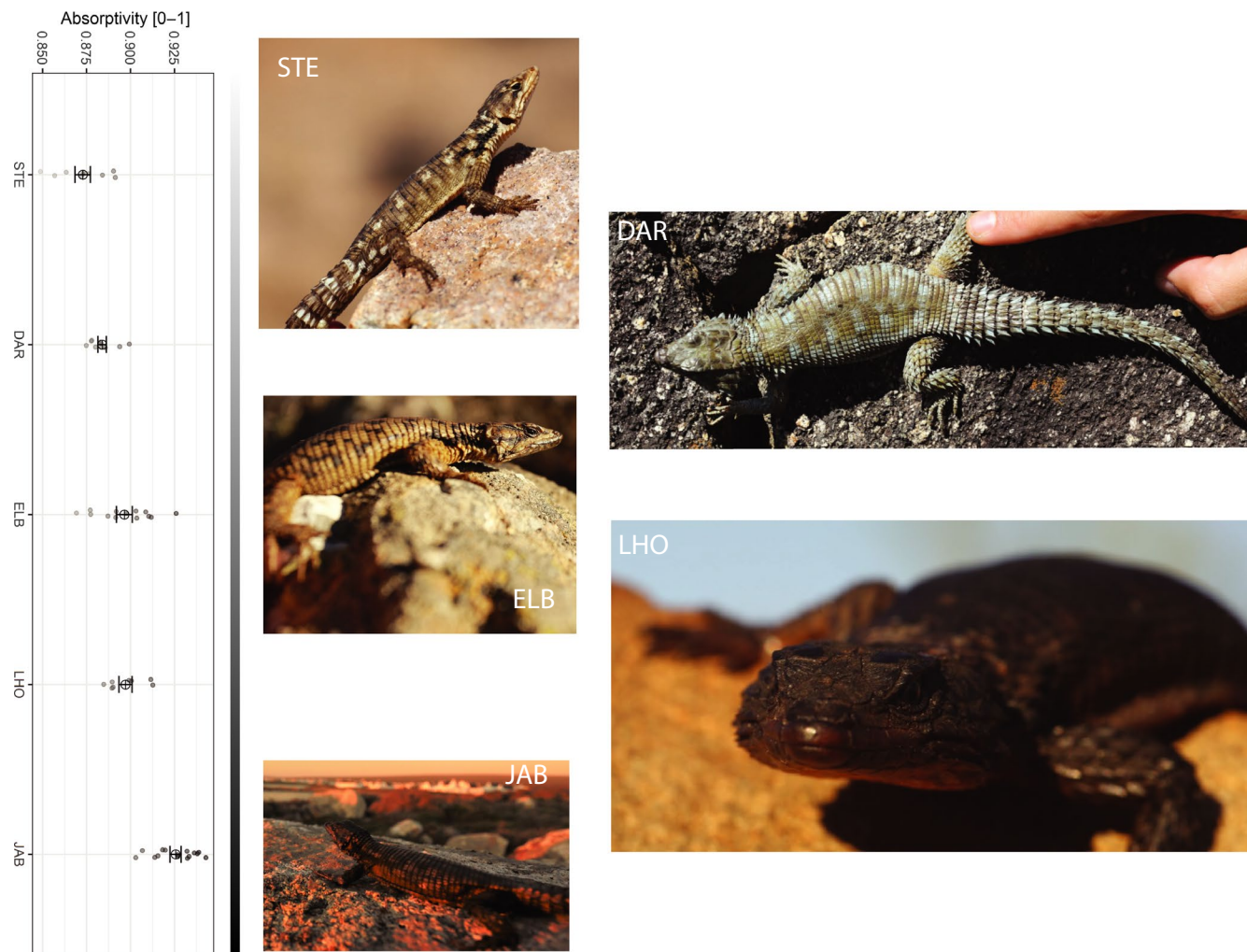
FIGURE 1 Colour polyphenism in the Karoo Girdled lizard *Karusasaurus polyzonus* across the five sampled sites showing different degrees of integumentary melanin content. Absorptivity (1 – reflectance) values were derived from reflectance measurements (0: bright and 1: dark). Acronyms reflect location sites. For a visualization of site locations, see Figure S1. Photograph credits Federico Massetti and Jonathan Goldenberg

2 | MATERIALS AND METHODS

2.1 | Species collection and sampling

We analysed 56 healthy adult individuals [11.2 (mean *n* per population) ± 2.4 σ: standard deviation; sex ratio 2.11:1 F:M ± 0.56 σ] of *Karusasaurus polyzonus* from five sites in South Africa (Figure S1) during December 2018–April 2019. Despite some geographical clustering, these sites display different lizard colour morphs (Figure 1) and climate regimes (Figure 3). We collected lizards with standard handheld noosing techniques, and, to ensure a correct release at site of capture, took GPS coordinates for each lizard. We placed the lizards in breathable cloth bags to transport them from each sampling site to its respective nearby (<20 km) field research station, and then placed each individual in a ventilated, transparent plastic terrarium, where we kept them for a maximum of 3 days until analyses were completed. We provided each individual with shelter and ad libitum water.

In addition, we collected rock samples at the site of capture to measure substrate properties. To avoid uneven water content within samples, we collected them during dry conditions between 12 and 4 p.m., placed them in separate 20-ml plastic tubes and kept them in a dry and cool environment until further analysis.

2.2 | Morphology and reflectance measurements

To account for the effect of body size on thermoregulation (Azócar et al., 2015), we weighed the lizards (Mettler Toledo, New classic MF ML303/01, ±0.001 g; for variation across populations, see Table S1). Then, to measure absorptivity (assuming no transmission: 1-reflectance), we took the reflectance of 14 selected dorsal spots (three on the head, nine on the trunk and two on the tail) of lizards across the 380–2100 nm range using an ASD Fieldspec 3 (range: 350–2500 nm; FieldSpec® 3, ASD Inc) coupled with an ASD Fiber Optic Illuminator connected to a bifurcated probe with 6-around-1

configuration on the distal end, and held at a 90° with a probe holder allowing for a constant (1) distance of the light source (2.2 mm) and (2) skin-surface area per measurement. To account for measurement variability, we repeated the measurements three times at each spot and calculated the mean. However, we removed the tail measurements from our data as the spiky anatomy caused inconsistent values. We also measured the reflectance of the rock samples selecting three random spots on the exposed surface following the protocol described above.

2.3 | Climate data

For the current climate conditions, we used monthly averaged macroclimate data from the global climate database published by New et al. (1999, 2002). It is averaged over the time period of 1961–1990. For projected future monthly climate conditions, we used the database of the Climate Change Knowledge Portal (CCKP: World Bank Group (2015)) based on CMIP5 simulations (Taylor et al., 2012). We included the output of all the 16 different climate models from the CCKP for precipitation, and minimum and maximum temperatures. These models displayed diverse patterns that could individually lead to variations in results (Figure S2). However, a multi-model ensemble of randomly selected models and equal weights yield the best model performances by reducing random errors (Pierce et al., 2009). For this reason, we took the average of the 16 models. We chose two time periods over which the data were averaged to analyse the effect of climate change: 2040 to 2059 and 2080 to 2099. Moreover, we picked the Representative Concentration Pathway (RCP) 8.5 (Allen et al., 2014; Taylor et al., 2012) as greenhouse gas concentration scenario, which assumes no mitigation of climate change, because we aimed to analyse the effect of climate change rather than comparing the outcome of different mitigation scenarios. Moreover, as few effective measures have yet been taken to lower greenhouse gas emissions, the RCP 8.5 scenario is more likely to occur (Andrew, 2008; Helm, 2010; Spash, 2016). Finally, it could be argued that the climate database of New et al. (1999, 2002) may be outdated. However, the future climate predictions provided in the CCKP are based on that database, so we used it for comparative and methodological consistency.

2.4 | Niche model

We used the R (v. 4.0.3; R Core Team (2020)) implementation of the mechanistic biophysical niche model Niche Mapper ('NicheMapR'; Kearney, 2016) to compare the activity pattern variation of individuals within and among the sampled populations over time. We considered activity time as proxy of viability because activity time can have a strong impact on the ecology of organisms (Porter et al., 2000, 2002). Following Kearney and Porter (2020), we defined activity time as the sum of hours a lizard is active between Tf_{min} (minimum foraging body temperature) and Tf_{max} (maximum foraging

body temperature) throughout 12 days per year (one average day per month), and each month represents the average climate output over the examined time period (i.e. 1961–1990, 2040–2059 and 2080–2099). With the mechanistic biophysical niche model, we constructed the fundamental niche of lizards through thermodynamic constraints on their energy and mass budgets. This procedure consists of two major parts. The first part models the microclimate over 24-hr cycles at the height (from the ground) of the organism of interest (Kearney & Porter, 2017). This is done based on macroclimate data from weather stations and information on the terrain such as elevation, slope (i.e. inclination of ground), aspect (i.e. cardinal direction of inclination), soil type and shading opportunities (Table S2). The second part models the biophysical performance of the organism of interest within that microclimate (Kearney & Porter, 2020). By including morphological, physiological and behavioural information, it captures the heat and water exchanges of the organism with its environment (Figure 2) to compute the core body temperature.

'NicheMapR' (Kearney, 2016) uses by default the climate database of New et al. (1999, 2002). To simultaneously analyse different climate databases, we developed an R package ('LizardsAndNiches') provided in the supplied supplementary data, which is built upon 'NicheMapR'.

2.4.1 | Microclimate model

We applied the microclimate model to the average day cycle of each month over 1 year at each of our five locations. The input parameters were the location-specific macroclimate and the terrain parameters elevation, slope and aspect as well as reflectance and specific heat capacity of the substrate (Table S2). To automatize acquisition of elevation, slope and aspect of locations, we made use of 'elevatr' (Hollister & Shah, 2018) within the *micro_ncep* function. The resulting values were then entered into the *micro_global* function to obtain the microclimate of each lizard. We could not use *micro_ncep* to model the microclimate of individuals, because *micro_ncep* accepts 6-and-hourly weather data, while *micro_global* provides the option for hourly and mean-monthly weather data. Future climate data are available monthly, so for comparative and standardization purposes in this study we used *micro_global*. As *K. polyzonus* is a rock-dwelling lizard, the soil type was always defined as rock. To obtain the specific heat capacity of the rock samples at different sites, we first collected a representative rock sample from each location. Once in the laboratory, we employed a differential scanning calorimetry (DSC) using a DSC1/700 from Mettler Toledo (Switzerland). We then powdered and compacted 20–45 mg from each sample onto the bottom of a 40-μl aluminium pan to enhance the reading quality, and recorded the released energy over the range of 0–40°C with a heating rate of 0.5 K/min. Measures of specific heat capacity were obtained by performing a TOPEM® evaluation—an analytical technique which allows to measure specific heat capacity values by overlaying the isothermal with a time series of random temperature pulses of different duration—using the STARe software. Furthermore, we kept
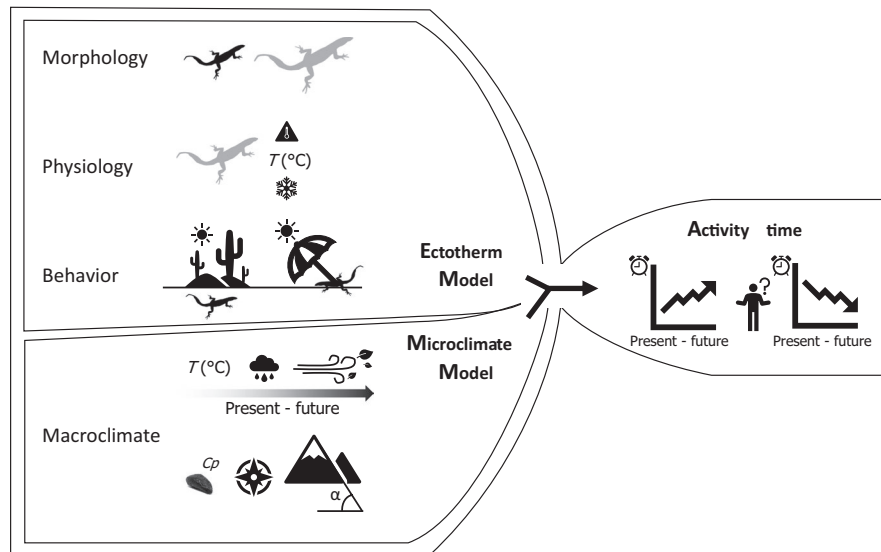
FIGURE 2 Schematic diagram illustrating the variables collected to run the mechanistic biophysical niche model. For the ectotherm model, at individual level [56 adults: 11.2 (mean *n* per population) ± 2.4 σ], we acquired skin absorptivity and body size data (morphology). At species level, we compiled physiological information (thermal preferences) from the literature (Table S3) and behavioural adaptations (burrow depth, burrow type, min. and max. shade availability) from personal observations in the field (described in Table S2). To obtain the microclimate data of each individual, we collected macroclimate data over three time periods: 1960–1991 (New et al., 1999, 2002), 2040–2059 (World Bank Group, 2015) and 2080–2099 (World Bank Group (2015)). For each of those, we obtained monthly averages for: maximum and minimum experienced (1960–1991) and forecasted (2040–2059 and 2080–2099) temperatures (T°C at 1.2 m height), and precipitation (mm) patterns. We kept the wind speed (m/s) from New et al. (1999, 2002) as a constant. Furthermore, we measured the substrate specific heat capacity (c_p) of a representative rock from each location (rock formations were all similar within the sites) and derived terrain data (elevation, slope and aspect) for each location through the *micro_ncep* function. Finally, we ran the two models (ectotherm and microclimate) in 'LizardsAndNiches', built upon 'NicheMapR', to obtain the predicted activity time of individuals. All data and R scripts are available at the provided repository. Diagram by Karen Bisschop and Jonathan Goldenberg

the shading parameters constant with 0% as minimum shade and 50% as maximum shade. We did not observe high vegetation cover at the sampling sites and thus assumed the modelled lizards would seek shelter in rock crevices, where they are usually found (Bates et al., 2014). We simulated rock crevices by applying a rock substrate to the lizards' burrow and assumed lizards would be at the temperature of the rock at a given depth. Burrows represent the next step of shelter after seeking shade (while maintaining activity) to prevent thermal stress (Kearney & Porter, 2020). We set the local height at which the microclimate was computed to 1 cm above ground based on lizard dimensions.

2.4.2 | Biophysical model

Next, we used the biophysical model on each individual's parameter set to include the variability at each location. The input parameters varying between individuals were absorptivity [1 – reflectance; ranging from 0 (all radiation is reflected) to 1 (all radiation is absorbed)] and body weight. The latter accounts for variation in thermal inertia between individuals, as body mass affects heating and cooling rates (Azócar et al., 2016). The physiological temperature thresholds were kept constant over all populations (Table S3). These are the critical minimum (CT_{min}) and maximum (CT_{max}) body temperature between which the lizard can survive, the minimum (Tf_{min}) and maximum

(Tf_{max}) foraging body temperature between which the lizard is considered active, the preferred body temperature (T_{pref}) and the body temperature at which the lizard moves out of its rock crevice and starts to actively regulate its body temperature (T_{bask}). We retrieved these parameters from the literature (Table S3). Specifically, the values of CT_{min} and CT_{max} were the means of critical limits measured for the cordylid family (Clusella-Trullas & Chown, 2014). For Tf_{min}, Tf_{max} and T_{pref}, we retrieved the values from Clusella-Trullas, Terblanche, et al. (2007), where T_{pref} reflects the mean of T_{pref}s, Tf_{min} the average of absolute minimum T_{pref}s and Tf_{max} the average of absolute maximum T_{pref}s. T_{bask} was defined as the minimum air temperature at which a *K. polyzonus* specimen was sighted basking (Broeckhoven & Mouton, 2015). Additionally, the model requires information on the type of retreat the lizard seeks to find shelter when the body temperature is close to critical temperature limits. We specified that shelter ('burrow' in 'NicheMapR') was at a depth of 1 m and either in the direct sunlight (when the body temperature is below CT_{min}) or in the shade (when the body temperature is above CT_{min}) defined as maximum shade.

2.5 | Activity pattern at locations

'NicheMapR' is a deterministic model, therefore there is no variance (or confidence interval) around the outcome (i.e. activity time).

Analysing the data via statistical analyses would be redundant as any significant result in the output would reflect differences in the input parameters (e.g. integument absorptivity, body size). Nevertheless, to facilitate the reading and for graphical interpretation, we compared the impact of climate change on the activity pattern of individuals between locations, and we built a GLM with 'glmmTMB' (Brooks et al., 2017) setting activity time of individuals as dependent (outcome) variable and locations, time periods and their interaction as independent (fixed) effects. We selected Gaussian (AIC: 671.6) as family distribution because it performed better than Poisson (AIC: 1050.7) and Tweedie distributions did not converge, and we adjusted for multiple comparisons using the Tukey method.

2.6 | The effect of absorptivity—Sensitivity analyses

To assess how the output (i.e. activity time) of the deterministic model may vary given a different set of the key input morphological parameters (i.e. integument reflectance and body mass), we ran the model 100 times with different input parameters via iterative Latin Hypercube Sampling (McKay et al., 1979) in 'LHS' (Carnell, 2020), and allowed the parameters to vary within their measured ranges—that is min-max values (Table 1). Besides exploring the influence of changes in the input of a single morphological parameter, we also tested the influence of variation in the parameter entries by simultaneously varying both morphological parameters (Table 1). To identify possible effects of the location, we ran the same model 100 times, but now using the min-max values per location and not the general min-max value from the entire community as used before (Table 1). Furthermore, the output may be affected by specific individual measurements, so we produced an extra set of 100 models running random 80% subsets using '*sample()*' (Table 1). Then, to quantify how the input uncertainty impacts the model output, we produced Partial Rank Correlation Coefficients (PRCC) in 'sensitivity' (Iooss et al., 2021), which measures the linear association between input and output and varies between −1 and +1 (Marino et al., 2008). We considered the two examined morphological parameters (i.e. integument reflectance and body mass) together with

rainfall and microhabitat temperature experienced by individuals at the three time periods (i.e. present, 2040–2059 and 2080–2099). We did not consider other non-morphological input parameters because (a) they were either kept constant across individuals and time (e.g. physiology, wind speed), or (b) they were used to derive the microclimate and were thus autocorrelated with microhabitat temperature (e.g. elevation, slope, aspect, substrate c_p).

Finally, to measure the influence of uncertainty around physiological input values (CTmin, CTmax, T_pref, Tf_max, Tf_min, T_bask) on activity time, we produced a sensitivity analysis where a regular sequence of ±2°C from the reported value (Table S2) with an increment of 0.25°C was performed for the five populations. We selected three time periods, so the analysis yielded a total of 306 models (6 physiological parameters × 17 possible variations for each physiological parameter × 3 time periods).

2.7 | Ethical clearance and permit applications

This project was approved by the Research Ethics Committee of Stellenbosch University (protocol number 0224), and field research was conducted under the permits 0056-AAA007-00226 (Cape Nature - Western Cape), Fauna 0010/2018 (Northern Cape Conservation Act) and JM 5065/2018 (Destea - Free State).

3 | RESULTS

3.1 | Exploratory climate analysis

We visualized the variation of temperature and precipitation across the five selected sites over time and found that, as expected, all locations are cooler in winter (i.e. June–August), but the magnitude of temperature change between warmer and cooler months is site specific (Figure 3). Specifically, LHO and STE are those with a highest difference between summer and winter temperatures, while DAR, ELB and JAB display relatively more uniform temperatures across the year (Figure 3). Interestingly, the latter locations are more southern

TABLE 1 Overview of input parameters and model runs used in the sensitivity analysis. We ran the same model multiple times for the selected input parameters, varying their values between minimum and maximum ranges across and within populations. LHS: Latin Hypercube Sampling; Temperature: microhabitat temperature; Absorptivity = 1 − reflectance; and *N*: number of model runs

		Absorptivity	Rainfall	Temperature	Body weight	*N*
	Predicted	✓	✓	✓	✓	1
	80% subset	✓	✓	✓	✓	100
Across locations	LHS reflectance	✓	✓	✓	✓	100
	LHS body weight	✓	✓	✓	✓	100
	LHS both	✓	✓	✓	✓	100
Within locations	LHS reflectance	✓	✓	✓	✓	100
	LHS body weight	✓	✓	✓	✓	100
	LHS both	✓	✓	✓	✓	100

Note: Each LHS model is repeated for the three time periods (present, 40–59 and 80–99), for a total of 2,103 models.
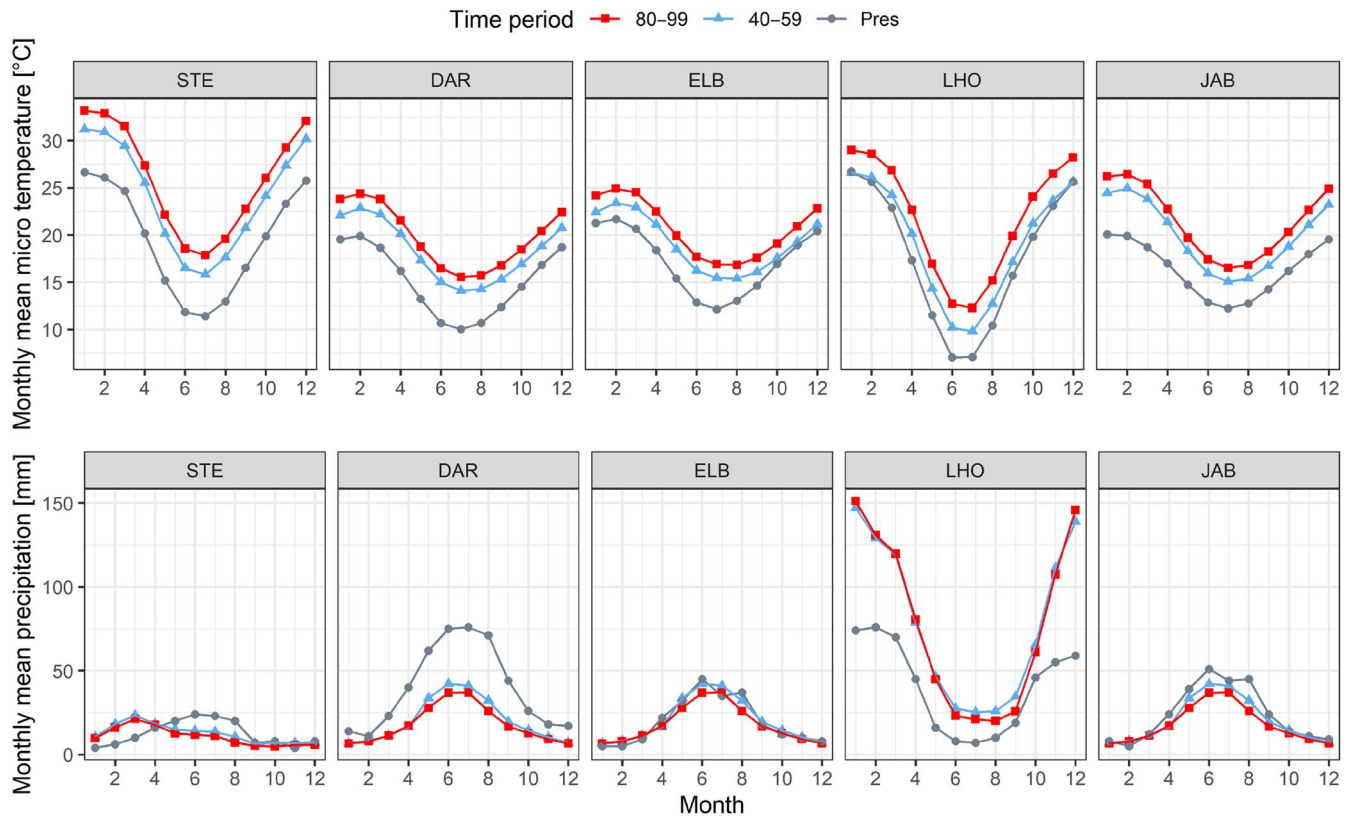
FIGURE 3 Climate regimes at all locations at different time periods. The top row displays microhabitat temperature (°C) for each month of the year and the bottom row shows monthly mean precipitation (mm). Different time periods are distinguished by colour and shape (red: 2080–2099, blue: 2040–2059 and grey: present time)

and closer to the coast than the former (Figure S1). Furthermore, temperature is predicted to increase across all locations, following a trend similar to that of the present time.

Precipitation patterns are predicted to be more variable among locations than the forecasted temperatures (Figure 3). While STE, ELB and JAB show a moderate variation of precipitation over time with STE shifting the precipitation peak from June–July to March, DAR is predicted to experience a dramatic decrease, and LHO an increase.

3.2 | Activity pattern at locations over time

To study the general impact of climate change on single populations, we analysed the variation of activity patterns over time across the five locations. Overall, we found an increase in activity over time for most locations (Figure 4; Tables S4–S7). The only exception was the last time period at Steinkopf (STE), where we observed a substantial decline (Figure 4).

3.3 | The effect of integument absorptivity

To assess the differential effect of climate change across colour morphs, we analysed the influence of skin absorptivity on activity pattern at different time periods.

Overall, darker individuals are predicted to have larger activity windows (Figure 5). Specifically, all time periods, that is 'present', '2040–2059' and '2080–2099', display an overall negative relationship between activity time and integumentary absorptivity. Interestingly, this trend decreases over time, where we observed that the slopes (i.e. the magnitude of activity change between bright and dark individuals) increase over time (Figure 5a). Moreover, in the last time period (i.e. '2080–2099'), brighter individuals are predicted to decrease their activity compared to the previous one (i.e. '2040–2059').

Then, to isolate the effect of activity change over time based on melanization, we visualized the magnitude of activity change relative to the present time. Relatively to the current activity time, dark individuals will more substantially increase their activity pattern than their brighter counterparts (Figure 5b).

3.4 | Sensitivity analyses

To evaluate the effect of integument brightness on the activity time over the three examined periods, we analysed the mechanistic model through sensitivity analysis. Overall, we found that the input parameter microhabitat temperature has the strongest influence on the activity pattern of individuals, regardless of time period (Figure 6; Table S8). Moreover, our results show a linear negative relationship between integument absorptivity and the
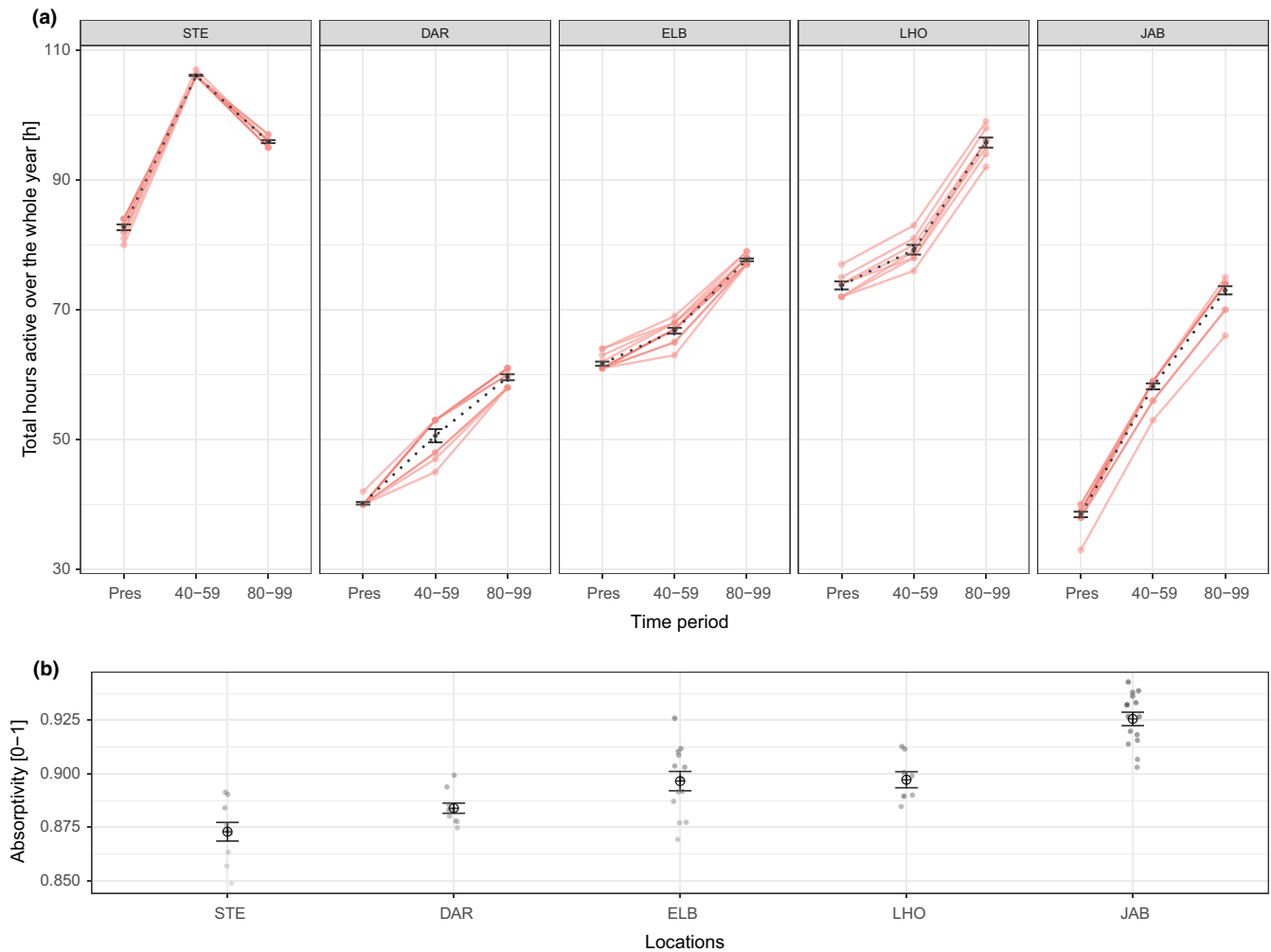
FIGURE 4 Projected activity patterns and skin absorptivity of *K. polyzonus* populations in South Africa. (a) The total activity time, summed over the whole year with one average day per month, at each location over time. Each time period is defined by different climate conditions averaged over the range of that period: 'pres(ent)' is averaged over the time period of 1960–1991; '(20)40-(20)59' and '(20)80-(20)99' over those years. For the future climate conditions, we averaged multiple climate models following the RCP 8.5 gas concentration scenario. Three red points connected by a line are each the results for one individual's parameter set. The black points with standard error connected with a dotted black line are the means at each location and time period. (b) The integument absorptivity of single individuals (points) and integument absorptivity means of populations with standard error (cross-circles with error bar)

predicted model output (Figure 6). Specifically, over time, the relationship decreases, and, coupled with Figure 5, this result likely suggests a stronger effect of dark integuments on the activity time of lizards compared to brighter individuals as time advances (Figure 6; Table S8). Indeed, the steeper increase in activity time of darker individuals lessens the difference between differently melanized individuals.

Moreover, the LHS on integument reflectance for values varying between locations (Figure 6a) shows that if values are randomly assigned the effect of absorptivity on the activity time is widespread, regardless of time period. Interestingly, varying the input of reflectance does not substantially affect the PRCC of body weight (Figure 6a: LHS REFL). Similarly, if body weight is randomly assigned (Figure 6a: LHS W), the influence of absorptivity on activity time is remarkably similar to the predicted model. These results suggest a decoupling between the influence of the two morphological

parameters on the activity time of lizards. The same pattern is observed if both parameters are simultaneously randomly assigned (Figure 6a: LHS REFL+W), where the PRCC for both absorptivity and body weight are similar—with a larger variation for body weight—to the previous models (i.e. LHS REFL and LHS W).

Then, to identify the possible effects of the location, we ran the same models allowing the values of input parameters to vary within the range of populations (Figure 6b). The predicted PRCC of absorptivity are all within the range of the LHS PRCC, and, comparing with Figure 6a, the result indicates a strong location effect on regulating integument reflectance. By contrast, despite the predicted PRCC of body weight are nested as well within the range of the LHS PRCC, the LHS PRCC follows the same pattern observed in the previous results (Figure 6a), suggesting a lack of location effect for body weight.

Next, to analyse how predictable the effect of data input is on the model output and to rule out possible individual entries to
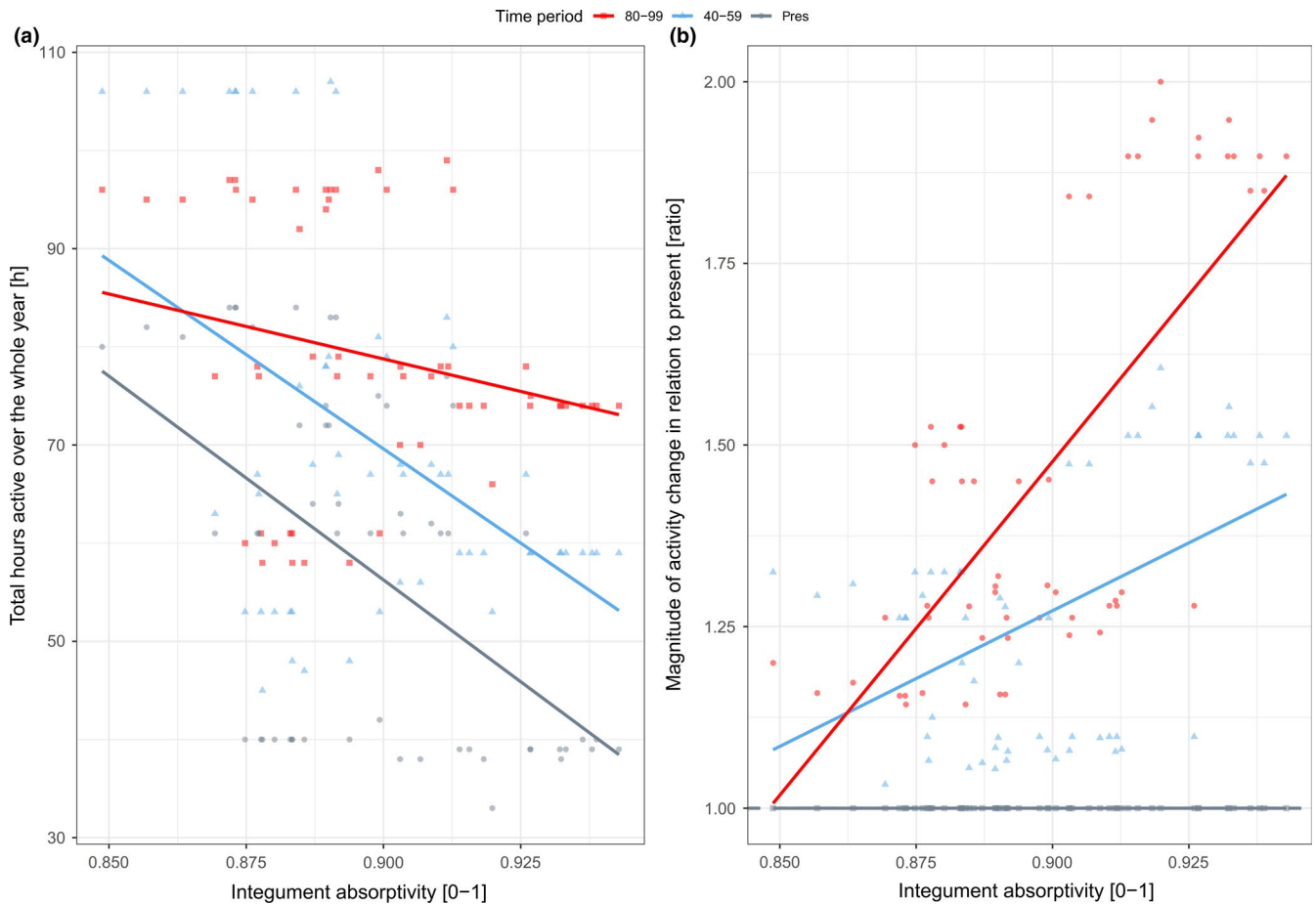
FIGURE 5 (a) The total activity time along individual absorptivity. (b) The magnitude of activity change relative to activity under present climate conditions in correlation with absorptivity. Therefore, present activity (dark-grey line) is set to 1 as that is the reference of this ratio scale. The different time periods are displayed by different colours and shapes: 'present' as dark-grey dots, '40–59' as light-blue triangles and '80–99' as red squares. Note that we defined activity time as the sum of hours a lizard is active between TF_{min} and TF_{max} throughout 12 days per year (one average day per month), and each month represents the average climate output over the examined time period (i.e. 1961–1990, 2040–2059 and 2080–2099). Solid lines represent the mean trend for each time period from the geom_smooth function in 'ggplot2'. These panels are for illustrative purposes only

affect the results, we randomly subsampled 80% of data points in the initial dataset. Our findings show that the predicted PRCC are all well within the subset PRCC ranges (Figure S5), providing us with a robust result that the predicted effect of input parameters on the model output (i.e. activity time) is a reliable estimation.

Finally, to assess the influence of uncertainty around physiological input values (CTmin, CTmax, T_pref, Tf_max, Tf_min, T_bask) on activity time, we produced a sensitivity analysis with regular sequence increments. Our results show that there is a limited deviation in activity time due to variations in thermal traits, with greater variation around Tf_min followed by T_pref, and patterns of activity increase-and-decrease over time are very similar (Figure S6).

4 | DISCUSSION

In this study we mechanistically modelled and compared the activity times of five colour-polyphenic South African Karoo girdled lizard *K.*

polyzonus populations over time. To compare the ability of populations to cope with climate conditions, we defined the activity time of lizards as proxy for viability due to its substantial effect on the ecology of organisms (Porter et al., 2000, 2002). We hypothesized that populations would decline in activity time in response to climate change, and that darker individuals would be more affected due to the likely stronger heating effect of darker integuments (Galván et al., 2018). In contrast to our expectations, we found that all populations were predicted to increase activity time with an increase in micro-ambient temperature. Furthermore, our models propose that over time darker individuals will increase their activity time more substantially than brighter ones. This suggests that dark individuals might actually benefit from the projected temperature increase.

The positive effect of climate warming on activity levels was consistent over almost all populations and time points. The only exception was STE, where we observed a negative trend from 2040–2059 to 2080–2099 (Figure 4). This increase was surprising, considering the extreme average temperature rise expected by the end of this
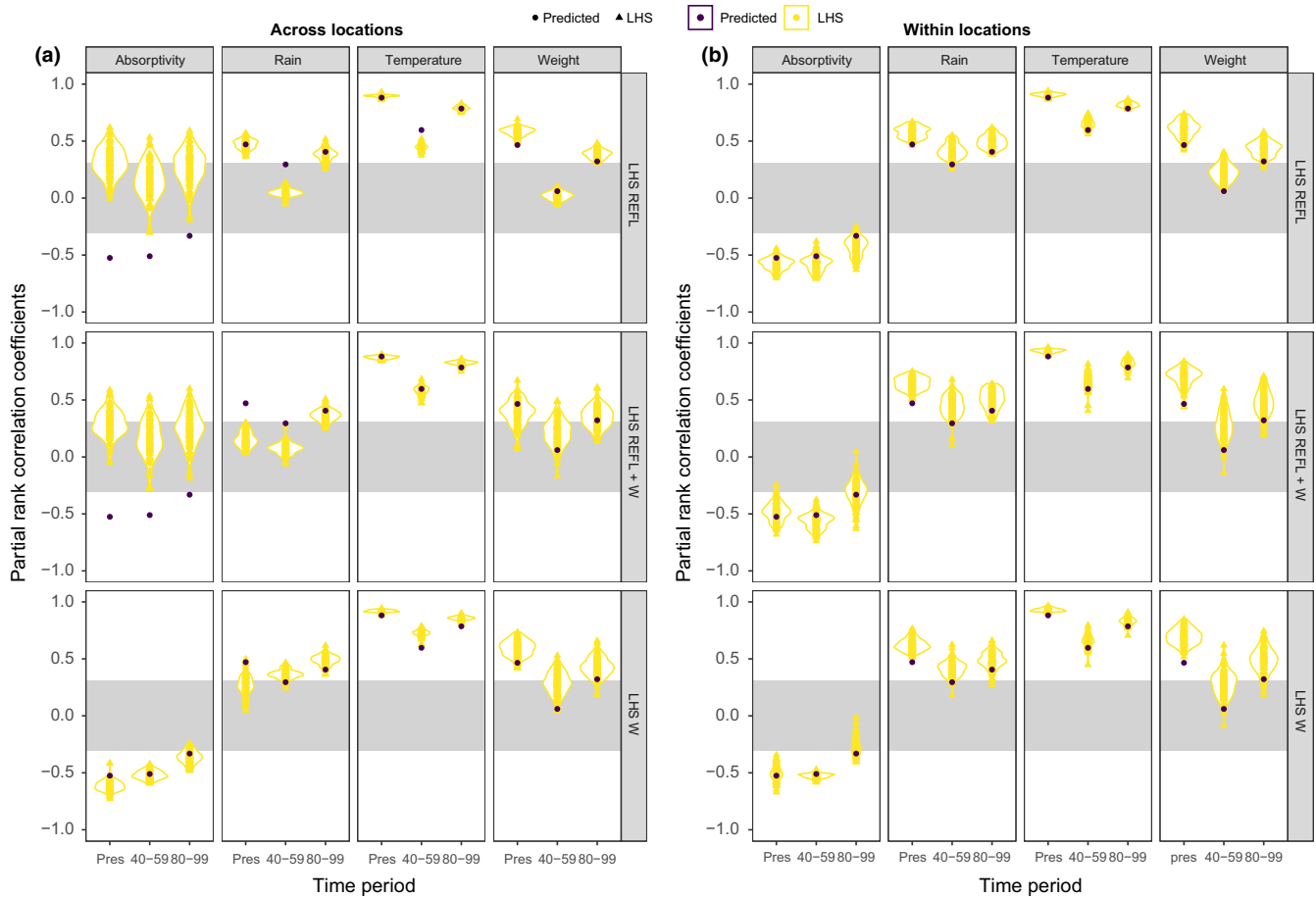
FIGURE 6 Partial Rank Correlation Coefficients (PRCC) testing the linear association between the model output (i.e. activity time) and input parameters (absorptivity, rainfall, microtemperature and body weight) across three time periods (present, 2040–2059 and 2080–2099). Both panels show the PRCC for the models output performing a Latin Hypercube Sensitivity (LHS) on (first row) reflectance ('LHS REFL') and keeping the raw input data for the other parameters, (second row) reflectance and body weight ('LHS REFL +W') and keeping the raw input data for the other parameters and (third row) body weight ('LHS W') while keeping the raw input data for the other parameters. Panel (a) allows the LHS to vary between minimum and maximum ranges of selected parameters found across all populations, while (b) values are allowed to vary between minimum and maximum ranges measured within the respective population. Absorptivity = 1 – reflectance. Shaded area (−0.3 to 0.3) indicates weak or no relationship between input parameter and output (i.e. activity time). Black dots show the PRCC of the predicted model

century (i.e. 4.8°C, RCP 8.5). However, similar to Clusella-Trullas et al. (2009), our results suggest that all populations, regardless of their coloured integuments, have high potential activity times, indicating that their current activities are likely limited by cold temperatures rather than warm ones. Indeed, activity time in 2080–2099 is expected to be on average 22.3 hr (27%) higher than under current conditions, suggesting that the sampled locations exhibit average temperatures colder than the optimum for *K. polyzonus*. Steinkopf is the hottest sampled location (Figure 3) showing the highest increase in temperature by 2080–2099 (i.e. 6.6°C). The observed relative decrease in activity time predicted by the end of the century for this population might be a response to the lizards' body temperature exceeding their maximum foraging temperature during summer (Figure S4). Therefore, we suggest that environmental temperature will become too high for the lizards to benefit further, regardless of the coloured integument. Based on the comparisons of field temperatures with physiological temperature optima and critical

thresholds, lizard species in cold environments might increase their viability in response to climate warming (Cabezas-Cartes et al., 2019; Clusella-Trullas et al., 2009). Furthermore, several large-scaled studies on ectotherms found a decreasing gradient of climate change impact with latitude and concluded that temperate species might be less negatively, if not positively, affected (Deutsch et al., 2008; Huey et al., 2009; Sunday et al., 2011). These results provide another line of evidence that the sampled *K. polyzonus* populations may gain some benefits from climate warming. Moreover, our results support previous findings (e.g. Luke, 1989) that regulation of integument reflectance is highly dependent on location, suggesting adaption to local conditions. However, we found no effects of location on body mass, in contrast with Grant and Dunham (1990) who detected a significant interplay between elevation gradient, temperature and precipitation patterns in determining body mass of *Sceloporus merriami*. The smaller body size of *S. merriami* suggests that body mass has a more substantial influence on thermoregulation in this species than

in the lighter *K. polyzonus*, because the coloured integument might compensate for slower heating rates in larger organisms (Azócar et al., 2015). This likely explains the contrasting results between our study and Grant and Dunham (1990).

The TMH states that under the same environmental conditions, melanistic ectotherms heat up faster and reach a higher steady-state body temperature than their non-melanistic counterparts given the same body properties; thus cooler environments may select for darker integuments (Clusella-Trullas, Terblanche, et al., 2007; Gates, 1980). Engelbrecht et al. (2011) found that melanistic populations of *K. polyzonus* are indeed ecotypes and are associated with low solar radiation in coastal areas through higher cloud cover (Janse van Rensburg et al., 2009). Hence, darker populations of *K. polyzonus* may compensate for lower environmental temperatures, with higher solar absorption (Azócar et al., 2015; Clusella-Trullas et al., 2008).

In butterfly and dragonfly species across Europe, local populations shifted to brighter colours (Zeuss et al., 2014). This suggests that melanism might be disadvantageous during climate change—unless trait plasticity or evolutionary adaptations will counteract this effect (Basson & Clusella-Trullas, 2015). As another line of evidence, melanism in two beetle species in temperate and subarctic areas was strongly selected against during the last decades, arguably as adaptation to warmer climate conditions (Brakefield & De Jong, 2011; Zvereva et al., 2019). In squamates, most studies demonstrate associations between climate and colour variation (e.g. Clusella-Trullas et al., 2008; Reguera et al., 2014), but there is a lack of knowledge of the heritable/genetic basis of colour change and the extent to which it increases fitness in the field (but see Lepetz et al., 2009). Although our findings show an increase rather than a decrease in activity time due to warming temperatures, it is stronger for darker individuals. Behavioural buffer mechanisms to avoid heat stress likely play a minor role here. Indeed, as activity mostly increases, we propose that there is little need to avoid heat stress by retreating and reducing activity (except for STE towards the latest time period). However, as observed for the STE population, we argue that due to higher heating rates, darker individuals will need to retreat earlier than brighter ones and will ultimately be more constrained by even higher temperatures.

We caution that our study does not address important ecological mechanisms such as biotic interactions (Jiménez-Valverde et al., 2008; see also discussion in Buckley et al., 2010), the potential of phenotypic plasticity or evolutionary adaptation to buffer negative impacts of climate change (Fuller et al., 2010) and the possible pleiotropic effect of genes involved in melanin production where dark integuments might be a side-product of selection on other specific traits (Ducrest et al., 2008). Moreover, local adaptation of thermal traits may also influence results (Porcelli et al., 2017). However, we did not try to provide accurate predictions of species' viability; instead, we aimed to underline the complexity of climate change impact not only on species but also on populations with contrasting integumentary colorations. Conservation strategies should account for variation between populations to correctly identify evolutionary

significant units. We have shown that the degree of melanization is one of these important traits.

5 | CONCLUSIONS

We have presented a novel approach to study the effects of thermal melanism on viability of lizards under changing climatic conditions (but see MacLean et al. (2019) who tracked morphological shifts through climate change in a butterfly). In line with the TMH, we found that integumentary absorptivity affects the body temperature and ultimately activity times of ectotherms. Moreover, the activity of darker individuals is predicted to be more affected by increasing temperatures than their brighter counterparts. Our results provide evidence that squamates, next to insects (Brakefield & De Jong, 2011; Zeuss et al., 2014), will be likely affected in the light of their coloured integument. Future research should expand these findings to other ectothermic species and possibly identify the phenotypic plasticity of the coloured integument to understand how species, such as our study system—*Karusasaurus polyzonus*—will cope with fast changing environments. We hope that our study will encourage further visions into the differential effects of climate change and will promote conservation strategies that include such interacting factors into their efforts.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS
J.G. and S.M. wrote the manuscript; F.M., K.B., L.D.A., R.S.E., S.C.-T. and M.D. contributed to the revision of the manuscript and the interpretation of the results; J.G., F.M., L.D.A., S.C.-T. and M.D. conceived the project; S.M., J.G., F.M. and K.B. performed fieldwork and the analyses.

DATA AVAILABILITY STATEMENT
Supporting tables and figures are available at our supporting information. Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.0k6djhb1t (Goldenberg et al., 2021). The R package 'LizardAndNiches' is available at: 'https://github.com/sebmader/LizardsAndNiches'.

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REFERENCES

Allen, S. K., Plattner, G. S., Nauels, A., Xia, Y., & Stocker, T. F. (2014). *Climate Change 2013: The Physical Science Basis. An Overview of the Working Group 1 Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*, 16 (May) (p. 3544). http://adsabs.harvard.edu/abs/2014EGUGA.16.3544A

Andrew, B. (2008). Market failure, government failure and externalities in climate change mitigation: The case for a carbon tax. *Public Administration and Development: The International Journal of Management Research and Practice*, 28(5), 393–401.

Angilletta, M. J. Jr (2009). *"Adaptation to Anthropogenic Climate Change" in thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press.

Azócar, D. M. L., Bonino, M. F., Perotti, M. G., Schulte, J. A., Abdala, C. S., & Cruz, F. B. (2016). Effect of body mass and melanism on heat balance in *Liolaemus* lizards of the goetschi clade. *Journal of Experimental Biology*, 219(8), 1162–1171.

Azócar, D. M. L., Perotti, M. G., Bonino, M. F., Schulte, J. A., Abdala, C. S., & Cruz, F. B. (2015). Variation in body size and degree of melanism within a lizards clade: Is it driven by latitudinal and climatic gradients? *Journal of Zoology*, 295(4), 243–253. https://doi.org/10.1111/jzo.12193

Basson, C. H., & Clusella-Trullas, S. (2015). The behavior-physiology nexus: Behavioral and physiological compensation are relied on to different extents between seasons. *Physiological and Biochemical Zoology*, 88(4), 384–394. https://doi.org/10.1086/682010

Bates, M. F., Branch, W. R., Bauer, A. M., Burger, M., Marais, J., Alexander, G. J., & De Villiers, M. S. (2014). *Atlas and red list of the reptiles of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.

Bornman, J. F., Barnes, P. W., Robson, T. M., Robinson, S. A., Jansen, M. A., Ballaré, C. L., & Flint, S. D. (2019). Linkages between stratospheric ozone, UV radiation and climate change and their implications for terrestrial ecosystems. *Photochemical & Photobiological Sciences*, 18(3), 681–716. https://doi.org/10.1039/C8PP90061B

Brakefield, P. M., & De Jong, P. W. (2011). A steep cline in ladybird melanism has decayed over 25 years: A genetic response to climate change? *Heredity*, 107(6), 574–578. https://doi.org/10.1038/hdy.2011.49

Brenner, M., & Hearing, V. J. (2008). The protective role of melanin against UV damage in human skin. *Photochemistry and Photobiology*, 84(3), 539–549. https://doi.org/10.1111/j.1751-1097.2007.00226.x

Broeckhoven, C., & Mouton, P. L. F. N. (2015). Some like it hot: Camera traps unravel the effects of weather conditions and predator presence on the activity levels of two lizards. *PLoS ONE*, 10(9), e0137428. https://doi.org/10.1371/journal.pone.0137428

Brooks, M. E., Kristensen, K., Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21(9), 873–885. https://doi.org/10.1111/j.1466-8238.2011.00737.x

Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J., & Sears, M. W. (2010). Can mechanism inform species' distribution models? *Ecology Letters*, 13(8), 1041–1054. https://doi.org/10.1111/j.1461-0248.2010.01479.x

Cabezas-Cartes, F., Fernández, J. B., Duran, F., & Kubisch, E. L. (2019). Potential benefits from global warming to the thermal biology and locomotor performance of an endangered Patagonian lizard. *PeerJ*, 7, e7437. https://doi.org/10.7717/peerj.7437

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., & Wiens, J. J. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), 20121890. https://doi.org/10.1098/rspb.2012.1890

Carnell, R. (2020). *lhs: Latin hypercube samples*. R package version 1.1.1. https://CRAN.R-project.org/package=lhs

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Clusella-Trullas, S., & Chown, S. L. (2014). Lizard thermal trait variation at multiple scales: A review. *Journal of Comparative Physiology B*, 184(1), 5–21. https://doi.org/10.1007/s00360-013-0776-x

Clusella-Trullas, S., & Nielsen, M. (2020). The evolution of insect body coloration under changing climates. *Current Opinion in Insect Science*, 41, 25–32. https://doi.org/10.1016/j.cois.2020.05.007

Clusella-Trullas, S., Terblanche, J. S., Blackburn, T. M., & Chown, S. L. (2008). Testing the thermal melanism hypothesis: A macrophysiological approach. *Functional Ecology*, 22(2), 232–238. https://doi.org/10.1111/j.1365-2435.2007.01377.x

Clusella-Trullas, S., Terblanche, J. S., van Wyk, J. H., & Spotila, J. R. (2007). Low repeatability of preferred body temperature in four species of cordylid lizards: Temporal variation and implications for adaptive significance. *Evolutionary Ecology*, 21(1), 63–79. https://doi.org/10.1007/s10682-006-9124-x

Clusella-Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, 32(5), 235–245. https://doi.org/10.1016/j.jtherbio.2007.01.013

Clusella-Trullas, S., Wyk, J. H., & Spotila, J. R. (2009). Thermal benefits of melanism in cordylid lizards: A theoretical and field test. *Ecology*, 90(8), 2297–2312. https://doi.org/10.1890/08-1502.1

Crisp, M., Cook, L. M., & Hereward, F. V. (1979). Color and heat balance in the lizard *Lacerta dugesii*. *Copeia*, 2, 250–257. https://doi.org/10.2307/1443410

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Ducrest, A. L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, 23(9), 502–510. https://doi.org/10.1016/j.tree.2008.06.001

Engelbrecht, H. M., Mouton, P. L. F. N., & Daniels, S. R. (2011). Are melanistic populations of the Karoo girdled lizard, *Karusasaurus polyzonus*, relics or ecotypes? A molecular investigation. *African Zoology*, 46(1), 146–155.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R. S., Mitchell, D., & Maloney, S. K. (2010). Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology*, 83(5), 713–720. https://doi.org/10.1086/652242

Galván, I., Rodríguez-Martínez, S., & Carrascal, L. M. (2018). Dark pigmentation limits thermal niche position in birds. *Functional Ecology*, 32(6), 1531–1540. https://doi.org/10.1111/1365-2435.13094

Gates, D. (1980). *Biophysical ecology*. Springer Verlag.

Goldenberg, J., Mader, S., Massetti, F., Bisschop, K., D'Alba, L., Etienne, R. S., Clusella-Trullas, S., & Shawkey, M. D. (2021). Data from: How melanism affects the sensitivity of lizards to climate change. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.0k6djhb1t

Grant, B. W., & Dunham, A. E. (1990). Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology*, *71*(5), 1765–1776. https://doi.org/10.2307/1937584

Helm, D. (2010). Government failure, rent-seeking, and capture: The design of climate change policy. *Oxford Review of Economic Policy*, *26*(2), 182–196. https://doi.org/10.1093/oxrep/grq006

Hollister, J., & Shah, T. (2018). *elevatr: Access elevation data from various APIs (Version 0.2.0)*. Retrieved from https://CRAN.R-project.org/package=elevatr

Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J., & Garland Jr., T. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1664), 1939–1948.

Huey, R. B., & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution*, *4*(5), 131–135. https://doi.org/10.1016/0169-5347(89)90211-5

Huey, R. B., & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *American Zoologist*, *19*(1), 357–366. https://doi.org/10.1093/icb/19.1.357

Iooss, B., Da Veiga, S., Janon, A., & Pujol, G. (2021). *sensitivity: Global sensitivity analysis of model outputs*. R Package 'sensitivity' version 1.24.0. Retrieved from https://cran.r-project.org/web/packages/sensitivity

Janse van Rensburg, D. A., Mouton, P. L. F., & Van Niekerk, A. (2009). Why cordylid lizards are black at the south-western tip of Africa. *Journal of Zoology*, *278*(4), 333–341. https://doi.org/10.1111/j.1469-7998.2009.00581.x

Jiménez-Valverde, A., Lobo, J. M., & Hortal, J. (2008). Not as good as they seem: The importance of concepts in species distribution modelling. *Diversity and Distributions*, *14*(6), 885–890. https://doi.org/10.1111/j.1472-4642.2008.00496.x

Kearney, M. R. (2016). *NicheMapR: R implementation of niche mapper software for biophysical modelling*. R package version 1 (0).

Kearney, M. R., & Porter, W. P. (2017). NicheMapR–an R package for biophysical modelling: The microclimate model. *Ecography*, *40*(5), 664–674. https://doi.org/10.1111/ecog.02360

Kearney, M. R., & Porter, W. P. (2020). NicheMapR–an R package for biophysical modelling: The ectotherm and Dynamic Energy Budget models. *Ecography*, *43*(1), 85–96. https://doi.org/10.1111/ecog.04680

Lawler, J. J., Shafer, S. L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R., & Bartlein, P. J. (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, *90*(3), 588–597. https://doi.org/10.1890/08-0823.1

Lepetz, V., Massot, M., Chaine, A. S., & Clobert, J. (2009). Climate warming and the evolution of morphotypes in a reptile. *Global Change Biology*, *15*(2), 454–466. https://doi.org/10.1111/j.1365-2486.2008.01761.x

Luke, C. A. (1989). *Color as a phenotypically plastic character in the side-blotched lizard, Uta stansburiana* (Doctoral dissertation). University of California.

Lusis, J. J. (1961). On the biological meaning of colour polymorphism of ladybeetle *Adalia bipunctata* L. *Latvijas Entomologs*, *4*, 3–29.

MacLean, H. J., Nielsen, M. E., Kingsolver, J. G., & Buckley, L. B. (2019). Using museum specimens to track morphological shifts through climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1763), 20170404. https://doi.org/10.1098/rstb.2017.0404

Maclean, I. M., & Wilson, R. J. (2011). Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings*

of the National Academy of Sciences of the United States of America, *108*(30), 12337–12342. https://doi.org/10.1073/pnas.1017352108

Marino, S., Hogue, I. B., Ray, C. J., & Kirschner, D. E. (2008). A methodology for performing global uncertainty and sensitivity analysis in systems biology. *Journal of Theoretical Biology*, *254*(1), 178–196. https://doi.org/10.1016/j.jtbi.2008.04.011

McKay, M. D., Beckman, R. J., & Conover, W. J. (1979). A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics*, *21*(2), 239–245.

Moore, M. P., Hersch, K., Sricharoen, C., Lee, S., Reice, C., Rice, P., Kronick, S., Medley, K. A., & Fowler-Finn, K. D. (2021). Sex-specific ornament evolution is a consistent feature of climatic adaptation across space and time in dragonflies. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(28), e2101458118. https://doi.org/10.1073/pnas.2101458118

Muri, D., Schuerch, J., Trim, N., Golay, J., Baillifard, A., El Taher, A., & Dubey, S. (2015). Thermoregulation and microhabitat choice in the polymorphic asp viper (*Vipera aspis*). *Journal of Thermal Biology*, *53*, 107–112. https://doi.org/10.1016/j.jtherbio.2015.06.009

New, M., Hulme, M., & Jones, P. (1999). Representing twentieth-century space–time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, *12*(3), 829–856.

New, M., Lister, D., Hulme, M., & Makin, I. (2002). A high-resolution data set of surface climate over global land areas. *Climate Research*, *21*(1), 1–25. https://doi.org/10.3354/cr021001

Norris, K. S. (1967). Color Adaptation in desert reptiles and its thermal relationships. In W. W. Milstead (Ed.), *Lizard ecology: A symposium* (pp. 162–229). University of Missouri Press.

Olalla-Tárraga, M. Á., & Rodríguez, M. Á. (2007). Energy and interspecific body size patterns of amphibian faunas in Europe and North America: Anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography*, *16*(5), 606–617. https://doi.org/10.1111/j.1466-8238.2007.00309.x

Pierce, D. W., Barnett, T. P., Santer, B. D., & Gleckler, P. J. (2009). Selecting global climate models for regional climate change studies. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(21), 8441–8446. https://doi.org/10.1073/pnas.0900094106

Porcelli, D., Gaston, K. J., Butlin, R. K., & Snook, R. R. (2017). Local adaptation of reproductive performance during thermal stress. *Journal of Evolutionary Biology*, *30*(2), 422–429. https://doi.org/10.1111/jeb.13018

Porter, W. P., Budaraju, S., Stewart, W. E., & Ramankutty, N. (2000). Calculating climate effects on birds and mammals: Impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist*, *40*(4), 597–630. https://doi.org/10.1093/icb/40.4.597

Porter, W. P., Sabo, J. L., Tracy, C. R., Reichman, O. J., & Ramankutty, N. (2002). Physiology on a landscape scale: Plant-animal interactions. *Integrative and Comparative Biology*, *42*(3), 431–453. https://doi.org/10.1093/icb/42.3.431

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reguera, S., Zamora-Camacho, F. J., & Moreno-Rueda, G. (2014). The lizard *Psammodromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biological Journal of the Linnean Society*, *112*(1), 132–141.

Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change. *Global Change Biology*, *20*(11), 3344–3350. https://doi.org/10.1111/gcb.12594

Seebacher, F., & Franklin, C. E. (2005). Physiological mechanisms of thermoregulation in reptiles: A review. *Journal of Comparative Physiology B*, *175*(8), 533–541. https://doi.org/10.1007/s00360-005-0007-1

Spash, C. L. (2016). This changes nothing: The Paris Agreement to ignore reality. *Globalizations*, *13*(6), 928–933. https://doi.org/10.1080/14747731.2016.1161119

Spence, A. R., & Tingley, M. W. (2020). The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography*, *43*(11), 1571–1590. https://doi.org/10.1111/ecog.05170

Stevenson, R. D. (1985). The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *The American Naturalist*, *126*(3), 362–386. https://doi.org/10.1086/284423

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1713), 1823–1830.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experimental design. *Bulletin of the American Meteorological Society*, *93*, 485–498.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Siqueira, M. F. D., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571–573.

Warren, R., Price, J., Fischlin, A., de la Nava Santos, S., & Midgley, G. (2011). Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise. *Climatic Change*, *106*(2), 141–177. https://doi.org/10.1007/s10584-010-9923-5

Watt, W. B. (1968). Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution*, *22*(3), 437–458.

World Bank Group. (2015). *Climate change knowledge portal*. https://climateknowledgeportal.worldbank.org

Zeuss, D., Brandl, R., Brändle, M., Rahbek, C., & Brunzel, S. (2014). Global warming favours light-coloured insects in Europe. *Nature Communications*, *5*(1), 1–9. https://doi.org/10.1038/ncomms4874

Zvereva, E. L., Hunter, M. D., Zverev, V., Kruglova, O. Y., & Kozlov, M. V. (2019). Climate warming leads to decline in frequencies of melanic individuals in subarctic leaf beetle populations. *Science of the Total Environment*, *673*, 237–244. https://doi.org/10.1016/j.scitotenv.2019.03.458

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