

# Intraspecific diversity alters the relationship between climate change and parasitism in a polymorphic ectotherm

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## Funding information

National Natural Science Foundation of China, Grant/Award Number: 32001124; Ohio University International Travel Grants; Laboratoire d'Excellence TULIP, Grant/Award Number: ANR-10-LABX-41; National Science Foundation, Grant/Award Number: DEB1950636 and EF1241848; Agence Nationale de la Recherche, Grant/Award Number: ANR MOBIGEN; Make Our Planet Great Again

## Abstract

Climate-modulated parasitism is driven by a range of factors, yet the spatial and temporal variability of this relationship has received scant attention in wild vertebrate hosts. Moreover, most prior studies overlooked the intraspecific differences across host morphotypes, which impedes a full understanding of the climate-parasitism relationship. In the common lizard (*Zootoca vivipara*), females exhibit three colour morphs: yellow (Y-females), orange (O-females) and mixed (mixture of yellow and orange, M-females). *Zootoca vivipara* is also infested with an ectoparasite (*Ophionyssus* mites). We therefore used this model system to examine the intraspecific response of hosts to parasitism under climate change. We found infestation probability to differ across colour morphs at both spatial (10 sites) and temporal (20 years) scales: M-females had lower parasite infestations than Y- and O-females at lower temperatures, but became more susceptible to parasites as temperature increased. The advantage of M-females at low temperatures was counterbalanced by their higher mortality rates thereafter, which suggests a morph-dependent trade-off between resistance to parasites and host survival. Furthermore, significant interactions between colour morphs and temperature indicate that the relationship between parasite infestations and climate warming was contingent on host morphotypes. Parasite infestations increased with temperature for most morphs, but displayed morph-specific rates. Finally, infested M-females had higher reductions in survival rates than infested Y- or O-females, which implies a potential loss of intraspecific diversity within populations as parasitism and temperatures rise. Overall, we found parasitism increases with warming temperatures, but this relationship is modulated by host morphotypes and an interaction with temperature. We suggest that epidemiological models incorporate intraspecific diversity within species for better understanding the dynamics of wildlife diseases under climate warming.

## KEYWORDS

climate change, colour polymorphism, intraspecific diversity, lizards, morphotype-by-environment interaction, morphotype-dependent trade-off, parasitism, spatio-temporal variation

## 1 | INTRODUCTION

Recent studies have identified climate change as one of the leading drivers for parasitism outbreaks, given that climatic conditions have direct and multiplicative effects on transmission dynamics and life cycles of parasites (Altizer et al., 2013; Caldwell et al., 2021; Claar & Wood, 2020; Rohr & Cohen, 2020; Shocket et al., 2018). Rising temperatures are anticipated to influence the physiology, behaviour, life history and phenology of hosts and parasites, which may exacerbate disease prevalence and severity (Altizer et al., 2013; Harvell et al., 2002). As a consequence, most hosts are predicted to suffer more frequent or severe infections in the near future (Harvell et al., 2002; but see Lafferty, 2009; Stireman et al., 2005). Yet, there remains a lack of consensus about the potential effects of climate change on host–parasite interactions (Morales-Castilla et al., 2021).

The rate of climate change tends to be heterogeneous across regions and can vary over short periods of time (Ebi et al., 2016). Thus, spatial and temporal dynamics in climate will lead to substantial variation in host–parasite interactions. Dissimilar regimes of climate change can operate across space, generating a mosaic of thermal sites across the landscape and exposing hosts and parasites to varying environmental temperatures (Ebi et al., 2016; Ostfeld et al., 2005). In addition, host–parasite interactions also can exhibit temporal variation, because of seasonality or inter-annual variability in climate (Altizer et al., 2006). Neglecting these sources of variation may result in inaccurate estimates of climate impacts on host–parasite interactions. In this context, data collected at both spatial and temporal scales might help to refine our understanding of host–parasite interactions while accounting for the variability of climate change.

Recent reviews also point out that the influence of global change on host–parasite interactions may depend on intraspecific variability in parasite resistance and tolerance of the host (Altizer et al., 2013; Cable et al., 2017; Côte et al., 2018; Tompkins et al., 2011). Intraspecific diversity has been demonstrated to be an essential driver in infection risks (Garrett et al., 2009; Zhu et al., 2000). In addition, individuals within a population may exhibit differences in their capacity to cope with abiotic stressors such as climate warming (Llewelyn et al., 2016). Whether one individual suffers more or less from infection therefore depends not only on its own genotype/phenotype, but also on the prevailing environmental context (Wolinska & King, 2009). Such potential interactive effects between intraspecific variability and environment can have major implications in our understanding of how hosts respond to the threats from parasitism and climate change (Côte et al., 2018). Nonetheless, few studies have incorporated intraspecific diversity of hosts into a conceptual framework for characterizing parasitism dynamics under climate change. Moreover, previous studies on how host intraspecific variability influences host–parasite dynamics focused on genetic diversity (e.g. Ekroth et al., 2019), but little attention has been paid to the phenotypic diversity of wild vertebrate hosts across spatial and temporal scales.

Intraspecific diversity can be characterized as different genotypes and phenotypes within or among populations (Raffard et al., 2019). A classic example is the manifestation of colour polymorphism (the coexistence of multiple colour morphs in the same population) among individuals. Colour morphs are thought to represent alternative phenotypic optima resulting from correlational selection, that is, selection for optimal combinations of traits (Miles et al., 2007; Sinervo & Svensson, 2002) and are often associated with a suite of life-history, behavioural and physiological traits (Ducrest et al., 2008; McKinnon & Pierotti, 2010; Roulin, 2004). Through the variation in direct effects of colours (more or less visible/attractive to parasites) or through indirect coadapted traits (behaviour/physiology), different colour morphs may vary in exposure to or encounter rates with parasites. Infected individuals of different morphs may also vary in immunocompetence, resulting in distinct capacities to cope with parasite infections (Côte et al., 2018). For example, differences in parasite loads and immune responses have been observed among colour morphs in several lizard species (Hacking et al., 2018; Huyghe et al., 2010; Sacchi et al., 2017). It is well established that immunity is costly and trades off with other fitness traits (Smith & French, 2017). Moreover, the cost of immunity can be affected by an individual's colour morph (Gasparini et al., 2009). Thus, by comparing how morph-specific variation in resistance to parasites affects the trade-off against key life-history traits (e.g. reproduction and survival), we may gain a deeper understanding of the role of morphotype diversity in the response of parasitism to climate (Côte et al., 2018).

In viviparous populations of the common lizard (*Zootoca vivipara*), females are characterized by a polymorphism in ventral colouration. The colours vary from pale yellow to bright orange. Past analyses have shown that females can be placed into three discrete categories: yellow, orange and mixed colouration (Vercken & Clobert, 2008; Vercken et al., 2007, 2010; but see Cote et al., 2008). The morphs exhibit alternative reproductive patterns (Vercken et al., 2007), behaviours (Vercken & Clobert, 2008) and dispersal decisions (Vercken et al., 2012), and these traits are influenced by the dynamics of colour morph frequencies in the population (see Table 1 for additional information). Specifically, yellow females are the most aggressive, orange females are non-aggressive and mixed females pursue a putative conditional bully strategy that depends on the social context (the presence of other morphs, Vercken et al., 2010).

Common lizards in our study sites are mainly infested by an ectoparasite, the haematophagous mites in the genus *Ophionyssus*. The infestation probability of this ectoparasite varies with the type of habitat, sex and body condition of common lizards (Wu et al., 2019). Because aggressive behaviours and energy allocated to reproduction diverge among colour morphs, some morphotypes may experience elevated levels of stress and variation in immunocompetence. Previous studies in common lizards showed that sustained levels of stress can make individuals more susceptible to parasite infections (Oppliger et al., 1998), which suggests the potential for heterogeneous patterns of parasitism among morphs. Moreover, divergence in rates of parasitism may be exacerbated by rising temperatures as climate warming lowers the thermal suitability of environment and raises daily costs of

**TABLE 1** Description of alternative reproductive, behavioural and dispersal strategies across the three colour morphs in female *Zootoca vivipara*

Trait	Yellow females (Y)	Orange females (O)	Mixed females (M)
Reproduction <sup>1</sup>	<ol style="list-style-type: none"> <li>1. Lower clutch size than O- and M-females</li> <li>2. Lower hatching success than M-females</li> </ol>	<ol style="list-style-type: none"> <li>1. Higher clutch size than Y-females</li> <li>2. Lower hatching success than M-females</li> </ol>	<ol style="list-style-type: none"> <li>1. Higher clutch size than Y-females</li> <li>2. Higher hatching success than Y- and O-females</li> </ol>
Behaviour <sup>2,3</sup>	<ol style="list-style-type: none"> <li>1. Rare exposure to aggression</li> <li>2. Dominant over other morphs</li> </ol>	<ol style="list-style-type: none"> <li>1. The least aggressive</li> <li>2. Avoids social interactions</li> </ol>	<ol style="list-style-type: none"> <li>1. Exposed to aggression</li> <li>2. Aggressive behaviour dependent on the colour of the opponent</li> </ol>
Dispersal <sup>4</sup>	Offspring from Y-females disperse more often in O-prevalent populations	Offspring from O-females disperse less often in Y-prevalent populations	Offspring from M-females disperse less often in Y-prevalent populations
Colour-frequency based influence <sup>1,4,5</sup>	<p>A higher frequency of Y-females:</p> <ol style="list-style-type: none"> <li>1. implies higher social stresses</li> <li>2. reduces juvenile body condition of all morphs</li> <li>3. positively correlates with clutch size</li> <li>4. negative effects on hatching success of Y- and O-females</li> <li>5. reduces juvenile dispersal of M- and O-females</li> </ol>	<p>A higher frequency of O-females:</p> <ol style="list-style-type: none"> <li>1. infers lower social stresses</li> <li>2. positively correlates with a higher hatching success of M-females</li> </ol>	No effects of the frequency of M-females have been detected

Note: References: 1. Vercken, E., Massot, M., Sinervo, B., & Clobert, J. (2007). *Journal of Evolutionary Biology*, 20(1), 221–232; 2. Vercken, E., & Clobert, J. (2008a). *Herpetological Journal*, 18(4), 223–230; 3. Vercken, E., & Clobert, J. (2008b). *Ecoscience*, 15(3), 320–326; 4. Vercken, E., Sinervo, B., & Clobert, J. (2012). *Behavioral Ecology*, 23(5), 1059–1067; 5. Vercken, E., Clobert, J., & Sinervo, B. (2010). *Oecologia*, 162(1), 49–5.

existence (Sinervo et al., 2010). Indeed, recent evidence has revealed common lizards display phenotypic responses to a warming climate, such as an accelerated pace of life (Bestion et al., 2015), which increases the risk of local population extinction (Dupoué et al., 2017).

Here, we investigate the effects of intraspecific diversity on the relationship between parasitism and climate warming at both a spatial and a temporal scale. Based on the results from earlier studies, we make the following predictions: (i) Climate warming will increase parasite infestations in female common lizards, after accounting for spatial and temporal variability; (ii) colour morphs should display differences in parasite infestation as a result of their specific behavioural and life-history strategies; (iii) parasite infestation among colour morphs should vary across environmental contexts; (iv) the risk of parasite infestation should trade-off with either host reproduction or host survival in a colour-dependent way. We addressed these predictions using two different datasets. The first dataset focuses on spatial variation and comprises 10 distinct populations distributed in the Massif-Central, France. The second dataset is from a long-term capture–mark–recapture (+20 years) sampling program on a single population in the same region.

## 2 | MATERIALS AND METHODS

### 2.1 | Focal species

*Zootoca vivipara* is a small-sized lizard (adult snout–vent length, SVL 50–70 mm) distributed across Europe and Asia. Individuals inhabit a variety of environments including peat bogs, mesic meadows,

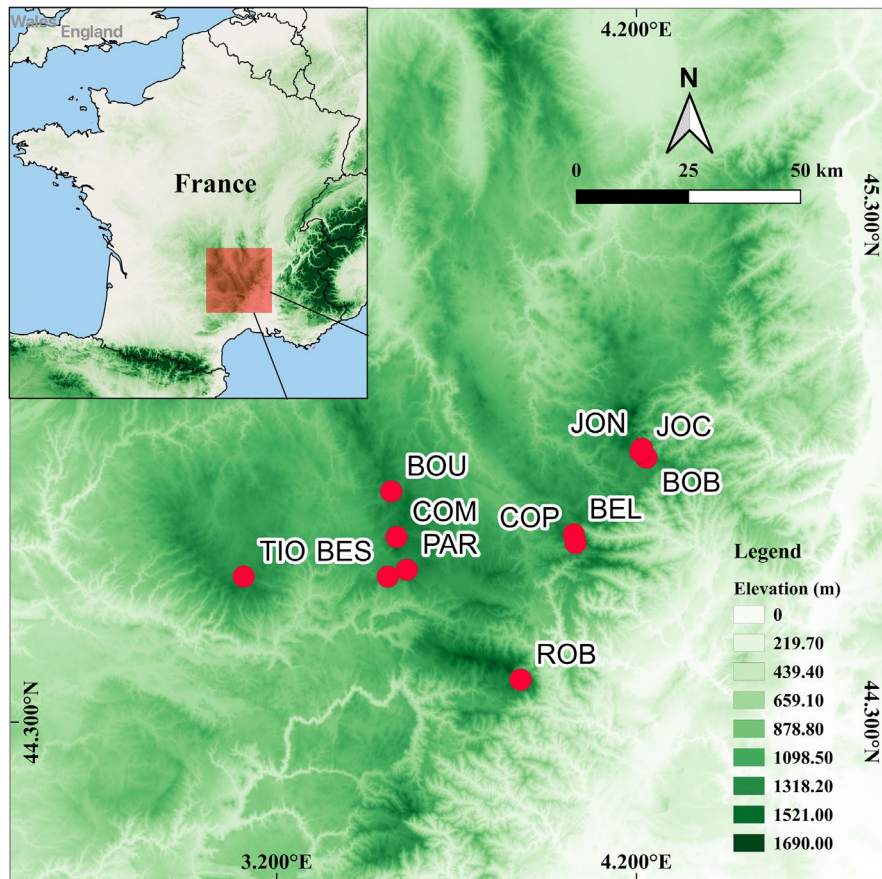
heathlands or humid grasslands. Males emerge from hibernation in April prior to adult females. Mating takes place early in May, immediately after the emergence of females. Parturition occurs between mid-July and mid-August. On average, females lay five soft-shelled eggs (range 1–13) and hatchlings emerge from the egg membrane within 1 h (Bleu et al., 2013).

Adult females from populations in the Massif-Central display a discernible polymorphism in ventral colouration, varying from pale yellow to bright orange. In contrast, adult males almost always remain orange. The ventral colour pattern of an adult individual remains stable after reaching adulthood (Vercken et al., 2007). Colour morphs have been found to be heritable ( $h^2 = 0.48$ , Vercken et al., 2007).

### 2.2 | Population monitoring and animal husbandry

We captured ~20 adult females from 10 populations in the Massif-Central (France). These sites were selected based on the variation in climatic conditions and anthropogenic disturbance (hereafter MC for 'Massif-Central populations', Figure 1). We sampled the MC populations over the course of 3 years: 2012, 2014 and 2015. Most sites were sampled each year, but due to logistical constraints some sites were only sampled once (Table 2). The mean capture date of pregnant females was June 27 ( $\pm 3.5$  days, Rutschmann et al., 2016).

At the temporal scale, we used a 20-year capture–mark–recapture study (located near the 'Rocher-de-la-Barque', hereafter ROB population, Figure 1). We used capture data from 1992 to



**FIGURE 1** Sample sites of common lizards (*Zootoca vivipara*) in the Massif-Central, France. We used a long-term capture-mark-recapture study at one population (ROB, bottom of the map) for the analysis of temporal patterns. The remaining 10 populations (centre of the map) are used in the spatial analysis. The elevation is from the SRTM database with 90 m resolution

**TABLE 2** Description of the capture sites in Massif-Central with sampling efforts, sample size and environmental factors, including elevation, vegetation cover index (VCI), human disturbance (1-3) and grazing condition (0 no grazing, 1 grazing)

Site	Mountain range	Number of visits	Sample size	Elevation(m)	VCI	Human disturbance	Grazing
BOB	Mont du Vivarais	2	26	1450	0.04	2	0
JOC	Mont du Vivarais	1	15	1300	0.02	2	1
JON	Mont du Vivarais	2	22	1405	0.19	2	0
BEL	Mont du Velay	1	10	1350	0.30	1	0
COP	Mont du Velay	3	27	1360	0.07	2	0
TIO	Mont d'Aubrac	2	34	1300	0.00	2	1
BES	Margeride	2	24	1220	0.10	3	1
BOU	Margeride	2	19	1410	0.12	2	1
COM	Margeride	3	32	1435	0.19	1	1
PAR	Margeride	2	24	1415	0.32	1	0

2012, for a total of 3768 captures consisting of 1498 unique females. The capture probability of a female within the ROB study site is independent of its colour (Vercken et al., 2007).

We brought lizards from the MC and ROB sites to a field laboratory where we measured SVL ( $\pm 0.1$  cm) and body mass ( $\pm 0.01$  g). For lizards from the ROB population, we first visually counted mites in the field and performed a second count in the laboratory. Based on two decades data from ROB, we found that no mites were dislodged from a lizard during transport to the laboratory. For MC populations, we counted

parasites in the laboratory, but checked all the terrariums after arrival to the laboratory to verify no mites have dropped during this process.

We assigned each female to one of the three discrete colour morph categories: yellow (Y-females), orange (O-females) and mixed (mixture of yellow and orange, M-females) using a Pantone® reference scale. Females were maintained in individual terrarium (11 × 18 × 11 cm, with damp soil and a small cardboard box as a shelter) under standardized rearing conditions (see Massot & Clobert, 2000). Six hours of light and water were provided every day and

females were fed every other day. At parturition, we recorded lay date, litter size and total litter mass. Three days after parturition, each female was released with her offspring at the exact capture location.

### 2.3 | Patterns of parasitism

Haematophagous mite species in the genus *Ophionyssus* are one of the most common ectoparasites of lizards. *Ophionyssus* mites are both thermophilic and hygrophilic and their life cycles usually include larval, nymph and adult stages (Bannert et al., 2000; Capinera, 2008). Individual mites are free living in the soil and cling onto a host for a blood meal (Cooper & Jackson, 1981). In our study sites, *Z. vivipara* is the main reptile host of mites. We will hereafter use the term 'infestation' instead of 'infection' as the former is more appropriate for ectoparasites.

### 2.4 | Environmental and climatic variables

Environmental factors (Table 2) of MC sites were measured following the methods of Rutschmann et al. (2016). We included data on elevation, vegetation cover, human disturbance and grazing condition. Vegetation cover was calculated from aerial photographs of each site (scaled Google Earth© views, Mountain View, CA, USA, collected in January 2015) as the proportion of pixels representing trees or bushes within the total capture area (Rutschmann et al., 2016; Wu et al., 2019). Human disturbance (intensity of grazing and openness) was estimated as a rank order from 1 to 4, with 1 being the least disturbed site and 4 being the highest one. Grazing condition was represented by 0 (no grazing) or 1 (grazing). Because some variables are categorical, we extracted patterns of covariation among variables using a principal coordinates analysis (PCoA) based on a Gower distance metric as implemented in the 'ape' package (Paradis & Schliep, 2019). We retained the scores from only the first axis ( $PC1_{Env}$ ), which explained 75.5% of the total variation.

For each MC site, the climatic conditions were obtained from the nearest meteorological station (Table S1). We also placed three temperature data loggers (Thermochron iButtons; Waranet Solution) at each site from mid-June to the end of July 2014. We used linear regression to relate the temperatures recorded by data loggers with those from the nearest meteorological station. The regression coefficients of each site were then used to predict the local temperatures for all the sampling periods (see more details of this method in Rutschmann et al., 2016). Air temperatures at ROB were collected from the Mt. Aigoual MeteoFrance<sup>R</sup> meteorological station (50 km south, similar elevation, Table S2) because of its availability of data through all sampling years. Previous studies found that temperatures measured in Mt. Aigoual station had a significant and high correlation with temperatures recorded at ROB by a portable meteorological station (Chamaillé-Jammes et al., 2006; Massot et al., 2008).

We used the mean daily maximum temperature in June ( $T_{max6}$ ) as the indicator of climate for the following reasons: (1) monthly means of daily maximum temperature appear to be a more pertinent predictor of thermoregulation opportunities for reptiles (Huey, 1982); (2) June temperature has been demonstrated as the best descriptor of thermal conditions during gestation in the common lizard (Le Galliard et al., 2010); and (3) the embryonic development in this species is most sensitive to environmental conditions at the mid-gestation stage, which corresponds to June in our study sites (Bleu et al., 2013; Le Galliard et al., 2010; Rutschmann et al., 2016).

### 2.5 | Statistical analysis

We included only those females with scores for ventral colouration in one of the three categories: yellow (Y-females), orange (O-females) and mixed (M-females). We excluded females with missing data for either ventral colour or parasites. The resulting sample size consisted of 233 females (only one recaptured individual) for the MC dataset and 1877 females (1025 unique females) for the ROB dataset. We first compared mite prevalence among MC populations and fitted a generalized additive mixed model against year to examine the temporal variation of prevalence for the ROB population. We then focused on the infestation probability of mites (presence/absence, hereafter MP), because parasite intensity had low variability among individuals. Further analyses using negative binomial mixed models confirmed that no differences existed between morphs in parasite intensity (see Table S3).

#### 2.5.1 | Infestation probability in relation to colour morph and temperature

To determine the factors affecting mite infestation probability (binomial distribution), we used generalized linear mixed models (GLMMs) as implemented in the 'lme4' package (Bates et al., 2015). The MC and ROB datasets were analysed separately. We included either site (MC populations) or the interaction of individual-by-year (some females were captured multiple times over multiple years at ROB) as random effects.

Our analysis of the MC dataset used ventral colour as a fixed effect (categorical variable), with body condition (residuals of body mass regressed against SVL),  $PC1_{Env}$  (environmental variation), annual  $T_{max6}$  and several interaction terms (ventral colour  $\times T_{max6}$ , ventral colour  $\times$  body condition, ventral colour  $\times PC1_{Env}$ ) as covariates.

Our analysis of the ROB dataset also included ventral colour as a fixed effect and body condition, age, annual frequencies of colour morphs and annual  $T_{max6}$  as covariates. We also included several interaction terms (ventral colour  $\times T_{max6}$ , ventral colour  $\times$  body condition, ventral colour  $\times$  age). Annual frequencies of females' colour morphs (Figure S1) in the ROB population were estimated from the sample of females brought to the laboratory



(Vercken et al., 2007). There were no significant correlations between  $T_{\max 6}$  and annual frequencies of colour morphs ( $|r|$  values all below .3). To account for the fact that colour frequencies sum to one (Aitchison, 1986), we summarized the changes in morph frequencies over time using a PCoA based on a Hellinger distance matrix. The first two PCoA axes explained 88% of the total variation and we retained them for subsequent statistical analyses ( $PC1_{\text{Freq}}$  and  $PC2_{\text{Freq}}$ ). The frequency of mixed females ( $F_{\text{mix}}$ ) increased with  $PC1_{\text{Freq}}$ . The second PCoA axis ( $PC2_{\text{Freq}}$ ) described a pattern of a negative association between the frequency of yellow females ( $F_Y$ ) and orange females ( $F_O$ ) (Figure S2).

We first fit a full model and used backward elimination to obtain the most parsimonious model for each dataset. We assessed the significance of fixed effects by backward selection, which involved removing non-significant terms (Zuur et al., 2009). Associated  $p$  values of the likelihood ratio test were obtained by bootstrap with 1000 replications (Faraway, 2006).

### 2.5.2 | Infestation and host reproduction

We investigated how mite infestations may affect host reproduction across the colour morphs. We included four reproductive traits: litter size, hatching success (the proportion of live neonates within one clutch), relative clutch mass (RCM, the difference of female body mass before and after parturition divided by body mass before parturition) and investment per offspring of females (INV, the difference of female body mass before and after parturition divided by litter size). We used a GLMM for litter size, hatching success and RCM, and a linear mixed model ('nlme' package, Pinheiro et al., 2017) for female's INV, with the site (for MC) or the interaction of individual by year (for ROB) as random effects. The fixed effects and covariates tested for reproduction are as follows:

**MC dataset:** Ventral colour, infestation probability (MP), SVL,  $PC1_{\text{Env}}$ ,  $T_{\max 6}$ , Labdays and interactions (up to three-way interactions between Ventral colour, MP and  $T_{\max 6}$ ). The term 'Labdays' represents the duration of time a female spent in captivity until parturition, which is used as a proxy for the stage of gestation at the day of capture.

**ROB dataset:** Ventral colour, infestation probability (MP), SVL, age,  $T_{\max 6}$ , Labdays and interactions (up to three-way interactions between Ventral colour, MP and  $T_{\max 6}$ ). We also included the annual frequencies of colour morphs (represented by  $PC1_{\text{Freq}}$  and  $PC2_{\text{Freq}}$ ). A minimum adequate model was obtained by backward selection of non-significant terms via maximum likelihood-based methods (Zuur et al., 2009).

### 2.5.3 | Host survival

We used program MARK (White & Burnham, 1999) through the package 'RMark' (Laake, 2013) to analyse the rates of survival in the ROB population. Female apparent survival rate was estimated by using

a Cormack–Jolly–Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965) extended to group effects (Clobert et al., 1988; Lebreton et al., 1992). As the capture sessions were concentrated in time and emigration or immigration rate was low in our study site (Massot et al., 1992), estimates of apparent survival rates reflect actual survival rates (Vercken et al., 2007). We tested the effects of colour morphs, infestation probability of mites (MP), annual  $T_{\max 6}$ , year and their interactions (up to three-way interaction) on the survival rates of females. Capture probabilities were tested by year or held as constant (capture probability did not vary between colour morphs, see Vercken et al., 2007). We used the corrected Akaike information criterion (AICc) to compare a set of candidate models (both  $\Delta\text{AICc} < 2$  or accumulative model weights  $\leq 95\%$  gave similar results, Burnham & Anderson, 2002). Final estimates of survival rates were computed by model averaging on all models within the kept range. All the analyses in this study were conducted in R software (version 4.0.2, R Core Team, 2020).

## 3 | RESULTS

### 3.1 | Temperature trends and spatial and temporal variation in mite prevalence

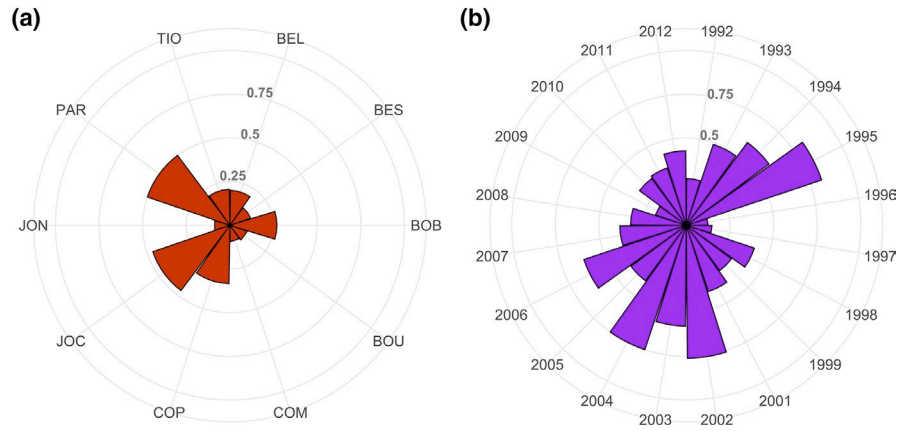
We observed significant differences in mean maximal daily temperature ( $T_{\max 6}$ ) among the 10 MC populations (one-way ANOVA:  $F_{9,20} = 18.69, p < .001$ ). JOC was the warmest study site and had significantly higher temperatures than the other nine sites. BES, COP and JON had higher temperatures than BEL and TIO (Tukey post-hoc test, see Figure S3). In ROB,  $T_{\max 6}$  displayed a gradual increasing trend during the study period ( $F_{1,19} = 4.41, p = .049$ ). From 1992 to 2012, annual  $T_{\max 6}$  in ROB increased around 3°C (Figure S4).

Mite prevalence exhibited significant geographic variation among the 10 MC populations and ranged from 9.4% to 50% (Figure 2a, Fisher's exact test  $p = .003$ ). We also found substantial temporal variation in mite prevalence in ROB population (Figure S5, generalized additive mixed model: estimated degree of freedom = 8.38,  $F = 20.85, p < .001$ ). Females varied in annual mite prevalence from 12.5% to 81.8% in ROB (Figure 2b).

### 3.2 | Mite infestation, colour morphs and temperature

After controlling for spatial variation in MC populations, the probability of mite infestation was affected by colour morphs,  $T_{\max 6}$  and the interaction between colour morphs and  $T_{\max 6}$  (Table 3). Among the three colour morphs, infestation probability of mites was generally lower for M-females than either Y- or O- females, whereas the opposite was true when temperature increased (Table 4; Figure 3a). Moreover, the relationship between infestation probability and temperature was contingent on colour morphs of the host: temperature

**FIGURE 2** Variation of mite prevalence from spatial and temporal perspectives respectively. (a) Mite prevalence across 10 spatially distinct populations in the Massif-Central. (b) Mite prevalence in the ROB population over 20 years



**TABLE 3** Main effects of statistical models for the infestation probability of mites with respect to MC and ROB dataset

Response	$\chi^2$ (type III Wald chi-square test)	df	<i>p</i> value
MC dataset (spatial)			
Intercept	7.57	1	<b>.0059</b>
Colour	6.42	2	<b>.0403</b>
$T_{\max 6}$	5.46	1	<b>.0195</b>
Colour $\times T_{\max 6}$	5.71	2	<b>.0576 (marginal)</b>
ROB dataset (temporal)			
Intercept	16.58	1	<b>&lt;.0001</b>
Colour	9.41	2	<b>.0090</b>
$T_{\max 6}$	13.71	1	<b>.0002</b>
PC2 <sub>Freq</sub>	24.69	1	<b>&lt;.0001</b>
Colour $\times T_{\max 6}$	7.75	2	<b>.0207</b>

Values shown in boldface are significant *p*-values.

had positive effects on mite infestation for M- and Y-females, but a weak negative effect for O-females (Figure 3a).

Similar results were found for females in the ROB population after accounting for temporal variation in infestation (Tables 3 and 4; Figure 3b). In addition, there was an effect of the frequency of colour morphs in the population on mite infestation. Specifically, the probability of mite infestation had a negative correlation with PC2<sub>Freq</sub> (Table 3; Figure 4,  $\beta = -5.54 \pm 1.12$ ,  $z = -4.97$ ,  $p < .001$ ). This result indicated that mite infestation increased with the frequency of yellow females and decreased with the frequency of orange females.

### 3.3 | Female reproductive traits

In MC populations (Table S4), we found no evidence that M-females exhibited lower values in litter size, RCM and investment per offspring (INV) compared to Y- or O-females. Hatching success was affected by the interaction of colour  $\times T_{\max 6}$  ( $\chi^2 = 14.54$ ,  $df = 2$ ,  $p < .001$ ), with O-females showing lower hatching success than M- and Y-females at higher temperatures (Table S4). Furthermore, parasites and  $T_{\max 6}$  had no negative effects on reproduction.

In the ROB population (Table S5), litter size, hatching success, RCM and INV did not differ among colour morphs after post-hoc analyses, nor were they influenced by any interactions involving colour morphs. The results from the analysis of both the temporal and spatial data suggest that M-females share similar reproductive patterns with Y- or O-females.

### 3.4 | Survival rates

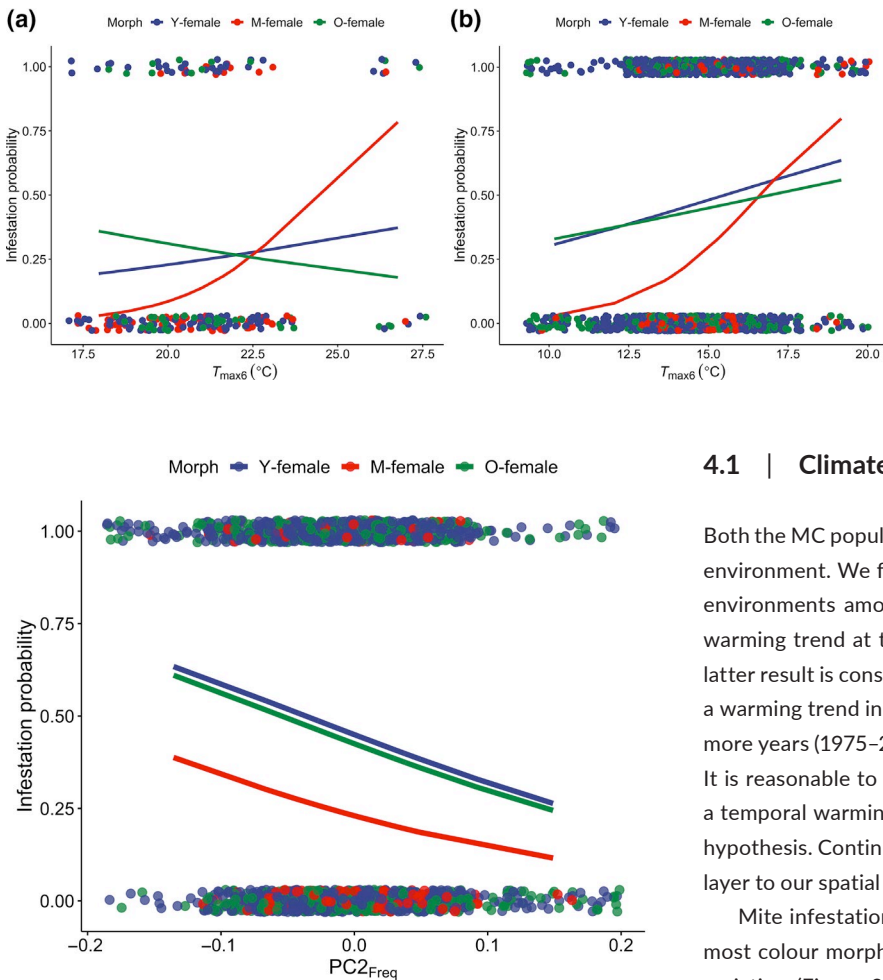
The most parsimonious model (the model with the lowest AICc values) indicated that survival rates were associated only with ventral colour. However, this model was indistinguishable from other retained models (Table S6), such as the model including the interaction between colour morphs and parasites ( $\sim MP \times$  colour). Average survival rates from the retained models suggest that survival differed among colour morphs, with M-females having lower average survival rates than Y- or O-females (Kruskal–Wallis test with Dunn's multiple comparison: M-female vs. Y-female:  $z = -5.14$ ,  $p < .001$ , M-female vs. O-female:  $z = -10.29$ ,  $p < .001$ , Figure 5a). The pattern of infested M-females having lower survival than infested Y- or O-females remains when excluding individuals without parasites (all adjusted  $p < .001$ ). Moreover, M-females also experienced the greatest reduction of survival rates under parasitism. When infested by parasites, the average survival was reduced by 26.7% for M-females, compared to a reduction of only 2.8% for O-females and an increase of 1.9% for Y-females. A final pattern in survival rates showed that M-females exhibited a slight decline with increasing  $T_{\max 6}$ , but only to a lesser extent compared to the other morphs (differences in slopes of a beta regression with post-hoc analysis, M- vs. Y-female:  $z = -2.09$ ,  $adjust-p = .09$ ; M- vs. O-female:  $z = -1.33$ ,  $adjust-p = .38$ , Figure 5b). It is possible that  $T_{\max 6}$  and MP play a similar statistical role since they are correlated (Table 3).

## 4 | DISCUSSION

Understanding the relationship between climate change and parasitism is vital to improve our abilities to predict disease risks in wildlife.

Effect	Yellow versus Mixed	Orange versus Mixed	Yellow versus Orange
MC dataset (spatial)			
Infestation probability	$z = 2.016$ adjust- $p = .107$ (marginal)	$z = 2.467$ adjust- $p = .036$	$z = 0.956$ adjust- $p = .602$
ROB dataset (temporal)			
Infestation probability	$z = 2.885$ adjust- $p = .010$	$z = 3.046$ adjust- $p = .005$	$z = 0.537$ adjust- $p = .846$

Values shown in boldface are significant  $p$ -values.



**FIGURE 4** Infestation probability of mites in relation to the annual frequency of colour morphs (represented by  $PC2_{Freq}$ ) in the ROB population

However, a particular challenge is to account for spatial and temporal variation in climate and to incorporate intraspecific diversity in estimating parasite infestation dynamics as ambient temperatures increase. Here we addressed both challenges using female common lizards as a model system. Overall, our study provides evidence of a relationship between colour morphs, temperature and parasitism, confirming our prediction that intraspecific diversity influences the infestation dynamics in a warming environment.

**TABLE 4** The results of multiple comparison with post-hoc tests for colour effects on infestation probability of mites

**FIGURE 3** Infestation probability of mites in relation to annual mean maximal temperature in June ( $T_{max6}$ ) with respect to each colour morphs. (a) Variation in mite infestation among colour morphs in the MC populations (spatial). (b) Variation in mite infestation among colour morphs in the ROB population (temporal)

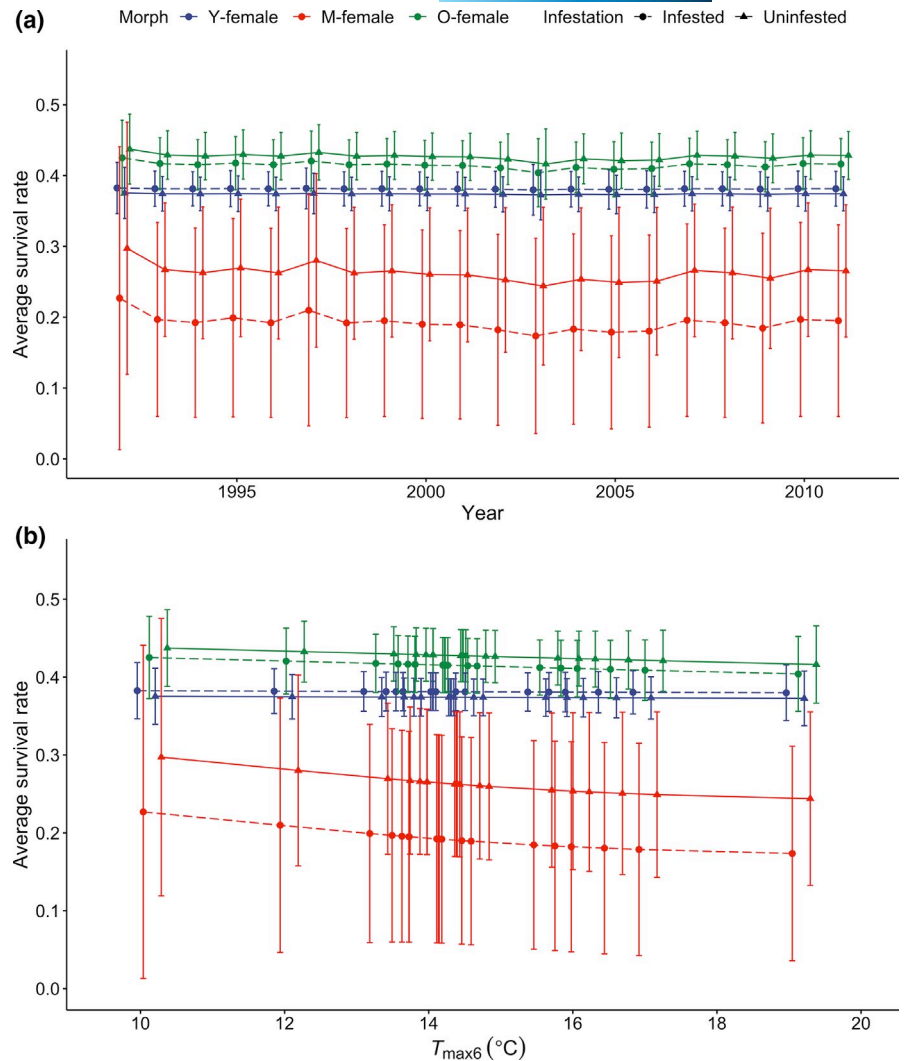
#### 4.1 | Climate and parasite prevalence

Both the MC populations and ROB exhibited variation in the thermal environment. We found significant spatial heterogeneity in thermal environments among the MC sites. In addition, we documented a warming trend at the ROB site during the study (1992–2012). This latter result is consistent with previous studies at ROB that reported a warming trend in temperature of June by using a dataset spanning more years (1975–2005; see fig. 2 in Chamaillé-Jammes et al., 2006). It is reasonable to speculate that MC populations also experienced a temporal warming trend, but our limited data cannot confirm this hypothesis. Continued monitoring on MC sites can add the temporal layer to our spatial dataset.

Mite infestation probability increased with the temperature for most colour morphs after controlling for both temporal and spatial variation (Figure 3). This pattern, in part, supports the hypothesis that warming temperatures increase the risk of parasitic infestation in common lizards. Parasites and their hosts often experience the same environmental milieu, thus changes in ambient temperatures of hosts are also expected to influence the life history of parasites (Löhmus & Björklund, 2015). Elevated temperatures could enhance development, survival rates, metabolism and distribution range of parasites, which results in an increase in encounter rates and disease transmission (Harvell et al., 2002). Meanwhile, warmer temperatures may also enhance the immune response of hosts (e.g. Adamo & Lovett, 2011 in the cricket *Gryllus texensis*). However, Altizer et al. (2013) asserted that positive effects of rising temperature on parasite growth and reproduction may outweigh a potential increase in the immune function of the host. An experimental manipulation



**FIGURE 5** Average survival rates of female adults in the ROB population with respect to different colour morphs and infestation status. (a) Average survival rates across different years. (b) Average survival rates in relation to annual mean maximal temperature in June ( $T_{\max 6}$ ). The points represent the estimated mean survival with standardized error (mean  $\pm$  SE). Infested individuals are represented by the solid circle, while uninfested individuals by the solid triangle



using an *Argulus* ectoparasite and the goldfish (*Carassius auratus*) demonstrated that higher temperatures enhanced the mean infestation intensity of ectoparasites with a concomitant reduction in several innate immune traits and survival of hosts (Shameena et al., 2021).

Another mechanism underlying the increasing rate of parasitism due to climate change could be the *thermal mismatch hypothesis*. This hypothesis posits that hosts should be more susceptible to infestations when environmental conditions deviate from the thermal optima of hosts (Cohen et al., 2017, 2019, 2020). Small organisms, such as parasites, often possess broader thermal performance curves and therefore adapt to new environments better than larger organisms, such as hosts (Rohr et al., 2018). In other words, when climate warming deviates lizards from their thermal optima (Bestion et al., 2015; Dupoué et al., 2017), parasite growth might outperform the host defence at warmer temperatures. These potential mechanisms warrant further studies in our system and other environmental factors of the study sites (such as precipitation) may also shape the parasitism of hosts (Rozen-Rechels et al., 2021). One should also be cautious when interpreting the results from MC populations as some extreme endpoints

and the unbalanced sampling may partially drive the observed pattern (Makin & Orban de Xivry, 2019). Future studies in our system should aim at collecting data over longer temporal periods for the same set of populations to provide more robust estimates.

## 4.2 | Morph-dependent parasite infestations

We found heterogeneous patterns of mite infestation among colour morphs: M-females had a lower probability of being infested than Y- or O-females, but became more susceptible to parasites when temperature increased (Figure 3). Previous studies demonstrated colour-specific reproductive, physiological and behavioural patterns in female common lizards (Table 1). Y-females are the most aggressive (Vercken & Clobert, 2008) and have higher levels of plasma testosterone (Vercken, 2007). Based on the immunocompetence handicap hypothesis (Folstad & Karter, 1992), Y-females should suffer from the immunosuppressive effects of a pace-of-life with higher physiological and energetic costs. In contrast, O-females are the least aggressive and tend to avoid agonistic interactions (Vercken & Clobert, 2008). O-females might then be excluded from optimal

habitats by other colour morphs, resulting in reduced foraging opportunities and diminished immunocompetence. O-females may also be sequestered in habitats with more parasites. Finally, M-females appear to have an intermediate condition-dependent strategy that relies on the frequency of the other two colour morphs (Vercken & Clobert, 2008). Assuming that increased competitive ability may decrease host immunocompetence (Luong & Polak, 2007), this putative condition-dependent strategy (bully strategy, Vercken et al., 2010) may release M-females from the elevated energetic costs of competitive interactions, hence resulting in a higher investment in the immune function. However, as ambient temperatures increased, M-females became more susceptible to parasitism (Figure 3). Previous studies have revealed that immune responses often differ among distinct ecotypes (Scharsack & Kalbe, 2014; Scharsack et al., 2007) and are highly temperature dependent in ectotherms (Raffel et al., 2006). Thus, it is possible that certain morphs (M-females here) have greater immunocompetence than others, but are simultaneously more susceptible to the negative effects of higher temperatures. Further data collected on the thermal sensitivity of the immune response among colour morphs are needed here to examine this untested hypothesis.

Mite infestation was also found to correlate with the social context of the population (i.e. composition of colour morphs): increasing with the frequency of Y-females but decreasing with the frequency of O-females. In common lizards, the social strategies displayed by different colour morphs constitute the social context of the population. A greater Y-female environment in the population should increase intraspecific competition compared to an O-female environment. Shifts in female morph frequencies may in turn alter investment in immune function (Luong & Polak, 2007). Such a pattern has already been observed in another colour polymorphic lizard, the side-blotched lizard (*Uta stansburiana*): female individuals surrounded by aggressive territorial neighbours were found to have suppressed immune responses (Svensson et al., 2001). Whether or not the stress-immunity relationships in *U. stansburiana* can be applied in *Z. vivipara* requires further investigation.

### 4.3 | Interaction between temperature and colour morphs on parasitism

We detected significant interactions between colour morphs and habitat temperature ( $T_{\text{max}0}$ ) on parasitism. This pattern suggests that the increasing trend of parasitism with warmer environments depends on the colour morphs, that is, the relationship between parasitism and temperature (and potentially climate change) is modulated by host morphotypes. It appears that one morphotype might have an adaptive advantage at one condition, but becomes maladaptive under another (Figure 3a,b). This scenario can be overlooked if one only considers average responses to climate change, but neglects the role of intraspecific diversity within populations or species.

Although intraspecific diversity has been documented to buffer disease risks in various ecosystems (Ekroth et al., 2019; Reiss

& Drinkwater, 2018), it might be a different situation under changing environments. Disparate responses to parasitism across colour morphs imply that warming temperatures may affect the phenotype frequencies within a population (e.g. through the change in survival). If heterogeneous patterns of parasitic infestation promote the maintenance of phenotypic diversity (and potentially genetic diversity) in host populations (Hamilton, 1982), then climate warming may destabilize the influence of parasites on each phenotype. In turn, climate warming may jeopardize the maintenance of colour polymorphism and its associated reproductive strategies or even threaten population persistence by increasing the maladaptive responses of certain morphs to their changing environments (i.e. the potential loss of intraspecific diversity). This hypothesis is based on phenotypic data, which might not correspond with genetic diversity. However, a recent unpublished project has identified two genes for female colour production in *Z. vivipara* (Kathryn Elmer, personal communication). Future genomic studies focusing on genes associated with both colour production and coadapted traits can greatly help to decipher the complex relationships among colour morphs, parasitism and climate warming.

### 4.4 | Colour morph-dependent trade-offs and climate warming

Putative trade-offs between immunity and reproductive investment are common (Smith & French, 2017 and references therein), but we have little support for such trade-offs among the three colour morphs in this study. The absence of effects of climate warming or parasitism on reproductive parameters has been documented by other studies on common lizards (Chamaillé-Jammes et al., 2006; Sorci & Clobert, 1995; Wu, 2018). However, it is possible that the geometry of trade-offs lies along axes other than those involving reproduction (Sinervo & Clobert, 2008). In particular, a recent meta-analysis indicated that a main cause of animal mortality events involves parasitism and disease, whereas other interacting stressors may play a relatively minor role (Fey et al., 2015). Since previous studies found that heavy infestations incur a higher mortality in common lizards (Sorci & Clobert, 1995), we may expect the existence of trade-offs linking parasitism with survivorship.

Indeed, we detected a trade-off involving host survival and susceptibility to parasitism. M-females had higher mortality rates when being infested, but also lower infestation probability in comparison with Y- or O-females. Combining these two findings, we hypothesize the existence of a trade-off between resistance to parasites and host mortality rates, and that the position of an individual on the trade-off continuum is contingent on the colour morph. This trade-off does not contradict the results of a previous study (Sorci & Clobert, 1995, only occurring in laboratory), as it is only meaningful to compare the mortality and infestation probability within a colour morph-dependent context here. Moreover, other factors may also affect the survival rates here because our study is based on natural populations. The colour morph-dependent trade-off involving

individual fitness has also been found in other systems such as a polymorphic damselfly (*Ischnura elegans*, Willink & Svensson, 2017). The differences in defensive mechanism between morphs may result from correlational selection (Miles et al., 2007; Sinervo & Svensson, 2002). Specifically, M-females may allocate more energy to support a higher avoidance of, or defence against parasites, but it is counterbalanced by their lower survival rates thereafter. In contrast, Y- or O-females exhibit a different strategy. The success of each strategy, through survival rates, might then depend on climate since the level of parasite infestation of each colour morph is mediated by temperature as indicated by our results.

## 5 | CONCLUSIONS

Our work demonstrates the role of intraspecific diversity in shaping climate-modulated parasitism. We found that infestation probability of mites in *Z. vivipara* increases with warmer temperature but with a different colour-dependent rate. We hypothesize that the trade-off between resistance to parasites and survival is at the basis of the colour morphs' susceptibility to parasites and its dependence to an increase in temperature. In the context of climate warming, the interplay between temperature and parasitism is likely to alter the diversity of alternative strategies in female common lizards and may even imply a decrease in population size as the rate of climate warming proceeds. While most studies focus on average responses of parasitism with increasing temperature, our work highlights that alternative morphotypes can interact with temperature to influence the infestation dynamics. We advocate additional studies that include host intraspecific diversity in the framework of climate-disease research.

## ACKNOWLEDGEMENTS

We are grateful to the handling editor and two anonymous reviewers for their insightful comments in improving a previous version of this manuscript. We thank all the assistants who collected the data used in this study. We also thank Meng Zhang for assistance in map creation. Population monitoring was supported by the 'Agence Nationale de la Recherche (ANR MOBIGEN) and the Laboratoire d'Excellence TULIP (ANR-10-LABX-41). QW is supported by the National Natural Science Foundation of China (no. 32001124). DBM acknowledges support from NSF (EF1241848, DEB1950636), Make Our Planet Great Again, Laboratoire d'Excellence TULIP and Ohio University International Travel Grants. The authors declare that they have no conflict of interest.

## AUTHOR CONTRIBUTIONS

Qiang Wu and Jean Clobert designed the study. All authors contributed to the data of this study. Qiang Wu performed the statistical analysis and wrote the first draft with substantial inputs from Jean Clobert, Donald B. Miles and Murielle Richard. Donald B. Miles, Alexis Rutschmann and Jean Clobert led the revision of the paper. All authors contributed to the manuscript writing and approved the final version.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.16895380> (Wu et al., 2021).

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**How to cite this article:** Wu, Q., Miles, D. B., Richard, M., Rutschmann, A., & Clobert, J. (2021). Intraspecific diversity alters the relationship between climate change and parasitism in a polymorphic ectotherm. *Global Change Biology*, 00, 1–14. <https://doi.org/10.1111/gcb.16018>