



**HAL**  
open science

# Climate warming and temporal variation in reproductive strategies in the endangered meadow viper

Jean-François Le Galliard, Malo Jaffré, Thomas Tully, Jean-Pierre Baron

## ► To cite this version:

Jean-François Le Galliard, Malo Jaffré, Thomas Tully, Jean-Pierre Baron. Climate warming and temporal variation in reproductive strategies in the endangered meadow viper. *Oecologia*, 2024, 207 (1), pp.12. 10.1007/s00442-024-05645-5 . hal-04859756

**HAL Id: hal-04859756**

**<https://cnrs.hal.science/hal-04859756v1>**

Submitted on 30 Dec 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NoDerivatives 4.0 International License

1 **Climate warming and temporal variation in**  
2 **reproductive strategies in the endangered meadow**  
3 **viper**

4 Jean-François Le Galliard<sup>1,2</sup>, Malo Jaffré<sup>1</sup>, Thomas Tully<sup>1</sup>, and Jean-Pierre Baron<sup>1</sup>

5 1. Sorbonne Université, CNRS, IRD, INRA, Institut d'écologie et des sciences de  
6 l'environnement (iEES Paris), 4 Place Jussieu, 75252 Paris Cedex 5, France

7 2. Ecole normale supérieure, PSL University, Département de biologie, CNRS, UMS 3194,  
8 Centre de recherche en écologie expérimentale et prédictive (CEREEP-Ecotron IleDeFrance),  
9 11 chemin de Busseau, 77140 Saint-Pierre-lès-Nemours, France

10

11 **Address correspondence to**

12 Jean-François Le Galliard, CNRS, UMR 7618

13 Sorbonne Université, Institut d'écologie et des sciences de l'environnement (iEES Paris), 4  
14 Place Jussieu, 75252 Paris Cedex 5, France

15 E-mail: galliard@biologie.ens.fr

16

17 **Author contributions:** JFLG, TT and JPB formulated the idea and designed the analyses,

18 JPB collected the data with help from JFLG and TT, JFLG performed the analyses, MJ

19 designed and analysed the model, JFLG wrote the manuscript and the other authors provided

20 editorial advice.

21 **Running headline:** Climate warming and reproductive strategies in a viper

## 22 **Summary**

23 Anthropogenic climate change poses a significant threat to species on the brink of extinction.  
24 Many non-avian reptiles are endangered, but uncovering their vulnerability to climate  
25 warming is challenging because this requires analysing the climate sensitivity of different life  
26 stages and modelling population growth rates. Such efforts are currently hampered by a lack  
27 of long-term life history data. In this study, we used over three decades of mark-recapture data  
28 from a natural population of the endangered meadow viper (*Vipera ursinii ursinii*) to unravel  
29 the patterns of temporal variation in reproductive traits, the local climatic determinants of  
30 inter-annual variation in reproduction and the potential buffering effects of life cycle on  
31 population growth rate. We found significant inter-annual variation in body growth, gestation  
32 length, post-parturition body condition, clutch success and offspring traits at birth, while  
33 reproductive effort showed little temporal variation. Temperature during gestation was the  
34 most critical factor, reducing gestation length and increasing both clutch success and post-  
35 parturition body condition. In contrast, neither air humidity nor global radiation affected  
36 reproductive outcomes. This population had a negative growth rate with minimal temporal  
37 variation, indicating a rapid decline largely independent of climatic conditions. Overall, the  
38 viper's life history traits appeared to be buffered against temporal variation in climatic  
39 conditions, with this declining population potentially benefiting on the short-term from rising  
40 local temperatures.

41

42 **Keywords:** reproduction, body growth, temperature, rainfall, gestation.

43

## 44 **Introduction**

45 Habitat loss, overexploitation of wild populations for food or resources, and introduced alien  
46 species have pushed many species to the brink of extinction (Ceballos et al. 2020).

47 Anthropogenic climate change is an aggravating extinction threat and thus plays a major role  
48 in the current biodiversity crisis (McLaughlin et al. 2002; Urban 2015). To improve our  
49 understanding of climate-driven extinction processes, a consensus has emerged on the need  
50 for integrated assessments of climate vulnerability (Williams et al. 2008; Huey et al. 2012). In  
51 this conceptual framework, extinction risk depends not only on exposure to climate change,  
52 but also on the sensitivity and resilience of the organism. Studying the extinction risk of  
53 species with complex life cycles, such as many iteroparous organisms or those living in highly  
54 seasonal environments, requires an understanding of the effects of climate change at different  
55 life stages, and the modelling of population growth rates (reviewed in Brodie et al. 2013).

56 In this context, long time series of demographic data from individually marked  
57 individuals are needed to decipher direct and delayed effects of climatic conditions, to account  
58 for potential compensatory responses across the life history, and to quantify specific effects of  
59 extreme weather events that rarely occur in nature (Williams et al. 2008; Brodie et al. 2013).

60 Integrated climate vulnerability assessments exist for a few plants and animals, but are scarce  
61 for non-avian reptiles (turtles, lizards, snakes, and crocodiles) due to the paucity of long-term  
62 data sets for these organisms (Le Galliard et al. 2012; Böhm et al. 2013; Winter et al. 2016).

63 Furthermore, non-avian reptiles are at high risk of extinction compared to other tetrapods,  
64 with more than 20% of existing species being currently threatened, but the specific threats  
65 posed by climate change remain highly uncertain for most of these organisms (Gibbons et al.  
66 2000; Falaschi et al. 2019; Cox et al. 2022). Thus, long-term studies of reptile population  
67 dynamics are needed to improve our understanding of the patterns and processes of their  
68 declines (Diele-Viegas and Rocha 2018; Diele-Viegas et al. 2020).

69 Non-avian reptiles are highly sensitive to the direct effects of global warming due to  
70 their behavioural thermoregulatory strategies (i.e., ectothermy). Direct, negative effects of  
71 climate change may include increased mortality risks due to overheating (e.g., Kingsolver et  
72 al. 2013), sublethal effects due to reduced basking and foraging activities (e.g., Sinervo et al.  
73 2010), disruption of energy balance (reviewed in Rutschmann et al. 2024), or increased  
74 likelihood of physiological dehydration (e.g., Kearney and Porter 2004). Such deleterious  
75 effects can alter early life stages, whose survival depends strongly on abiotic conditions, but  
76 also adult life stages, especially in viviparous species where females must optimally regulate  
77 their body temperature during a long gestation period (Shine 2003; Le Galliard et al. 2012).  
78 However, the cumulative effects of these stresses on population growth and viability are  
79 uncertain, as non-avian reptiles have also developed strategies to buffer the negative effects  
80 of climate variability (Le Galliard et al. 2012; Cox et al. 2022). For example, some are  
81 efficient thermoregulators and exploit habitat heterogeneity to maintain homeostasis, even  
82 under changing environmental conditions (Huey et al. 2012; Sunday et al. 2014). On the other  
83 hand, many iteroparous reptiles have low and flexible metabolic requirements and can cope  
84 with prolonged periods of starvation or chronic water deprivation (Shine 2005). Some are  
85 capital breeders, accumulating energy for several months or even years before breeding  
86 (Bonnet et al. 1998; Shine 2003). For these species, we expect small environmental  
87 fluctuations in cumulative lifetime reproductive success, even under changing climatic  
88 conditions. Unfortunately, studies quantifying the temporal variability of life history traits and  
89 population growth rates are rare in reptiles (but see Miller et al. 2011; Rodríguez-Caro et al.  
90 2021; Warret Rodrigues et al. 2021).

91 Climate change may also have indirect effects on non-avian reptile populations via its  
92 impact on the quantity and distribution of food resources, or the abundance of predators (see  
93 Diele-Viegas and Rocha 2018 for a review). The trophic effects of climatic conditions have

94 been well studied in ecosystems characterized by resource pulses; for example, high rainfall  
95 regimes in certain arid or tropical environments favour greater prey abundance and thus have  
96 positive effects on the growth, reproduction, or survival of certain snake species (e.g., Ujvari  
97 et al. 2010; Meik et al. 2024). In temperate regions, climate change may also alter the prey  
98 community, with potentially variable effects on reptile demography between studies (Diele-  
99 Viegas and Rocha 2018). For example, in a viper population in Italy, whose phenology is  
100 highly dependent on ambient temperature, prey availability reflects local habitat variation  
101 rather than climatic conditions (Rugiero et al. 2012, 2013). In contrast, in another viper  
102 population in Sweden, an extreme summer climatic event caused a potential decline in  
103 resources that was associated with a loss of body condition and a reduction in future adult  
104 survival (Madsen et al. 2023). These trophic effects of climate change are likely to be more  
105 pronounced in reptiles with specialized diets and inflexible foraging behaviour (Ujvari et al.  
106 2011; Diele-Viegas and Rocha 2018).

107       Among non-avian reptiles, vipers rank among the most endangered groups, with 16% of  
108 species threatened compared to 8% of all reptiles' species (Böhm et al. 2013; Maritz et al.  
109 2016; Cox et al. 2022). Many snake populations are declining globally, primarily due to  
110 habitat loss or reduced prey availability (Reading et al. 2010; Luiselli et al. 2011; Böhm et al.  
111 2013). However, changes in climatic conditions can also drive long-term population declines  
112 (e.g., Shine and Mason 2004; Pomara et al. 2014; Madsen et al. 2023). Snakes exhibit  
113 ecological traits that are sensitive to climate change, with higher temperatures generally  
114 enhancing activity levels, accelerating gestation, and improving the quality of reproduction in  
115 temperate species (Lourdais et al. 2004; Moreno-Rueda et al. 2009; Le Galliard et al. 2012;  
116 Rugiero et al. 2013). On the other hand, winter and summer climatic conditions can have  
117 variable effects on annual survival rates (Altwegg et al. 2005; Pomara et al. 2014; Elmberg et  
118 al. 2024). Extreme climate events, especially those leading to water shortage, are also likely to

119 disrupt resource availability and reproductive success (Dezetter et al. 2021; Holden et al.  
120 2022; Madsen et al. 2023).

121 Here, we analysed over three decades of mark-recapture data from a population of the  
122 meadow viper (*Vipera ursinii ursinii*, Bonaparte 1835) to uncover patterns of temporal  
123 variation in reproductive traits, to identify the local climatic factors influencing these  
124 variations, and assess the potential buffering effects of life cycle on population growth rates.  
125 *Vipera u. ursinii* is a small viper with a fragmented distribution across medium-altitude  
126 mountain ranges in the northern Mediterranean basin. This species is listed on the IUCN Red  
127 List of threatened European species, although climate change is not currently identified as a  
128 primary threat (Ferchaud et al. 2011). Previous research on our study population has revealed  
129 that the meadow viper has a slow life history with a continuous growth throughout life, a  
130 sexual maturation at 3-5 years of age, a biennial breeding, and a high and stable annual  
131 subadult and adult survival (Baron et al., 1996, 2013; Tully et al., 2020). In our study  
132 population, the vipers primarily feed on large grasshoppers, which represents up to 99% of the  
133 diet during summer (Baron 1992). Although growth rates and some reproductive traits  
134 fluctuate from year to year, it is unclear whether this variability is linked to climatic  
135 conditions, or to what extent life history traits variability contribute to temporal variation in  
136 the population growth rate.

137 In this study, we quantified the effects of climatic variables related to the most relevant  
138 thermal and water constraints. Since the meadow viper is a capital breeder, alternating  
139 between breeding and non-breeding years (Baron et al. 2013; Tully et al. 2020), we tested for  
140 the effects of climatic condition during gestation, during the mating period prior to gestation,  
141 and during the preceding non-reproductive year. We next parametrized a finite stochastic  
142 integral projection model (Easterling et al. 2000; Vindenes et al. 2011; Jaffré and Le Galliard  
143 2016) to (1) quantify the demographic and environmental variances in population growth rate,

144 and (2) identify the vital rates most critical for population growth. Our analysis revealed  
145 distinct patterns of climate-reproduction relationships, but minimal environmental variation in  
146 population growth rate. Our findings suggest limited potential for direct effects of climate  
147 warming on the vulnerability of this population.

## 148 **Materials and methods**

### 149 **Study species and site**

150 The meadow viper *V. u. ursinii* is a small insectivorous viper inhabiting open and dry  
151 calcareous grasslands between 900 and 2 200 m a.s.l. in the northern Mediterranean basin.  
152 This study was carried out in Mont Ventoux population (1430 m altitude, 44°18'N, 5°26'E), a  
153 population occupying an area of 100 ha that is isolated from the nearest populations 45 km  
154 away. A four hectares study area has been monitored continuously from 1979 until 2014,  
155 when monitoring was halted due to lack of support and conflicts with local landowners. The  
156 area is divided into two contiguous study sites of approximately two hectares each, including  
157 a north-facing and mesophilic hillside (habitat A), and a south-facing and xerophilic hillside  
158 (habitat B). Small home ranges averaging 0.09 ha (Baron et al. 1996), together with the  
159 presence of a 10 m wide asphalt road separating the two sites, make movements of snakes  
160 between these two sites extremely rare (only two such movements were reported during this  
161 study). In this population, females become sexually mature at approximately 4-6 years of age.  
162 Adult males and adult females emerge around mid-April and early May respectively.  
163 Vitellogenesis begins after hibernation and lasts 4 to 8 weeks. Mating occurs during the last  
164 two weeks of May, soon followed by ovulation and fertilization, which occurs during the first  
165 week of June. Parturition takes place between mid-August and mid-September, depending on  
166 weather conditions. Hibernation begins in October.



**167 Demographic data collection**

168 Snakes were individually marked by scale clipping upon their first capture during 56 primary  
169 capture sessions between 1979 and 2014 (n=1346 captures, mean duration per session of 10  
170 days). Although scale clipping is highly reliable, we also recorded ventral and head scales to  
171 confirm the ventral scale clipping pattern. Primary capture sessions were carried out by 1-3  
172 people for 1-2 weeks twice a year, including one session during the mating season and before  
173 ovulation, and one session before the end of gestation. All spotted animals were captured,  
174 identified and measured (snout-vent length, SVL to the nearest mm and body mass to the  
175 nearest dg). Sexual maturity and reproductive status (non-reproductive, reproductive: post-  
176 ovulation, gravid or post-partum) of each female was assessed. During the second capture  
177 session, ova were counted by palpation of the abdominal cavity to provide an accurate  
178 estimate of litter size (Baron et al. 2013). Snakes were released at their capture site in the  
179 evening of the day of capture, or after parturition for gravid females (see below). All  
180 applicable institutional and/or national guidelines for animal care and use were followed.

181 In 1983-1988 and from 1994 onwards, we obtained data on reproductive output by  
182 keeping gravid females in the laboratory until they gave birth (498 offspring, 162 litters, 109  
183 mothers, 28 years). Gravid females were kept in individual rearing boxes (350 × 180 × 210  
184 mm) with a shelter, damp soil, free access to water and a heat source to allow the snakes to  
185 thermoregulate. Body mass was measured daily. Immediately after parturition, the number of  
186 undeveloped ova, dead embryos, stillborns and healthy offspring were counted to calculate  
187 litter size and litter success (all variables are precisely defined in Baron et al. 2013). On  
188 average, females were kept in the laboratory for 15 days ( $\pm$  10.7 SD, range = 0-46) prior to  
189 parturition, a short period of captivity that should not influence reproductive parameters. The  
190 gestation period was defined as the time between the date of ovulation (assumed to start on 10  
191 June based on pers. obs.) and the date of parturition. Newborns were measured for SVL and

192 body mass, and sexed by counting sub-caudal scales. Mothers were released with their  
193 offspring at the maternal capture site on average 11 days ( $\pm 7$  SD) after parturition. Data on  
194 survival and growth during the juvenile stage and data on intermittent reproduction and  
195 longevity have been reported elsewhere (Baron et al. 2010a, 2013; Tully et al. 2020).

## 196 **Climate data collection**

197 Temperature and rainfall data were recorded since June 1992 by Météo France at a non-  
198 automated weather station at the study site (Beaumont-Mont Serein, 1445 m a.s.l.,  
199 44°10'48"N, 5°15'18"E). To reconstruct time series of weather data during the entire time  
200 period of the census (1980-2014), we gathered temperature and rainfall data from an  
201 automated meteorological station located 30 km south-west of the study site (Carpentras, 99  
202 m a.s.l., 44°05'00"N, 5°03'30"E), and temperature, rainfall, global radiation and specific  
203 humidity data calculated for the study site by the Safran model of Météo France (Quintana-  
204 Seguí et al. 2008). The Carpentras station provides high quality and long term meteorological  
205 data on temperature and precipitation, but is located at a lower altitude than the study site. The  
206 Safran model is a gauge-based analytical meteorological system that provides reconstructed  
207 and robust weather data through interpolation methods at 8 km resolution in France for the  
208 period 1958-2014 (Vidal et al. 2010). We obtained daily data on precipitation (including  
209 snowfall), minimum and maximum air temperature, specific humidity, wind speed and global  
210 radiation for a grid cell centred on the study site. For this study, we calculated daily maximum  
211 temperature ( $^{\circ}\text{C}$ ), daily cumulative rainfall (mm), daily cumulative global radiation ( $\text{J}/\text{cm}^2$ )  
212 and daily mean of atmospheric specific humidity (g/kg) as climate variables (Appendix A).  
213 We chose these variables because they are relevant to the thermal and water biology of  
214 reptiles such as the meadow viper (Lourdais et al. 2004; Guillon et al. 2009; Le Galliard et al.  
215 2012), and may correlate with environmental constraints on basking time (low daily  
216 maximum temperatures and low global radiation) and environmental constraints on

217 evaporative water loss and water uptake (limited rainfall and low air specific humidity). For  
218 each climate variable and each study year, we calculated stage-specific weather data during  
219 the mating period (the three first weeks of May), the average gestation period (from the first  
220 week of June to the first week of September), and the non-reproductive period of the previous  
221 year (from the second week of June to the last week of September of the previous year). The  
222 non-reproductive period of the previous year was included to account for intermittent biennial  
223 reproduction and the capital breeding strategy of the species (Baron et al. 2013). In addition,  
224 we calculated the temperature conditions experienced during three consecutive gestation  
225 stages, namely early gestation (first week of June to first week of July), mid-gestation (first  
226 week of July to first week of August) and late gestation (first week of August to first week of  
227 September).

## 228 **Statistical analyses**

229 We first used mixed-effects models to investigate temporal variation (between years) and  
230 spatial variation (between sites A and B) in gestation length, total clutch size and clutch  
231 success (percentage of viable offspring in the clutch) controlling for body size, variation in  
232 clutch mass (including water and residual tissue from amnion and allantois) and variation in  
233 post-partum body condition (log-transformed body mass after parturition, controlling for log-  
234 transformed body size). We analysed clutch mass including post-partum body mass as a  
235 covariate, which amounts to examining variation in “relative clutch mas” (Van Dyke and  
236 Beaupre 2011). We also calculated mass change and body size growth of females during their  
237 non-reproductive years (57 observations, 35 females), as we have previously shown that  
238 females stop growing and lose significant body mass during the reproductive years (Baron et  
239 al. 2013). Models for for body mass change and body size growth included initial body mass  
240 and initial body size as covariates in the models, respectively, to account for the slowing of  
241 growth with age (Baron et al. 2010b). Inter-individual differences were also tested prior to full

242 model implementation, but we found that these were negligible compared to inter-annual  
243 differences so we did not include them in our final models. We also analysed spatial and  
244 temporal variation in offspring characteristics, including mass and body condition at birth.  
245 Body condition at birth was defined as the residual of a linear regression of body mass against  
246 SVL. Body mass was preferred to SVL for analyses of variation in offspring size because (1)  
247 offspring mass can be measured more accurately than SVL, (2) mass better reflects maternal  
248 energy allocation to the offspring than SVL, and (3) mass at birth is often used in studies of  
249 temporal variation in offspring fitness traits in reptiles (Baron et al. 2010a).

250 In all cases, we followed the methodology of Pinheiro and Bates (2000) for general  
251 linear models (normally distributed data) and of Bolker et al. (2009) for generalized linear  
252 models (binomially distributed data). In all models, habitat (site A vs. B) was included as a  
253 fixed effect and year was included as a random effect. We used a random intercept model,  
254 which assumes that years vary in the mean values of each response trait. We also checked for  
255 temporal autocorrelation by calculating the empirical autocorrelation function for the within-  
256 group residuals of the fitted models and found that temporal autocorrelation was negligible.  
257 For offspring traits, we included the random effect of litter identity, nested within birth year  
258 and habitat effects. Mixed models were fitted using the *lme* package (Pinheiro et al. 2022) in  
259 R 3.2.4 software (R Core Team 2020). Model assumptions (normality, homoscedasticity  
260 and/or overdispersion) were checked and met in all cases.

261 We first used these models to quantify variation between years and maternal identity,  
262 controlling for fixed effects of critical covariates (body size and habitat). Fixed effects were  
263 tested with conditional F-tests based on REML and random effects were tested with likelihood  
264 ratio tests. Initial models included all factors and model selection was performed backwards  
265 by removing non-significant terms until a minimum adequate model was obtained (all factors  
266  $p > 0.05$  removed). From the minimum adequate model, we calculated the ratio of annual

267 variation to the sum of annual and residual variation, hereafter referred to as relative temporal  
268 variation (RTV).

269 In a second step, we used the minimum adequate model as a starting point to search for  
270 the most influential weather covariates at each life stage. Following our investigation of all  
271 climate variables (see below), we tested for effects of temperature, global radiation and  
272 specific humidity calculated during the mating, gestation and non-reproductive periods on  
273 reproductive traits with a significant inter-annual variation (see below). We compared all  
274 models with additive effects of each covariate and therefore did not test for interactions or  
275 quadratic effects. We however checked graphically for the absence of quadratic effects of  
276 climatic conditions (results not shown). We compared the independent effects of temperature,  
277 global radiation and specific humidity to determine which weather variable was the best  
278 predictor of inter-annual variation. Where climatic conditions during gestation were retained  
279 in the best model, we next tested more specifically for the effects climatic conditions  
280 calculated during early (first month), mid (second month) or late (third month) gestation  
281 period. Models were compared by Akaike Information Criterion corrected for small sample  
282 size (AICc), Akaike's weight ( $w_i$ ) and evidence ratio (ER) using the *MuMin* (Multiple-Model  
283 Inference) package (MuMIn, Bartoń 2022). In addition, we calculated the marginal pseudo-R<sup>2</sup>  
284 (R<sup>2</sup>m) and the conditional pseudo-R<sup>2</sup> (R<sup>2</sup>c) for each mixed-effects model using the  
285 *r.squaredGLMM* function of the *MuMin* package (Nakagawa and Schielzeth 2013). The best  
286 set of models included all models within a cumulative Akaike's weight < 0.95, and the best  
287 models were considered to be those with an AICc difference with the best model < 2  
288 (Burnham and Anderson 1998, see Appendix B for a list of model selection tables). Relative  
289 variable importance was calculated as the sum of  $w_i$  of all models including the variable, and  
290 parameter estimates were estimated using a model averaging procedure (conditional average).  
291 Results are presented as mean  $\pm$  SE unless otherwise stated.

## 292 **Results**

### 293 **Climate variation**

294 Supplementary information on temporal variation and correlation patterns between climate  
295 variables are provided in Appendix A. The weather at the study site showed marked seasonal  
296 variation, with harsh thermal conditions for reptile activity from November to April (daily  
297 maximum temperatures around and below 5°C and daily minimum temperatures below 0°C),  
298 a short summer season from June to August (daily maximum temperatures above 15°C and  
299 daily minimum temperatures above 10°C), and heavy rainfall or snowfall from September to  
300 May (cumulative monthly rainfall or snowfall greater than 100 mm). The temperature and  
301 rainfall data collected at the study site since 1992 were highly correlated with those of the  
302 Safran model available on a long-term basis, allowing time series of temperature and rainfall  
303 conditions to be reconstructed for the entire duration of the population survey. There was a  
304 weak pattern of increasing daily maximum temperatures in late spring and early summer over  
305 time during the study, but not for average summer temperatures (see Appendix A and Figure  
306 A1). Global radiation increased significantly over time during the survey (Figure A1).  
307 Cumulative rainfall and air specific humidity showed no temporal trend. Independent of these  
308 trends, weather data showed strong inter-annual variation at all reproductive stages. As  
309 rainfall at the study site was less well predicted by the Safran data, and was also negatively  
310 correlated with global radiation and positively correlated with air specific humidity, we did  
311 not use rainfall data in our statistical models of life history variation in vipers.

### 312 **Life history variation**

313 Similar to previous findings (Baron et al. 2013; Tully et al. 2020), certain reproductive traits  
314 and body growth were significantly influenced by maternal body size and habitat (Table 1).  
315 Larger females produced larger litters, exhibited higher clutch success, and gave birth to

316 larger offspring. Additionally, females from the xerophilic habitat (Habitat B) displayed  
317 similar size-independent fecundity and reproductive effort to those of females from the  
318 mesophilic habitat (Habitat A). However, they exhibited lower post-parturition body  
319 condition, reduced offspring condition, and smaller body size growth and annual change than  
320 females from Habitat A. Moreover, we detected significant inter-annual variation in all  
321 demographic traits, except for total clutch size (Table 1). RTV was generally low for  
322 reproductive effort, where it was largely driven by a few years with unusually low  
323 reproductive effort and also for offspring mass. Intermediate levels were observed for clutch  
324 success, post-parturition body condition, offspring condition and body size growth. The  
325 highest RTV was recorded for gestation length and annual changes in body mass during non-  
326 reproductive years (detailed results provided in Table 1).

### 327 **Climate effects on reproduction and growth**

328 Our model selection procedure included 17 candidate models and one null model (the  
329 minimum adequate models shown in Table 1, see Appendix B for the full list of all models).  
330 We excluded from the set of candidate models some models with additive effects of global  
331 radiation variables due to strong collinearity between the variables (see Appendix A). The  
332 combined outcomes from our model selection procedures for gestation length (Table B1),  
333 clutch success (Table B2), relative clutch mass (Table B3), post-parturition body condition  
334 (Table B4) and offspring mass and condition (Tables B5 and B6) showed very small effects of  
335 specific humidity, moderate effects of global radiation and significant positive effects of air  
336 temperature.

337 The gestation length shortened significantly with increasing average temperatures  
338 during both the mating period ( $-1.46 \text{ days}/^{\circ}\text{C} \pm 0.48$ ,  $z = 2.92$ ,  $P = 0.003$ ) and gestation ( $-2.76$   
339  $\text{days}/^{\circ}\text{C} \pm 0.96$ ,  $z = 2.73$ ,  $P = 0.006$ ; Figure 1, Table B1), with relative importance ( $w$ ) of 0.94  
340 and 0.93 respectively. It also tended to shorten with hotter thermal conditions during the

341 previous non-reproductive season ( $w = 0.46$ ). The best model, which included average  
342 temperature during gestation (Table B1,  $w_i = 0.49$ ), outperformed the three other gestation-  
343 stage dependent models. The second-best model included effects of temperature during early  
344 gestation ( $w_i = 0.45$ ). Upon re-analysing the data excluding the coldest summer season, which  
345 saw a high number of clutch failures (Figure 1A), we obtained similar results, with even  
346 stronger effects of temperatures (gestation:  $-3.75 \text{ days}/^\circ\text{C} \pm 0.79$ ,  $z = 4.5$ ,  $P < 0.0001$ ; mating:  
347  $-1.57 \text{ days}/^\circ\text{C} \pm 0.38$ ,  $z = 3.92$ ,  $P < 0.0001$ ).

348 Climatic conditions explained little variation in relative clutch mass, with all covariates  
349 showing relative importance below 0.25 (Table B2). The most influential covariate was global  
350 radiation during the previous summer season, and it negatively affected relative clutch mass ( $-$   
351  $0.009 \pm 0.004$ ,  $z = 1.97$ ,  $P = 0.05$ , result not shown). In sharp contrast, thermal conditions  
352 were major drivers of inter-annual variation in post-parturition body condition (Table B3).  
353 Average temperature during gestation was the most influential variable ( $w = 0.66$ ), followed  
354 by average temperature during the previous year (positive effect,  $w = 0.48$ ) and during the  
355 mating period (negative effect,  $w = 0.45$ ). Post-parturition body condition increased with  
356 rising average temperatures during gestation ( $0.031 \pm 0.014 \text{ g}/^\circ\text{C}$ ,  $z = 2.1$ ,  $P = 0.04$ ; Figure  
357 2A). Based on additional analyses, we found that late gestation thermal conditions were the  
358 primary driver of this pattern ( $w_i = 0.65$ ;  $0.024 \pm 0.009 \text{ g}/^\circ\text{C}$ ,  $z = 2.4$ ,  $P = 0.01$ ).

359 Clutch success increased on average with higher mean temperature during gestation  
360 (logit regression:  $0.45 \pm 0.21$ ,  $z = 2.1$ ,  $P = 0.04$ ; Figure 2B, Table B4,  $w = 0.51$ ), and was  
361 moderately influenced by temperature and humidity during the previous non-reproductive  
362 season ( $w = 0.34$  and  $w = 0.21$ , respectively). Additional analyses indicated that the model  
363 with average temperature during gestation fitted equally well the data than a model with  
364 average temperature during mid-gestation ( $w_i = 0.49$  and  $w_i = 0.45$ , respectively). Climatic  
365 conditions did not significantly influence offspring mass at birth (Table B5, all  $w < 0.22$ ).



366 However, both mean global radiation ( $w = 0.54, 0.0006 \pm 0.0002, z = 2.9, P = 0.004$ ) and  
367 temperature during gestation ( $w = 0.24, 0.05 \pm 0.02, z = 2.1, P = 0.04$ ) were positively  
368 correlated with offspring condition at birth. Lastly, annual changes in body mass and body  
369 growth during the non-reproductive years were unaffected by climatic conditions during the  
370 active summer season (all  $w < 0.23$ , not shown).

## 371 **Population growth analysis**

372 We fitted a finite stochastic integral projection model (IPM) to the meadow viper life cycle  
373 and analysed the stochastic IPM using the methodology described in Jaffré and Le Galliard  
374 (2016, see Appendix C). The deterministic IPM predicted a substantial annual population  
375 decline of approximately 12% (), consistent with previous findings using a matrix  
376 population model (Baron et al. 1996). Components of stochastic growth included a significant  
377 demographic variance () and a very weak environmental variance ()  
378 ), indicating that the iteroparous life cycle with a constant adult survival and breeding  
379 frequency buffered the population against temporal variation in growth, juvenile survival and  
380 reproduction. In addition, an analysis of the elasticity of the deterministic growth rate to  
381 changes in the kernel function of the IPM revealed (1) very low sensitivity to changes in adult  
382 reproduction, (2) strong sensitivity to the survival and growth of juveniles and immature  
383 females, and (3) moderate sensitivity to the survival and growth of older sexually mature  
384 individuals (Figure 3A). Using a realistic starting population size of 100 vipers, the stochastic  
385 model predicted a median extinction time of 25–30 years for this population, with complete  
386 extirpation of the population likely within less than a century (Figure 3B). Given the weak  
387 contribution of reproduction to growth rate, climate warming effects on reproductive traits is  
388 unlikely to significantly alter this extinction trajectory.

## 389 Discussion

390 Our analysis complements previous research on body growth rate strategies, survival,  
391 intermittent reproduction, and ageing in the same meadow viper population (Baron et al.  
392 2010a, b, 2013; Tully et al. 2020). In particular, our findings reveal that fecundity and  
393 reproductive effort are largely buffered against environmental variation and are primarily  
394 dictated by female body size. Female fecundity is strongly constrained by body size and  
395 exhibit little to no variability among years. Similarly, reproductive effort, defined as the  
396 relative mass lost during gestation (Bonnet et al. 2002; Van Dyke and Beaupre 2011), shows  
397 minimal inter-annual variation, except for one year marked by a notably poor reproduction  
398 without any clear climatic explanation (Table 1). These results contrast with the pronounced  
399 year-to-year variation in reproductive effort and frequency seen in other snake species, which  
400 often occurs in response to changes in food availability. For example, some snakes feed on  
401 prey whose populations fluctuate dramatically due to changes in rainfall patterns, leading to  
402 pronounced reproductive variability in those species (Madsen and Shine 1999; Lourdaï et al.  
403 2002; Ujvari et al. 2010). This discrepancy likely stems from the meadow viper's unique  
404 semi-insectivorous diet, which consists almost exclusively of crickets and grasshoppers. At  
405 our study site, these insects are both diversified and abundant during the summer activity  
406 season (Baron 1992), indicating that food resources are unlikely to be limiting factors and this  
407 stable supply of food may contribute to the low variability in reproductive traits observed in  
408 this population.

409 In contrast to fecundity and reproductive effort, we observed a strong temporal  
410 variability in annual growth rates during non-reproductive years, as well as in traits related to  
411 gestation speed, body condition, and reproduction quality. These variations were either  
412 unrelated to climatic conditions even during extreme climate years, such as body growth of  
413 adult females and body mass of young at birth, or were linearly correlated with ambient

414 temperature rather than air humidity (which indicates desiccation risk due to evaporative  
415 water loss) or global radiation (which indicates both thermoregulatory conditions and  
416 rainfall). In general, warmer ambient conditions are more favourable for reproduction by  
417 accelerating gestation, improving post-parturition condition, and ensuring better offspring  
418 condition at birth.

419       The flexibility of gestation length and post-partum body condition, which is driven by  
420 warmer temperatures, is not surprising but demonstrates that reproductive traits can be  
421 flexible without significantly affecting reproductive effort or frequency. This should be  
422 understood in the light of the meadow viper's bioenergetic strategy of biennial reproduction  
423 and resource capitalization (Bonnet et al. 1998; Baron et al. 2013; Huang et al. 2013). Females  
424 alternate between breeding years – marked by a halt in structural growth and depletion of  
425 body reserves – and non-breeding years, during which growth resumes and body condition is  
426 restored to a threshold necessary for future reproduction (Baron et al. 2013). Our findings  
427 suggest that warmer ambient temperatures during gestation accelerate reserve capitalization  
428 dynamics but do not alter the biennial threshold for reproduction (Madsen and Shine 1999;  
429 Baron et al. 2013; Huang et al. 2013; Capula et al. 2016). These effects on reserve dynamics  
430 are unlikely to influence future survival, as survival is not linked to post-partum body  
431 condition (Baron et al. 2013).

432       In contrast, lowland populations of the asp viper (*Vipera aspis*) exhibit a more  
433 semelparous reproductive strategy, where higher gestation temperatures result in poorer body  
434 condition by the end of gestation (Lourdais et al. 2002, 2004). One explanation for this  
435 difference is that meadow vipers are able to feed during gestation, unlike carnivorous vipers  
436 that are anorexic due to the challenge of consuming large preys while gravid (Bonnet et al.  
437 2002; Baron et al. 2013). Thus, we hypothesize that warmer thermal conditions during  
438 gestation may favour maternal feeding in meadow vipers, enabling them to recoup the energy

439 expenditure of viviparity more efficiently. Our analysis further suggests that thermal  
440 conditions toward the end of gestation, during late summer, are particularly important for  
441 maintaining female energy balance and reserve dynamics.

442       The impact of ambient temperatures on the speed of gestation reflects a general effect of  
443 thermal conditions on the rate of biological processes in ectotherms, even including years of  
444 heat waves that might have slowed gestation by altering daily activities during the hottest  
445 times of the day. Such phenological changes are common in many temperate non-avian  
446 reptiles (Lourdais et al. 2004; Moreno-Rueda et al. 2009; Rugiero et al. 2013; Diele-Viegas  
447 and Rocha 2018). Here, it corresponded to a shift of about three weeks between the coldest  
448 and warmest years, a pattern very similar to that observed in the asp viper (Lourdais et al.  
449 2004; Lориoux et al. 2013). In this congeneric species, thermal conditions during mid-  
450 gestation are more strongly correlated with gestation length, whereas our study suggests that it  
451 is the average temperature over the entire gestation that is most important. Thus, generally  
452 warmer summer conditions, in early, mid or late gestation, will accelerate gestation similarly.  
453 The demographic consequences of shifts in reproductive phenology are likely to be small in  
454 meadow vipers, as the date of parturition does not affect the future maternal or neonate  
455 survival, growth and sexual maturation (Baron et al. 2010a, 2013).

456       A notable demographic effect of climatic conditions is a positive correlation between  
457 average temperatures during gestation and reproductive success, measured by the proportion  
458 of viable neonates in the litter. This trend holds even when accounting for data from the  
459 extreme heat wave of 2003, when summer temperatures were unusually high and could have  
460 imposed sublethal stress on reproduction. Overall, reproductive success is typically high in  
461 this species, but cooler years are associated with an increased frequency of developmental  
462 failures and prolonged, incomplete gestations. This reflects the importance of optimal  
463 thermoregulation during gestation for embryo development and viability in vipers (Lориoux et

464 al. 2013). Altogether, we found that some reproductive traits in this population are currently  
465 constrained by cold thermal conditions. Thus, assuming other factors remain constant, climate  
466 warming is likely to provide short-term benefits to this population, a pattern that may apply  
467 more generally to high-altitude reptiles, whose energy budgets are constrained by colder and  
468 shorter activity seasons (Huang et al. 2013). Comparative data and mechanistic models could  
469 be used to determine whether this trend is consistent across the species' range. For example,  
470 similar studies could examine populations in southern regions or at lower elevations, which  
471 are closer to the species' upper thermal limits, to see if they respond differently to climate  
472 warming.

473 We integrated the effects of the different vital rates and their temporal variability on  
474 long-run growth rate and population dynamics using the Integral Projection Model framework  
475 (Easterling et al. 2000; Ellner and Rees 2006; Vindenes et al. 2011). The motivation for  
476 building this model is the existence of a high variability in body size, with pervasive effects of  
477 individual size on growth, sexual maturation, fecundity, or the size of newborns at birth. Our  
478 analysis of an individual-based version of the model allows for both demographic fluctuations  
479 generated by random, identically and independently distributed temporal variability in each  
480 vital rate (i.e., environmental stochasticity) and random inter-individual variability in the  
481 demographic processes of growth, survival, and reproduction (i.e., demographic stochasticity).  
482 This shows that temporal fluctuations in the stochastic growth rate are negligible compared to  
483 random inter-individual demographic fluctuations in the meadow viper. Assuming that the  
484 average stochastic growth rate scales like  ~~$\lambda^{-1}$~~  (Vindenes et al. 2011;  
485 Jaffré and Le Galliard 2016), the population size at which the contribution of demographic  
486 variance equals contribution of environmental variance would be approximately 1,000  
487 females in this population, well above the estimated population size of a few hundred vipers  
488 (Baron et al. 1996). This result is expected for long-lived species with low temporal

489 variability in adult survival and an iteroparous reproductive mode that spreads fecundity over  
490 several years (Hilde et al. 2020). As a result, stochastic population dynamics are dominated  
491 first by a significant deterministic decay term that predicts rapid decline, and second by a  
492 strong demographic stochasticity term that accelerates this deterministic decline in small  
493 populations. Instead, climate variability is unlikely to slow down or accelerate average  
494 stochastic growth. These predictions confirm previous estimates from matrix population  
495 models and are consistent with the population decline observed at this isolated site (Ferrière et  
496 al. 1996). Climate warming could still benefit the population by improving clutch success, a  
497 vital rate positively related to population growth. Yet, average clutch success is already high  
498 (around 80%) and our analysis shows that the population growth rate is not as sensitive to  
499 components of the life cycle related to reproduction as it is to those related to growth and  
500 survival.

501       Our study has implications for assessing the conservation status of the meadow viper  
502 and designing measures to protect at least the Mont Ventoux population in France. We show  
503 that temporal variability and climatic conditions currently have a limited demographic impact  
504 on this population, with warmer temperatures even providing beneficial for breeding. Thus,  
505 climate change should not be considered an immediate threat to this population. However,  
506 continued monitoring is essential to track the potential effects of more extreme weather  
507 conditions, such as summer intense and prolonged hot and dry periods (Madsen et al. 2023).  
508 Future assessments should also consider indirect threats posed by climate warming, such as  
509 the upward migration of lowland species that could outcompete or prey on meadow vipers, as  
510 well as long-term changes in vegetation and habitat. Meanwhile, our analysis underlines the  
511 urgent need for strong conservation measures to prevent the expected rapid population of the  
512 Mont Ventoux meadow viper. The population's deterministic growth is low, and reversing the  
513 decline will require joint improvements of several critical life history traits such as growth and

514 survival. Previous research found that growth and late-life survival are enhanced in more  
515 humid microhabitats (Tully et al. 2020), suggesting that effective conservation actions could  
516 include habitat restoration. Strict protection measures to decrease disturbance and mortality  
517 could also be adopted. These could include physical barriers, clear signage, and active  
518 surveillance to safeguard the population.

## 519 **Acknowledgements**

520 We are grateful to DIREN PACA and MEEDDAT for providing capture permits  
521 (08/004/DEROG) during our fieldwork and to the many workers who helped to collect data in  
522 the field.

## 523 **Declarations**

524 **Funding.** This research has been partly supported by the Centre National de la Recherche  
525 Scientifique and by the Agence Nationale de la Recherche program 07-JCJC-0120. **Conflicts**  
526 **of interest.** Not applicable. **Ethics approval.** Ethics approval was not required for this study  
527 according to local legislation. **Consent to participate.** Not applicable. **Consent for**  
528 **publication.** Not applicable. **Availability of data and code.** The data and codes were  
529 deposited in Zenodo under the reference number DOI: 10.5281/zenodo.10219671.

## 530 **Supporting Information**

531 Supporting Information is available for this article online: Appendix A. Climate variability;  
532 Appendix B. Model selection tables; Appendix C. Integral projection model

533 **Literature cited**

- Altwegg R, Dummermuth S, Anholt BR, Flatt T (2005) Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos* 110:55–66. <https://doi.org/10.1111/j.0030-1299.2001.13723.x>
- Baron J-P (1992) Régime et cycles alimentaires de la vipère d’Orsini (*Vipera ursinii* Bonaparte 1835) au Mont Ventoux, France. *Rev Ecol Terre Vie* 47:287–311. <https://doi.org/10.3406/revec.1992.2408>
- Baron J-P, Ferrière R, Clobert J, Saint Girons H (1996) Stratégie démographique de *Vipera ursinii* au Mont-Ventoux. *Comptes Rendus Académie Sci Paris* 319:57–69
- Baron J-P, Le Galliard J-F, Tully T, Ferrière R (2013) Intermittent breeding and the dynamics of resource allocation to growth, reproduction and survival. *Funct Ecol* 27:173–183. <https://doi.org/10.1111/1365-2435.12023>
- Baron J-P, Le Galliard J-F, Tully T, Ferrière R (2010a) Cohort variation in offspring growth and survival: prenatal and postnatal factors in a late-maturing viviparous snake. *J Anim Ecol* 79:640–649. <https://doi.org/10.1111/j.1365-2656.2010.01661.x>
- Baron J-P, Tully T, Le Galliard J-F (2010b) Sex-specific fitness returns are too weak to select for non random patterns of sex allocation in a viviparous snake. *Oecologia* 164:369–378. <https://doi.org/10.1007/s00442-010-1660-y>
- Bartoń K (2022) MuMIn: Multi-Model Inference
- Böhm M, Collen B, Baillie JEM, et al (2013) The conservation status of the world’s reptiles. *Biol Conserv* 157:372–385. <https://doi.org/10.1016/j.biocon.2012.07.015>
- Bolker BM, Brooks ME, Clark CJ, et al (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Bonnet X, Bradshaw D, Shine R (1998) Capital versus income breeding: an ectothermic perspective. *Oikos* 83:333–342. <https://doi.org/10.2307/3546846>
- Bonnet X, Lourdais O, Shine R, Naulleau G (2002) Reproduction in a typical capital breeder: costs, currencies and complications in the aspic viper. *Ecology* 83:2124–2135. [https://doi.org/10.1890/0012-9658\(2002\)083\[2124:RIATCB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2124:RIATCB]2.0.CO;2)
- Brodie JF, Post ES, Doak DF (2013) *Wildlife Conservation in a Changing Climate*. University of Chicago Press
- Burnham KP, Anderson DR (1998) *Model selection and inference: a practical information-theoretical approach*. Springer Verlag, New York
- Capula M, Rugiero L, Capizzi D, et al (2016) Long-term, climate-change-related shifts in feeding frequencies of a Mediterranean snake population. *Ecol Res* 31:49–55. <https://doi.org/10.1007/s11284-015-1312-0>



- Ceballos G, Ehrlich PR, Raven PH (2020) Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc Natl Acad Sci* 117:13596–13602. <https://doi.org/10.1073/pnas.1922686117>
- Cox N, Young BE, Bowles P, et al (2022) A global reptile assessment highlights shared conservation needs of tetrapods. *Nature* 605:285–290. <https://doi.org/10.1038/s41586-022-04664-7>
- Dezetter M, Le Galliard JF, Guiller G, et al (2021) Water deprivation compromises maternal physiology and reproductive success in a cold and wet adapted snake *Vipera berus*. *Conserv Physiol* 9:. <https://doi.org/10.1093/conphys/coab071>
- Diele-Viegas LM, Figueroa RT, Vilela B, Rocha CFD (2020) Are reptiles toast? A worldwide evaluation of Lepidosauria vulnerability to climate change. *Clim Change* 159:581–599. <https://doi.org/10.1007/s10584-020-02687-5>
- Diele-Viegas LM, Rocha CFD (2018) Unraveling the influences of climate change in Lepidosauria (Reptilia). *J Therm Biol* 78:401–414. <https://doi.org/10.1016/j.jtherbio.2018.11.005>
- Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708. [https://doi.org/10.1890/0012-9658\(2000\)081\[0694:SSSAAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2)
- Ellner SP, Rees M (2006) Integral projection models for species with complex demography. *Am Nat* 167:410–428. <https://doi.org/10.1086/499438>
- Elmberg J, Palmheden L, Edelstam C, et al (2024) Climate change-induced shifts in survival and size of the worlds' northernmost oviparous snake: A 68-year study. *PLOS ONE* 19:e0300363. <https://doi.org/10.1371/journal.pone.0300363>
- Falaschi M, Manenti R, Thuiller W, Ficetola GF (2019) Continental-scale determinants of population trends in European amphibians and reptiles. *Glob Change Biol* 25:3504–3515. <https://doi.org/10.1111/gcb.14739>
- Ferchaud AL, Lyet A, Cheylan M, et al (2011) High genetic differentiation among French populations of the Orsini's viper (*Vipera ursinii ursinii*) based on mitochondrial and microsatellite data: implications for conservation management. *J Hered* 102:67–78. <https://doi.org/10.1093/jhered/esq098>
- Ferrière R, Sarrazin F, Legendre S, Baron J-P (1996) Matrix population models applied to viability analysis and conservation: theory and practice with ULM software. *Acta Oecologica* 17:629–656
- Gibbons JW, Scott DE, Ryan TJ, et al (2000) The global decline of reptiles, Deja Vu amphibians. *Bioscience* 50:653–666. [https://doi.org/10.1641/0006-3568\(2000\)050\[0653:TGDORD\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2)
- Guillon M, Guiller G, DeNardo DF, Lourdais O (2009) Microclimate preferences correlate with contrasted evaporative water loss in parapatric vipers at their contact zone. *Can J Zool* 92:81–86. <https://doi.org/10.1139/cjz-2013-0189>

- Hilde CH, Gamelon M, Sæther B-E, et al (2020) The Demographic Buffering Hypothesis: Evidence and Challenges. *Trends Ecol Evol* 35:523–538. <https://doi.org/10.1016/j.tree.2020.02.004>
- Holden KG, Gangloff EJ, Miller DAW, et al (2022) Over a decade of field physiology reveals life-history specific strategies to drought in garter snakes (*Thamnophis legans*). *Proc R Soc B Biol Sci* 289:20212187. <https://doi.org/10.1098/rspb.2021.2187>
- Huang S-P, Chiou C-R, Lin T-E, et al (2013) Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Funct Ecol* 27:446–458. <https://doi.org/10.1111/1365-2435.12040>
- Huey RB, Kearney MR, Krockenberger A, et al (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos Trans R Soc B Biol Sci* 367:1665–1679. <https://doi.org/10.1098/rstb.2012.0005>
- Jaffré M, Le Galliard J-F (2016) Population viability analysis of plant and animal populations with stochastic integral projection models. *Oecologia* 182:1031–1043. <https://doi.org/10.1007/s00442-016-3704-4>
- Kearney M, Porter WP (2004) Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131. <https://doi.org/10.1890/03-0820>
- Kingsolver JG, Diamond SE, Buckley LB (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct Ecol* 27:1415–1423. <https://doi.org/10.1111/1365-2435.12145>
- Le Galliard J-F, Massot M, Baron J-P, Clobert J (2012) Ecological effects of climate change on European reptiles. In: Brodie JF, Post E, Doak D (eds) *Wildlife conservation in a changing climate*. University of Chicago Press
- Lorioux S, Vaugoyeau M, DeNardo DF, et al (2013) Stage Dependence of Phenotypical and Phenological Maternal Effects: Insight into Squamate Reptile Reproductive Strategies. *Am Nat* 182:223–233. <https://doi.org/10.1086/670809>
- Lourdais O, Bonnet X, Guillon M, Naulleau G (2004) Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos* 104:551–560. <https://doi.org/10.1111/j.0030-1299.2004.12961.x>
- Lourdais O, Bonnet X, Shine R, et al (2002) Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *J Anim Ecol* 71:470–479. <https://doi.org/10.1046/j.1365-2656.2002.00612.x>
- Luiselli L, Madsen T, Capizzi D, et al (2011) Long-term population dynamics in a Mediterranean aquatic snake. *Ecol Res* 26:745–753. <https://doi.org/10.1007/s11284-011-0828-1>
- Madsen T, Loman J, Bauwens D, et al (2023) The impact of an extreme climatic event on adder (*Vipera berus*) demography in southern Sweden. *Biol J Linn Soc* 138:282–288. <https://doi.org/10.1093/biolinnean/blac147>

- Madsen T, Shine R (1999) The adjustment of reproductive threshold to prey abundance in a capital breeder. *J Anim Ecol* 68:571–580. <https://doi.org/10.1046/j.1365-2656.1999.00306.x>
- Maritz B, Penner J, Martins M, et al (2016) Identifying global priorities for the conservation of vipers. *Biol Conserv* 204:94–102. <https://doi.org/10.1016/j.biocon.2016.05.004>
- McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. *Proc Natl Acad Sci* 99:6070–6074. <https://doi.org/10.1073/pnas.052131199>
- Meik JM, Watson JA, Schield DR, et al (2024) Climatic temperature and precipitation jointly influence body size in species of western rattlesnakes. *R Soc Open Sci* 11:240345. <https://doi.org/10.1098/rsos.240345>
- Miller DA, Clark WR, Arnold SJ, Bronikowski AM (2011) Stochastic population dynamics in populations of western terrestrial garter snakes with divergent life histories. *Ecology* 92:1658–1671. <https://doi.org/10.1890/10-1438.1>
- Moreno-Rueda G, Pleguezuelos JM, Alaminos E (2009) Climate warming and activity period extension in the Mediterranean snake *Malpolon monspessulanus*. *Clim Change* 92:235–242. <https://doi.org/10.1007/s10584-008-9469-y>
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Pinheiro JC, Bates D, R Core Team (2022) *nlme: Linear and Nonlinear Mixed Effects Models*
- Pinheiro JC, Bates DM (2000) *Mixed-effect models in S and S-plus*. Springer, New York
- Pomara LY, LeDee OE, Martin KJ, Zuckerberg B (2014) Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. *Glob Change Biol* 20:2087–2099. <https://doi.org/10.1111/gcb.12510>
- Quintana-Seguí P, Le Moigne P, Durand Y, et al (2008) Analysis of near-Surface atmospheric variables: validation of the SAFRAN analysis over France. *J Appl Meteorol Climatol* 47:92–107. <https://doi.org/10.1175/2007JAMC1636.1>
- R Core Team (2020) *R: A Language and Environment for Statistical Computing*
- Reading CJ, Luiselli LM, Akani GC, et al (2010) Are snake populations in widespread decline? *Biol Lett* 6:777–780. <https://doi.org/10.1098/rsbl.2010.0373>
- Rodríguez-Caro RC, Capdevila P, Graciá E, et al (2021) The limits of demographic buffering in coping with environmental variation. *Oikos* 130:1346–1358. <https://doi.org/10.1111/oik.08343>
- Rugiero L, Milana G, Capula M, et al (2012) Long term variations in small mammal composition of a snake diet do not mirror climate change trends. *Acta Oecologica* 43:158–164. <https://doi.org/10.1016/j.actao.2012.07.002>

- Rugiero L, Milana G, Petrozzi F, et al (2013) Climate-change-related shifts in annual phenology of a temperate snake during the last 20 years. *Acta Oecologica* 51:42–48. <https://doi.org/10.1016/j.actao.2013.05.005>
- Rutschmann A, Perry C, Le Galliard J-F, et al (2024) Ecological responses of squamate reptiles to nocturnal warming. *Biol Rev* 99:598–621. <https://doi.org/10.1111/brv.13037>
- Shine R (2003) Reproductive strategies in snakes. *Proc R Soc Lond B* 270:995–1004. <https://doi.org/10.1098/rspb.2002.2307>
- Shine R (2005) Life-history evolution in reptiles. *Annu Rev Ecol Syst* 36:23–46. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152631>
- Shine R, Mason RT (2004) Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). *Biol Conserv* 120:201–210. <https://doi.org/10.1016/j.biocon.2004.02.014>
- Sinervo B, Mendez-de-la-Cruz F, Miles DB, et al (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899. <https://doi.org/10.1126/science.1184695>
- Sunday JM, Bates AE, Kearney MR, et al (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci* 111:5610–5615. <https://doi.org/10.1073/pnas.1316145111>
- Tully T, Galliard J-FL, Baron J-P (2020) Micro-geographic shift between negligible and actuarial senescence in a wild snake. *J Anim Ecol* 89:2704–2716. <https://doi.org/10.1111/1365-2656.13317>
- Ujvari B, Andersson S, Brown G, et al (2010) Climate-driven impacts of prey abundance on the population structure of a tropical aquatic predator. *Oikos* 119:188–196. <https://doi.org/10.1111/j.1600-0706.2009.17795.x>
- Ujvari B, Shine R, Madsen T (2011) How well do predators adjust to climate-mediated shifts in prey distribution? A study on Australian water pythons. *Ecology* 92:777–783. <https://doi.org/10.1890/10-1471.1>
- Urban MC (2015) Accelerating extinction risk from climate change. *Science* 348:571–573. <https://doi.org/10.1126/science.aaa4984>
- Van Dyke JU, Beaupre SJ (2011) Bioenergetic components of reproductive effort in viviparous snakes: costs of vitellogenesis exceed costs of pregnancy. *Comp Biochem Physiol -Mol Integr Physiol* 160:504–515. <https://doi.org/10.1016/j.cbpa.2011.08.011>
- Vidal J-P, Martin E, Franchistéguy L, et al (2010) A 50-year high-resolution atmospheric reanalysis over France with the Safran system. *Int J Climatol* 30:1627–1644. <https://doi.org/10.1002/joc.2003>
- Vindenes Y, Engen S, Saether BE (2011) Integral projection models for finite populations in a stochastic environment. *Ecology* 92:1146–1156. <https://doi.org/10.1890/10-0500.1>

- Warret Rodrigues C, Angin B, Besnard A (2021) Favoring recruitment as a conservation strategy to improve the resilience of long-lived reptile populations: Insights from a population viability analysis. *Ecol Evol* 11:13068–13080. <https://doi.org/10.1002/ece3.8021>
- Williams SE, Shoo LP, Isaac JL, et al (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLOS Biol* 6:e325. <https://doi.org/10.1371/journal.pbio.0060325>
- Winter M, Fiedler W, Hochachka WM, et al (2016) Patterns and biases in climate change research on amphibians and reptiles: a systematic review. *R Soc Open Sci* 3:160158. <https://doi.org/10.1098/rsos.160158>

534 **Figure legends**

535 **Figure 1.** Relationship between mean daily maximum temperatures during gestation (red) and  
536 during the mating season (green) and the gestation length, calculated as the difference  
537 between the parturition date and 10 June, for female meadow vipers at Mont Ventoux, France.  
538 Regression lines and confidence bands from the best model in Table B1 are plotted. Note that  
539 a cold summer (lowest values of the red data points) is associated with bimodal parturition  
540 dates due to reproductive failure (abortions) in several gravid females.

541  
542 **Figure 2.** Relationship between mean daily maximum temperatures during gestation and post-  
543 partum body condition (residual of a regression between body mass and body size, A) or  
544 clutch success (proportion of live newborns in a clutch, B) for female meadow vipers at Mont  
545 Ventoux, France. Regression lines and confidence bands from the best models in Tables B3  
546 and B4 are plotted in panels A and B, respectively. In panel B, the size of the data points is  
547 proportional to the total clutch size, which ranges from 2 to 8.

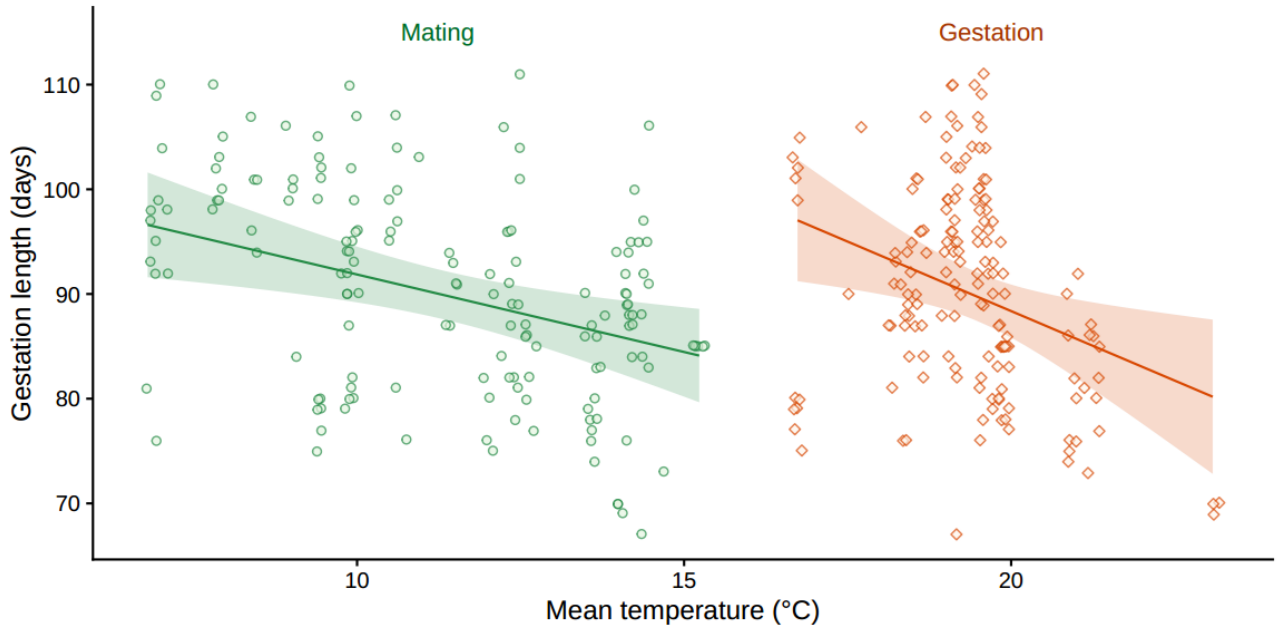
548  
549 **Figure 3.** Population viability analysis using an integration projection model (IPM) of the  
550 female component of the Mont Ventoux population. A. Elasticity surfaces representing the  
551 relative sensitivities of the deterministic growth rate to changes in the kernel function. B.  
552 Population viability analysis using a diffusion approximation and simulations of the IBM  
553 starting with 100 females randomly drawn from the equilibrium population structure of the  
554 deterministic model in the mean environment. Data shown are cumulative quasi-extinction  
555 risk during the first 50 years of the simulation for 50,000 population trajectories and three  
556 quasi-extinction thresholds ( $N=1$ , equivalent to true extinction,  $N=4$  and  $N=10$ ).

557 **Figure 1**

558

559

560



561

562

563

564

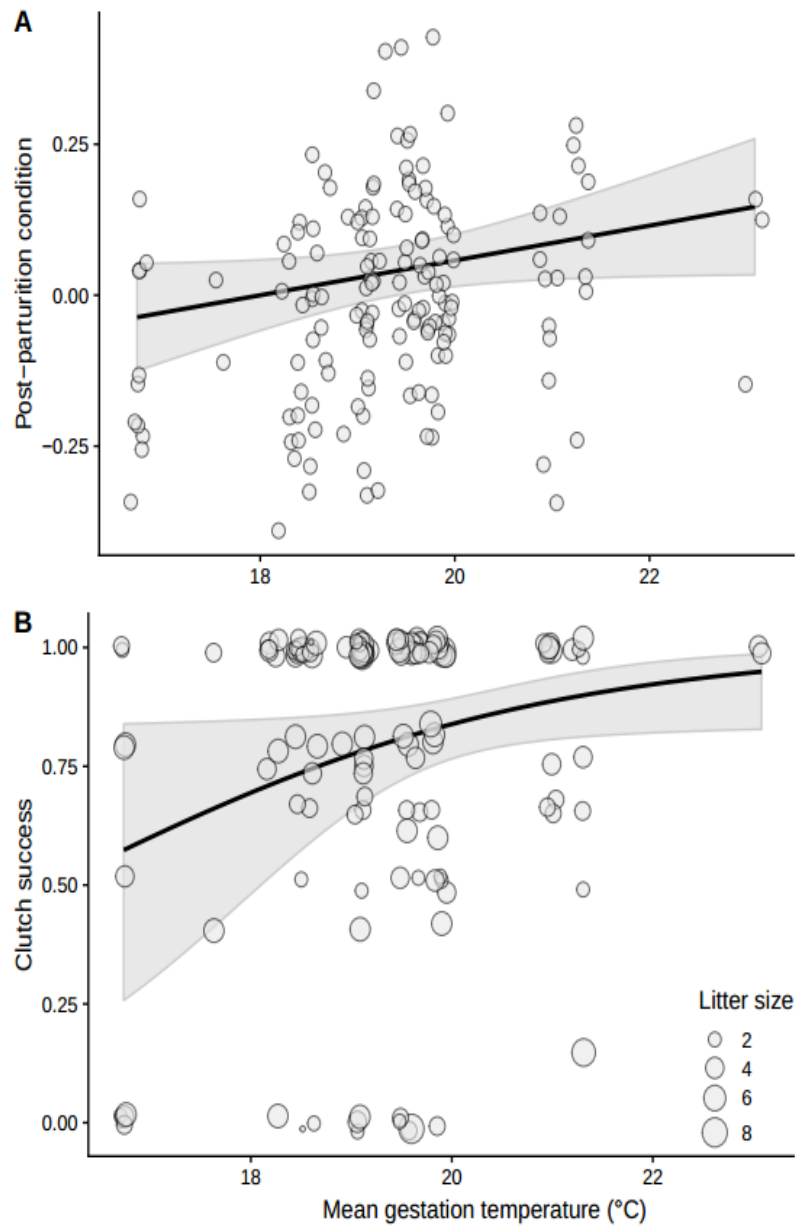
565

566

567 **Figure 2**

568

569



570



571 **Figure 3**

572

573

574

575

576

577

578

579

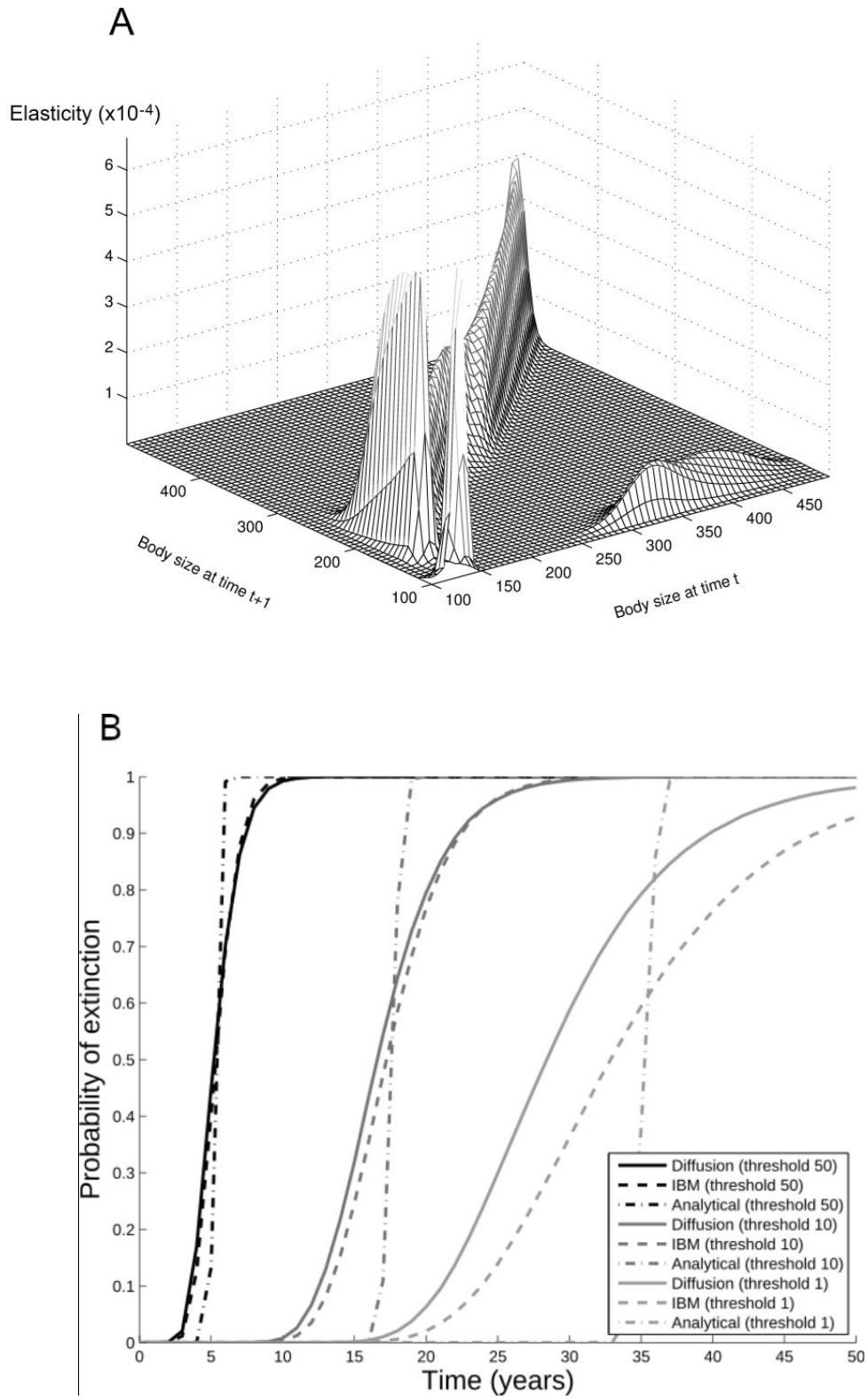
580

581

582

583

584



585 **Tables**

586 **Table 1.** Temporal variation in demographic parameters within the study population of the  
 587 meadow viper at Mont Ventoux, France. Results shown are number of years ( $N$ ), sample size  
 588 ( $n$ ), mean ( $\pm$  standard deviation for normal distribution and with 95% CI otherwise), best  
 589 statistical model from a full model including effects of body size, zone and a random year  
 590 effects, and the relative temporal variation (RTV). RTV measures the proportion of inter-  
 591 individual variation caused by yearly variation, and was obtained from variance components  
 592 of the best model.

Demographic parameter	$N$	$n$	Mean	Best model	RTV
<i>Reproductive traits</i>					
Gestation length*	28	159	90.4 $\pm$ 9.81	Year: $\chi^2 = 44.73$ , $P < 0.001$	0.51
Total clutch size	33	220	4.81 $\pm$ 1.31	SVL: $F_{1,186} = 58.2$ , $P < 0.0001$ Year: $\chi^2 = 0.001$ , $P = 0.97$	0.001
Clutch success (%)	27	155	0.79 [0.76, 0.82]	SVL: $z = -2.01$ , $P = 0.045$ Year: $\chi^2 = 107.2$ , $df = 26$ , $P < 0.0001$	0.25
Relative clutch mass (g)	24	152	15.4 $\pm$ 5.46	Year: $\chi^2 = 5.23$ , $P = 0.02$	0.12
Post-parturition condition (g)	27	157	30.4 $\pm$ 9.02	Zone: $F_{1,128} = 14.99$ , $P < 0.0001$ Year: $\chi^2 = 12.31$ , $P < 0.0001$	0.27
<i>Offspring traits</i>					
Offspring mass (g)	26	494	2.89 $\pm$ 0.45	Mother SVL: $F_{1,114} = 4.69$ , $P = 0.03$ Year: $\chi^2 = 188.2$ , $P < 0.0001$	0.11
Offspring condition (residual mass)	26	468	Not applicable (0)	Zone: $F_{1,109} = 3.98$ , $P = 0.05$ Year: $\chi^2 = 18.4$ , $P < 0.0001$	0.21
<i>Annual change in body mass and body size</i>					
Body mass change (g)	20	54	12.6 $\pm$ 7.29	Zone: $F_{1,32} = 30.2$ , $P < 0.0001$ Year: $\chi^2 = 13.8$ , $P = 0.0002$	0.59
Body size growth (mm)	22	57	14.6 $\pm$ 11.51	Zone: $F_{1,33} = 10.6$ , $P = 0.003$ Year: $\chi^2 = 6.76$ , $P = 0.009$	0.36

593 \* Number of days since June 10 (average ovulation and fertilization date)

594 SVL = snout to vent length

595

596 **Supplementary Information**597 **Appendix A – Climate variability**

598 Temperature data calculated for the three reproductive stages of the meadow vipers at the  
 599 weather station of the study site were strongly and linearly correlated with temperature data  
 600 collected at the weather station of Carpentras (Pearson's product moment correlation,  $n = 21$   
 601 years, mating stage:  $r = 0.95$ ,  $P < 0.001$ ; gestation stage:  $r = 0.93$ ,  $P < 0.001$ ; non-  
 602 reproductive stage:  $r = 0.91$ ,  $P < 0.001$ ) and with temperature data calculated with the Safran  
 603 model for the study site (mating stage:  $r = 0.97$ ,  $P < 0.001$ ; gestation stage:  $r = 0.95$ ,  $P <$   
 604  $0.001$ ; non-reproductive stage:  $r = 0.94$ ,  $P < 0.001$ ). To calculate the local weather conditions  
 605 on the long-term, we thus applied a linear correction factor to the temperature data calculated  
 606 on the long-term with the Safran model, which was more strongly correlated with local data  
 607 than data from the Carpentras weather station (mating stage:  $F_{1,19} = 274.4$ ,  $P < 0.0001$ ,  $R^2 =$   
 608  $0.93$ ; gestation stage:  $F_{1,20} = 176.8$ ,  $P < 0.0001$ ,  $R^2 = 0.90$ ; non-reproductive stage:  $F_{1,20} =$   
 609  $149.7$ ,  $P < 0.0001$ ,  $R^2 = 0.88$ ). We obtained similar results when we decomposed data  
 610 calculated for the gestation into three stages (early gestation, mid-gestation, and late gestation:  
 611 Pearson's product moment correlations, all  $r > 0.91$ ; linear regressions, all  $R^2 > 0.88$ ).

612 Cumulative rainfall data collected at the study site's weather station were also positively  
 613 correlated with those from Carpentras's weather (Pearson's product moment correlation,  $n =$   
 614  $21$  years, mating stage:  $r = 0.77$ ,  $P < 0.001$ ; gestation stage:  $r = 0.88$ ,  $P < 0.001$ ; non-  
 615 reproductive stage:  $r = 0.77$ ,  $P < 0.001$ ) and those calculated with the Safran model (mating  
 616 stages:  $r = 0.93$ ,  $P < 0.001$ ; gestation stages:  $r = 0.94$ ,  $P < 0.001$ ; non-reproductive stage:  $r =$   
 617  $0.94$ ,  $P < 0.001$ ). We used a linear correction factor to calculate local rainfall data from data  
 618 calculated with the Safran model, which correlated more strongly with local data than data  
 619 from the Carpentras weather station (linear regression, mating stage:  $F_{1,20} = 126.2$ ,  $P <$

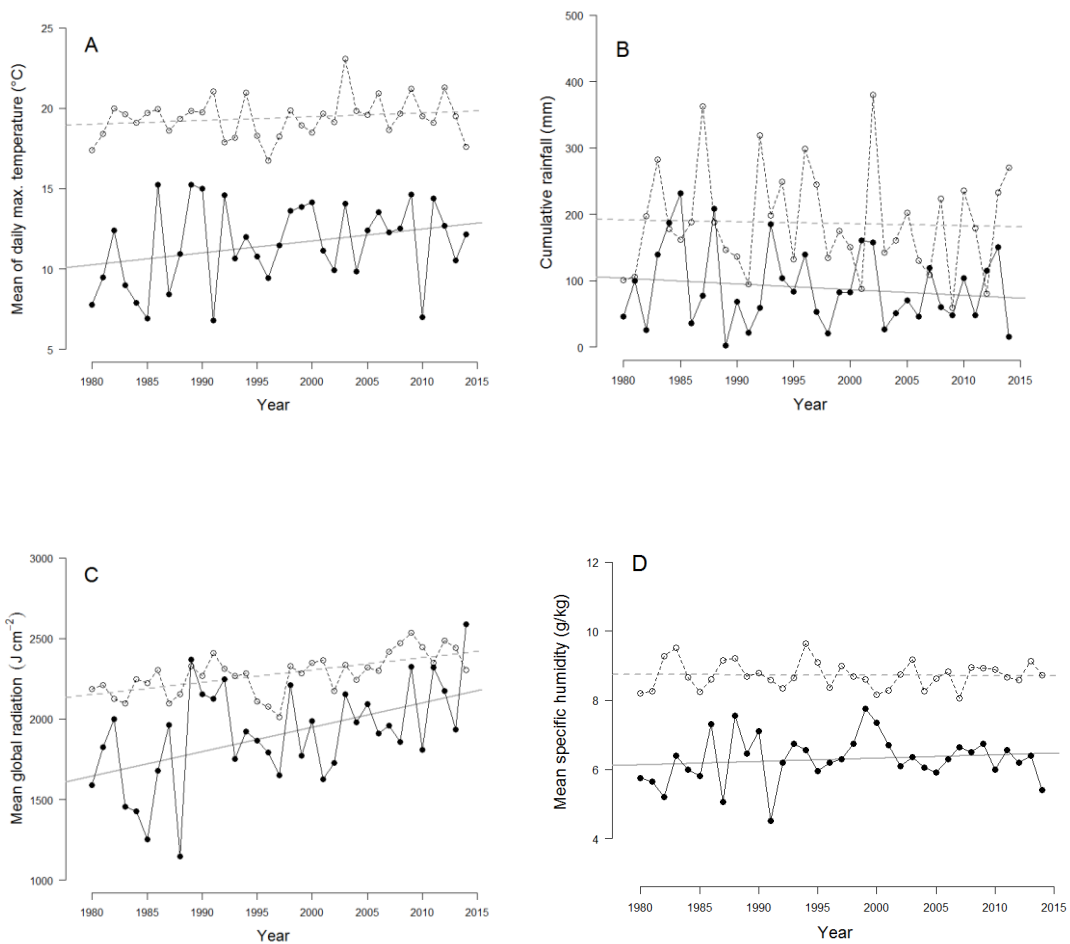
620 0.0001,  $R^2 = 0.86$ ; gestation stage:  $F_{1,21} = 152.2$ ,  $P < 0.0001$ ,  $R^2 = 0.88$ ; non-reproductive  
621 stage:  $F_{1,21} = 157.7$ ,  $P < 0.0001$ ,  $R^2 = 0.89$ ).

622 Temperature, rainfall, global radiation, and humidity varied markedly among years  
623 during the long-term study (Figure A1). Late spring and early summer mean temperatures  
624 increased weakly throughout the study period (mating stages:  $+ 0.07 \text{ }^\circ\text{C} \pm 0.04$  s.e. per year,  
625  $F_{1,33} = 3.16$ ,  $P = 0.08$ ; early gestation:  $+ 0.08 \text{ }^\circ\text{C} \pm 0.03$  s.e. per year,  $F_{1,33} = 6.41$ ,  $P = 0.02$ ),  
626 but this trend wasn't consistent across life stages (other life stages: all  $P > 0.25$ , see Figure  
627 A1). The rainfall and humidity data showed no consistent temporal trend; instead, they varied  
628 in a seemingly random way among years. Global radiation (mean of the cumulative daily  
629 global radiation) calculated with the Safran model for the study site increased through time  
630 during the study (mating stages:  $+ 15.13 \text{ J/cm}^2 \pm 4.6$  s.e. per year,  $F_{1,33} = 10.55$ ,  $P = 0.003$ ;  
631 gestation:  $+ 7.6 \pm 1.7$  s.e. per year,  $F_{1,33} = 20.23$ ,  $P < 0.0001$ , Figure A1).

632 Correlations of temperature and rainfall data between reproductive stages within a year  
633 were usually small and not significant, but there was a negative correlation between these two  
634 environmental factors at the mating and gestation stage, indicating that colder spring and  
635 summer climates were also characterized by stronger rainfall (Table A1). Global radiation was  
636 consistently positively correlated with temperature and negatively with rainfall within the  
637 reproductive stage, and there was also a steady positive correlation between global radiation  
638 data across stages within the same year. Humidity was consistently positively correlated with  
639 rainfall and temperature within a reproductive stage.

640

641 **Figure A1.** We calculated climate conditions for each reproductive year at two life stages of the meadow  
 642 viper (mating periods [black dots], summer gestation periods [white dots]) from 1980 to 2014. Data  
 643 from the non-reproductive stage aren't displayed because they had similar temporal trends than data  
 644 from the gestation stage. (A) Yearly changes in means of maximum daily temperatures (°C); note the  
 645 exceptionally warm 2003 summer and the warming trend during the mating period represented by the  
 646 linear regression. (B) Yearly changes in cumulative rainfall (mm); note the wide temporal fluctuations  
 647 in rainfall during gestation. (C) Yearly changes in daily global radiation (J/cm<sup>2</sup>) with the increasing trend  
 648 over time. (D) Yearly changes in mean daily humidity (g/kg).



649

650

651 **Table A1.** Pairwise correlations of temperature (TP), rainfall (RF), global radiation (GR) and specific humidity (SH) data between reproductive stages calculated  
 652 each year (upper triangular matrix: Pearson's product moment correlation coefficient, lower triangular matrix: sample size). Reproductive stage: M = mating, G  
 653 = gestation, and NR = non-reproductive stage of the previous year. Bolded correlations are significant without correction for multiple testing ( $p < 0.05$ ).  
 654

	TP_M	TP_G	TP_NR	RF_M	RF_G	RF_NR	GR_M	GR_G	GR_NR	SH_M	SH_G	SH_NR
TP_M		0.245	-0.055	<b>-0.490</b>	-0.183	-0.051	<b>0.546</b>	0.315	0.170	<b>0.584</b>	0.039	-0.223
TP_G	34		0.056	-0.195	<b>-0.384</b>	-0.019	0.181	<b>0.468</b>	0.087	0.04	<b>0.379</b>	-0.141
TP_NR	34	35		-0.048	-0.011	-0.212	0.104	0.290	<b>0.371</b>	-0.012	-0.139	<b>0.419</b>
RF_M	34	34	34		0.163	0.206	<b>-0.731</b>	-0.168	-0.114	0.192	-0.048	0.112
RF_G	34	35	35	34		0.006	-0.099	<b>-0.446</b>	-0.012	-0.153	<b>0.340</b>	-0.073
RF_NR	34	35	35	34	35		-0.185	-0.274	-0.235	0.134	0.321	<b>0.349</b>
GR_M	34	34	34	34	34	34		<b>0.461</b>	<b>0.403</b>	-0.183	-0.037	-0.053
GR_G	34	35	35	34	35	35	34		<b>0.664</b>	0.173	-0.199	-0.176
GR_NR	34	35	35	34	35	35	34	35		0.038	-0.135	-0.262
SH_M	34	34	34	34	34	34	34	34	34		-0.023	-0.057
SH_G	34	35	35	34	35	35	34	35	35	35		0.141
SH_NR	34	35	35	34	35	35	34	35	35	35	35	

655

656

657 **Appendix B – Model selection tables**

658 Notations in Appendix B are  $k$  (number of model parameters), LogLikelihood (natural logarithm of the likelihood function), AICc (Akaike  
659 Information Criterion corrected for small sample size),  $\Delta_i$  (difference between the AIC value of the best model and the AIC value for each other  
660 models),  $w_i$  (Akaike weight), ER (evidence ratio),  $R^2_m$  (marginal pseudo-R<sup>2</sup> for the mixed-effects model) and  $R^2_c$  (conditional pseudo-R<sup>2</sup> for the  
661 mixed-effects model). Abbreviations for the descriptions of the covariate are the same as in Table A1. First part corresponds to the kind of  
662 climate variable: TP = temperature, GR = global radiation, and SH = specific humidity. Second part corresponds to the kind of life stage: M =  
663 mating, G = gestation, and NR = non-reproductive stage of the previous year.

664

665 **Table B1.** Full set of linear models examining effect of climate variables on gestation length in the meadow viper population at Mont Ventoux,  
 666 France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold. Yellow filling indicates models with  $\Delta_i < 2$ .

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R <sup>2</sup> m	R <sup>2</sup> c
<b>1</b>	<b>TP_M+TP_G</b>	<b>5</b>	<b>-557.53</b>	<b>1125.46</b>	<b>0.00</b>	<b>0.47</b>		<b>0.27</b>	<b>0.47</b>
<b>2</b>	<b>TP_NR+TP_M+TP_G</b>	<b>6</b>	<b>-556.58</b>	<b>1125.71</b>	<b>0.25</b>	<b>0.41</b>	<b>1.13</b>	<b>0.28</b>	<b>0.46</b>
<b>3</b>	<b>TP_M</b>	<b>4</b>	<b>-561.17</b>	<b>1130.60</b>	<b>5.14</b>	<b>0.04</b>	<b>13.06</b>	<b>0.19</b>	<b>0.48</b>
<b>4</b>	<b>TP_NR+TP_G</b>	<b>5</b>	<b>-560.28</b>	<b>1130.94</b>	<b>5.48</b>	<b>0.03</b>	<b>15.51</b>	<b>0.17</b>	<b>0.48</b>
5	TP_G	4	-561.61	1131.49	6.03	0.02	20.34	0.15	0.50
6	TP_NR+TP_M	5	-560.91	1132.21	6.75	0.02	29.15	0.19	0.48
7	GR_M	4	-562.57	1133.40	7.93	0.01	52.81	0.12	0.49
8	1	3	-565.89	1137.94	12.48	0.00	512.75	0.00	0.51
9	TP_NR	4	-565.37	1138.99	13.53	0.00	868.01	0.03	0.51
10	GR_G	4	-565.37	1139.00	13.54	0.00	872.67	0.02	0.51
11	SH_M	4	-565.62	1139.50	14.04	0.00	1117.98	0.01	0.50
12	GR_NR	4	-565.65	1139.56	14.09	0.00	1149.60	0.01	0.51
13	SH_NR	4	-565.80	1139.87	14.41	0.00	1343.79	0.00	0.51
14	SH_G	4	-565.87	1140.00	14.54	0.00	1437.36	0.00	0.51
15	SH_NR+SH_M	5	-565.56	1141.51	16.05	0.00	3055.19	0.01	0.50
16	SH_M+SH_G	5	-565.61	1141.61	16.14	0.00	3203.81	0.01	0.50
17	SH_NR+SH_G	5	-565.79	1141.97	16.51	0.00	3839.25	0.00	0.51
18	SH_NR+SH_M+SH_G	6	-565.55	1143.65	18.19	0.00	8906.16	0.01	0.50

667



668 **Table B2.** Full set of linear models examining effect of climate variables on relative clutch mass in the meadow viper population at Mont  
 669 Ventoux, France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold. Yellow filling indicates models with  $\Delta_i < 2$ .

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R2m	R2c
<b>1</b>	<b>GR_NR</b>	<b>5</b>	<b>-453.22</b>	<b>916.85</b>	<b>0.00</b>	<b>0.25</b>		<b>0.21</b>	<b>0.29</b>
<b>2</b>	<b>GR_G</b>	<b>5</b>	<b>-453.80</b>	<b>918.01</b>	<b>1.16</b>	<b>0.14</b>	<b>1.79</b>	<b>0.19</b>	<b>0.30</b>
<b>3</b>	<b>1</b>	<b>4</b>	<b>-455.13</b>	<b>918.54</b>	<b>1.69</b>	<b>0.11</b>	<b>2.33</b>	<b>0.17</b>	<b>0.29</b>
<b>4</b>	<b>SH_G</b>	<b>5</b>	<b>-454.08</b>	<b>918.57</b>	<b>1.73</b>	<b>0.10</b>	<b>2.37</b>	<b>0.19</b>	<b>0.30</b>
5	SH_M+SH_G	6	-453.84	920.26	3.41	0.05	5.50	0.19	0.30
6	TP_M	5	-454.95	920.32	3.47	0.04	5.67	0.17	0.29
7	SH_M	5	-455.05	920.51	3.66	0.04	6.23	0.16	0.29
8	GR_M	5	-455.05	920.51	3.67	0.04	6.26	0.17	0.29
9	SH_NR+SH_G	6	-453.99	920.56	3.71	0.04	6.41	0.19	0.30
10	SH_NR	5	-455.09	920.58	3.74	0.04	6.47	0.17	0.29
11	TP_G	5	-455.10	920.62	3.77	0.04	6.59	0.16	0.29
12	TP_NR	5	-455.12	920.65	3.80	0.04	6.68	0.16	0.29
13	SH_NR+SH_M+SH_G	7	-453.69	922.16	5.31	0.02	14.22	0.20	0.30
14	TP_M+TP_G	6	-454.86	922.30	5.45	0.02	15.29	0.16	0.29
15	TP_NR+TP_M	6	-454.95	922.47	5.63	0.01	16.68	0.17	0.29
16	SH_NR+SH_M	6	-454.98	922.54	5.69	0.01	17.22	0.17	0.29
17	TP_NR+TP_G	6	-455.09	922.77	5.92	0.01	19.33	0.16	0.29
18	TP_NR+TP_M+TP_G	7	-454.86	924.50	7.65	0.01	45.90	0.16	0.29

670

671

672 **Table B3.** Full set of linear models examining effect of climate variables on post-parturition condition in the meadow viper population at Mont  
 673 Ventoux, France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold. Yellow filling indicates models with  $\Delta_i < 2$ .

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R2m	R2c
<b>1</b>	<b>TP_NR+TP_G</b>	<b>7</b>	<b>92.11</b>	<b>-169.45</b>	<b>0.00</b>	<b>0.18</b>		<b>0.81</b>	<b>0.84</b>
<b>2</b>	<b>TP_NR</b>	<b>6</b>	<b>90.76</b>	<b>-168.94</b>	<b>0.51</b>	<b>0.14</b>	<b>1.29</b>	<b>0.80</b>	<b>0.84</b>
<b>3</b>	<b>TP_NR+TP_M+TP_G</b>	<b>8</b>	<b>92.73</b>	<b>-168.45</b>	<b>1.01</b>	<b>0.11</b>	<b>1.65</b>	<b>0.82</b>	<b>0.84</b>
<b>4</b>	<b>GR_NR</b>	<b>6</b>	<b>90.42</b>	<b>-168.27</b>	<b>1.19</b>	<b>0.10</b>	<b>1.81</b>	<b>0.80</b>	<b>0.83</b>
<b>5</b>	<b>TP_G</b>	<b>6</b>	<b>90.42</b>	<b>-168.25</b>	<b>1.20</b>	<b>0.10</b>	<b>1.82</b>	<b>0.81</b>	<b>0.84</b>
<b>6</b>	<b>TP_M+TP_G</b>	<b>7</b>	<b>91.43</b>	<b>-168.08</b>	<b>1.37</b>	<b>0.09</b>	<b>1.99</b>	<b>0.81</b>	<b>0.84</b>
7	<b>1</b>	<b>5</b>	<b>88.74</b>	<b>-167.06</b>	<b>2.39</b>	<b>0.05</b>	<b>3.30</b>	<b>0.79</b>	<b>0.84</b>
8	<b>TP_NR+TP_M</b>	<b>7</b>	<b>90.90</b>	<b>-167.03</b>	<b>2.43</b>	<b>0.05</b>	<b>3.36</b>	<b>0.81</b>	<b>0.84</b>
9	<b>GR_G</b>	<b>6</b>	<b>89.61</b>	<b>-166.65</b>	<b>2.80</b>	<b>0.04</b>	<b>4.06</b>	<b>0.80</b>	<b>0.83</b>
10	<b>TP_M</b>	<b>6</b>	<b>89.06</b>	<b>-165.53</b>	<b>3.92</b>	<b>0.03</b>	<b>7.09</b>	<b>0.80</b>	<b>0.84</b>
11	<b>SH_M</b>	<b>6</b>	<b>89.00</b>	<b>-165.43</b>	<b>4.02</b>	<b>0.02</b>	<b>7.48</b>	<b>0.80</b>	<b>0.84</b>
12	<b>GR_M</b>	<b>6</b>	<b>88.88</b>	<b>-165.18</b>	<b>4.27</b>	<b>0.02</b>	<b>8.46</b>	<b>0.79</b>	<b>0.84</b>
13	SH_NR	6	88.75	-164.91	4.54	0.02	9.67	0.79	0.84
14	SH_G	6	88.74	-164.91	4.54	0.02	9.69	0.79	0.84
15	SH_NR+SH_M	7	89.00	-163.23	6.22	0.01	22.43	0.80	0.84
16	SH_M+SH_G	7	89.00	-163.23	6.22	0.01	22.44	0.80	0.84
17	SH_NR+SH_G	7	88.75	-162.73	6.72	0.01	28.81	0.79	0.84
18	SH_NR+SH_M+SH_G	8	89.00	-161.00	8.45	0.00	68.39	0.80	0.84

674  
675

676 **Table B4.** Full set of binomial models examining effect of climate variables on clutch success in the meadow viper population at Mont Ventoux,  
 677 France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold. Yellow filling indicates models with  $\Delta_i < 2$ . The set  
 678 of models did not include GR\_M effect due to lack of convergence.

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R2m	R2c
<b>1</b>	<b>TP_NR+TP_G</b>	<b>5</b>	<b>-157.85</b>	<b>326.10</b>	<b>0.00</b>	<b>0.21</b>		<b>0.06</b>	<b>0.10</b>
<b>2</b>	<b>TP_G</b>	<b>4</b>	<b>-159.13</b>	<b>326.53</b>	<b>0.43</b>	<b>0.17</b>	<b>1.24</b>	<b>0.04</b>	<b>0.09</b>
<b>3</b>	<b>SH_NR</b>	<b>4</b>	<b>-159.76</b>	<b>327.79</b>	<b>1.69</b>	<b>0.09</b>	<b>2.32</b>	<b>0.02</b>	<b>0.09</b>
4	TP_NR+TP_M+TP_G	6	-157.85	328.27	2.16	0.07	2.95	0.06	0.10
5	TP_M+TP_G	5	-159.08	328.56	2.46	0.06	3.42	0.05	0.09
6	1	3	-161.27	328.70	2.60	0.06	3.66	0.00	0.07
7	SH_NR+SH_M	5	-159.32	329.04	2.94	0.05	4.35	0.03	0.09
8	SH_M	4	-160.46	329.19	3.09	0.05	4.69	0.01	0.08
9	SH_NR+SH_G	5	-159.50	329.40	3.30	0.04	5.20	0.03	0.09
10	TP_NR	4	-160.67	329.60	3.50	0.04	5.76	0.09	0.08
11	TP_M	4	-160.97	330.21	4.11	0.03	7.81	0.10	0.08
12	GR_NR	4	-161.03	330.33	4.23	0.03	8.27	0.01	0.08
13	SH_G	4	-161.09	330.45	4.34	0.02	8.78	0.01	0.07
14	SH_NR+SH_M+SH_G	6	-158.94	330.45	4.35	0.02	8.78	0.04	0.09
15	GR_G	4	-161.12	330.50	4.40	0.02	9.02	0.01	0.07
16	SH_M+SH_G	5	-160.14	330.68	4.58	0.02	9.89	0.02	0.07
17	TP_NR+TP_M	5	-160.47	331.35	5.25	0.02	13.82	0.01	0.09

679  
 680  
 681

682 **Table B5.** Full set of linear models examining effect of climate variables on offspring mass at birth in the meadow viper population at Mont  
 683 Ventoux, France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold. Yellow filling indicates models with  $\Delta_i < 2$ .

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R2m	R2c
<b>1</b>	<b>1</b>	<b>6</b>	<b>-192.89</b>	<b>397.95</b>	<b>0.00</b>	<b>0.15</b>		<b>0.05</b>	<b>0.61</b>
<b>2</b>	<b>GR_NR</b>	<b>7</b>	<b>-192.30</b>	<b>398.84</b>	<b>0.88</b>	<b>0.09</b>	<b>1.55</b>	<b>0.06</b>	<b>0.61</b>
<b>3</b>	<b>TP_NR</b>	<b>7</b>	<b>-192.33</b>	<b>398.89</b>	<b>0.94</b>	<b>0.09</b>	<b>1.60</b>	<b>0.06</b>	<b>0.61</b>
<b>4</b>	<b>TP_G</b>	<b>7</b>	<b>-192.41</b>	<b>399.06</b>	<b>1.10</b>	<b>0.08</b>	<b>1.73</b>	<b>0.05</b>	<b>0.61</b>
<b>5</b>	<b>GR_M</b>	<b>7</b>	<b>-192.59</b>	<b>399.41</b>	<b>1.46</b>	<b>0.07</b>	<b>2.07</b>	<b>0.05</b>	<b>0.60</b>
<b>6</b>	<b>TP_NR+TP_G</b>	<b>8</b>	<b>-191.59</b>	<b>399.48</b>	<b>1.52</b>	<b>0.07</b>	<b>2.14</b>	<b>0.07</b>	<b>0.61</b>
<b>7</b>	<b>TP_M</b>	<b>7</b>	<b>-192.68</b>	<b>399.58</b>	<b>1.63</b>	<b>0.07</b>	<b>2.25</b>	<b>0.05</b>	<b>0.60</b>
<b>8</b>	<b>GR_G</b>	<b>7</b>	<b>-192.83</b>	<b>399.89</b>	<b>1.94</b>	<b>0.06</b>	<b>2.64</b>	<b>0.05</b>	<b>0.61</b>
<b>9</b>	<b>SH_M</b>	<b>7</b>	<b>-192.87</b>	<b>399.97</b>	<b>2.02</b>	<b>0.05</b>	<b>2.74</b>	<b>0.05</b>	<b>0.61</b>
<b>10</b>	<b>SH_NR</b>	<b>7</b>	<b>-192.88</b>	<b>399.99</b>	<b>2.03</b>	<b>0.05</b>	<b>2.76</b>	<b>0.05</b>	<b>0.61</b>
<b>11</b>	<b>SH_G</b>	<b>7</b>	<b>-192.89</b>	<b>400.01</b>	<b>2.06</b>	<b>0.05</b>	<b>2.80</b>	<b>0.05</b>	<b>0.61</b>
<b>12</b>	<b>TP_NR+TP_M</b>	<b>8</b>	<b>-192.17</b>	<b>400.64</b>	<b>2.69</b>	<b>0.04</b>	<b>3.83</b>	<b>0.06</b>	<b>0.61</b>
<b>13</b>	<b>TP_M+TP_G</b>	<b>8</b>	<b>-192.31</b>	<b>400.91</b>	<b>2.95</b>	<b>0.03</b>	<b>4.38</b>	<b>0.05</b>	<b>0.60</b>
<b>14</b>	<b>TP_NR+TP_M+TP_G</b>	<b>9</b>	<b>-191.55</b>	<b>401.47</b>	<b>3.51</b>	<b>0.03</b>	<b>5.79</b>	<b>0.07</b>	<b>0.61</b>
15	SH_NR+SH_M	8	-192.86	402.01	4.05	0.02	7.58	0.05	0.61
16	SH_M+SH_G	8	-192.87	402.04	4.08	0.02	7.69	0.05	0.61
17	SH_NR+SH_G	8	-192.88	402.05	4.10	0.02	7.76	0.05	0.61
18	SH_NR+SH_M+SH_G	9	-192.85	404.08	6.12	0.01	21.37	0.05	0.61

684

685

686 **Table B6.** Full set of linear models examining effect of climate variables on offspring body condition at birth in the meadow viper population at  
 687 Mont Ventoux, France. The best set of models (models whose cumulative Akaike weight  $\leq 0.95$ ) is in bold.

Model rank	Model name	k	-LogLikelihood	AICc	$\Delta_i$	$w_i$	ER	R2m	R2c
<b>1</b>	<b>GR_G</b>	<b>8</b>	<b>10.24</b>	<b>-4.17</b>	<b>0.00</b>	<b>0.54</b>		<b>0.63</b>	<b>0.80</b>
<b>2</b>	<b>TP_G</b>	<b>8</b>	<b>8.72</b>	<b>-1.13</b>	<b>3.04</b>	<b>0.12</b>	<b>4.58</b>	<b>0.63</b>	<b>0.80</b>
<b>3</b>	<b>GR_NR</b>	<b>8</b>	<b>8.18</b>	<b>-0.04</b>	<b>4.13</b>	<b>0.07</b>	<b>7.87</b>	<b>0.61</b>	<b>0.80</b>
<b>4</b>	<b>TP_M+TP_G</b>	<b>9</b>	<b>8.92</b>	<b>0.56</b>	<b>4.73</b>	<b>0.05</b>	<b>10.63</b>	<b>0.63</b>	<b>0.80</b>
<b>5</b>	<b>TP_NR+TP_G</b>	<b>9</b>	<b>8.82</b>	<b>0.75</b>	<b>4.92</b>	<b>0.05</b>	<b>11.70</b>	<b>0.63</b>	<b>0.80</b>
<b>6</b>	<b>1</b>	<b>7</b>	<b>6.38</b>	<b>1.48</b>	<b>5.66</b>	<b>0.03</b>	<b>16.91</b>	<b>0.61</b>	<b>0.81</b>
<b>7</b>	<b>TP_NR+TP_M+TP_G</b>	<b>10</b>	<b>9.08</b>	<b>2.32</b>	<b>6.49</b>	<b>0.02</b>	<b>25.68</b>	<b>0.63</b>	<b>0.80</b>
<b>8</b>	<b>TP_M</b>	<b>8</b>	<b>6.94</b>	<b>2.43</b>	<b>6.60</b>	<b>0.02</b>	<b>27.17</b>	<b>0.62</b>	<b>0.81</b>
<b>9</b>	<b>GR_M</b>	<b>8</b>	<b>6.88</b>	<b>2.55</b>	<b>6.72</b>	<b>0.02</b>	<b>28.75</b>	<b>0.62</b>	<b>0.81</b>
<b>10</b>	<b>SH_G</b>	<b>8</b>	<b>6.70</b>	<b>2.92</b>	<b>7.09</b>	<b>0.02</b>	<b>34.69</b>	<b>0.62</b>	<b>0.81</b>
<b>11</b>	<b>TP_NR</b>	<b>8</b>	<b>6.62</b>	<b>3.06</b>	<b>7.24</b>	<b>0.01</b>	<b>37.26</b>	<b>0.61</b>	<b>0.80</b>
12	SH_M	8	6.41	3.50	7.67	0.01	46.32	0.61	0.81
13	SH_NR	8	6.38	3.55	7.72	0.01	47.52	0.61	0.81
14	TP_NR+TP_M	9	7.32	3.76	7.93	0.01	52.76	0.61	0.80
15	SH_M+SH_G	9	6.71	4.98	9.15	0.01	96.97	0.62	0.81
16	SH_NR+SH_G	9	6.70	5.00	9.17	0.01	98.07	0.62	0.81
17	SH_NR+SH_M	9	6.41	5.57	9.74	0.00	130.45	0.61	0.81
18	SH_NR+SH_M+SH_G	10	6.71	7.07	11.24	0.00	275.50	0.62	0.81

688

689 **Appendix C – Integral projection model**690 *Model rationale*

691 The integral projection model (IPM) assumes that the life history is structured by body size (here,  
 692 snout-vent length), hereafter called  $y$ , such that snakes differ by  $y$  only and  $y$  is the sole determinant  
 693 of their vital rates. The population can then be described by a function  $N(y, t)$  where  $N(y, t)dy$  is  
 694 the discrete number of individuals between size values  $y$  and  $y + dy$  at time  $t$ . The total, finite  
 695 population size is called  $N(t)$ . To describe this population in a fluctuating environment, we used a  
 696 stochastic IPM formulated by Vindenes et al. (2011):

$$697 \quad N(y, t+1) = \int_{\Omega} K(y, x, Z_t) N(x, t) dx, \quad (C1)$$

$$698 \quad K(y, x, Z_t) = s(x, Z_t) f_s(y, x, Z_t) + b(x, Z_t) f_b(y, x, Z_t)$$

699 where  $K$  is a stochastic projection kernel,  $Z_t$  is a random vector describing parameter values at  
 700 time  $t$  and thus the environmental state, and  $\Omega$  is the domain of possible values for body size (Rees  
 701 and Ellner 2009).

702 The kernel describes transition rates from state  $x$  at time  $t$  to state  $y$  at time  $t+1$  in  
 703 environment  $Z$ . According to equation (C1), the kernel is decomposed into (1) the survival-growth  
 704 kernel where  $s(x, Z_t)$  is the survival probability of an individual with trait value  $x$ , and  
 705  $f_s(y, x, Z_t)dy$  is the probability of reaching trait value between  $y$  and  $y + dy$  at time  $t+1$  for an  
 706 individual of trait value  $x$ , and (2) the fecundity kernel where  $b(x, Z_t)$  is the fecundity of an  
 707 individual with trait value  $x$ , and  $f_b(y, x, Z_t)$  is the probability density function of the trait value of  
 708 offspring. Thus, the stochastic model described by equation (C1) is similar the deterministic model  
 709 of Easterling *et al.* (2000) conditional on  $Z$ .

710 This IPM can be considered as a stochastic matrix projection model (MPM) with an infinite  
 711 number of discrete classes. According to the seminal paper by Easterling *et al.* (2000), most of the  
 712 properties of MPMs can therefore be generalised to IPMs, including the calculation of the  
 713 deterministic population growth rate  $\lambda$ , equilibrium population structure, reproductive values and  
 714 deterministic elasticities of  $\lambda$ . Here, we used a numerical method to simulate the deterministic  
 715 IPMs by discretising the state-space  $\Omega$  into  $C$  classes of the same width  $\Delta y$  and computing  
 716 integrals using Simpson's 3/8 method, a more accurate numerical integration method than the  
 717 standard mid-point rule (Merow *et al.* 2014).

718 For stochastic environments and finite populations, we used individual based simulations and  
 719 considered that  $Z_t$  is a vector of year-specific parameters and assumed that parameter values vary  
 720 randomly over time according to the random effects model of Rees and Ellner (2009). This implies  
 721 that elements of the stochastic kernel of the IPM are drawn randomly each year from some  
 722 parametric statistical distributions. The dynamics of the expected population size at time  $t+1$  given  
 723 population size at time  $t$  can then be written as:

$$724 \quad E[N(t+1)|N(t)] = \int_{\Omega} \int_{\Omega} \bar{k}(y, x) N(x, t) dx dy \quad (C2)$$

725 where  $\bar{k}(y, x)$  is the mean kernel defined by averaging the stochastic kernel over all possible  
 726 environmental state values. This dynamics is characterised by an expected growth rate  $\bar{\lambda}$  and a  
 727 stable size structure  $\bar{u}(x)$ .

728 An important property of this stochastic IPM is the long-run logarithmic growth rate, denoted  
 729  $\ln \lambda_s$ , which describes the asymptotic exponential growth rate of the population size after a  
 730 sufficiently long time (Lande *et al.* 2003; Rees and Ellner 2009; Tuljapurkar 1990). The long-run  
 731 logarithmic growth rate can be approximated assuming a small environmental noise, which implies

732 that the population stays close to its stable distribution (e.g., for IPM Rees and Ellner 2009).

733 Vindenes et al. (2011) showed that the first-order approximation of the long-run growth rate of the  
 734 stochastic IPM writes like:

$$735 \quad \ln \lambda_s \approx \ln \bar{\lambda} - \frac{\sigma_e^2}{2\bar{\lambda}^2} - \frac{\sigma_d^2}{2\bar{\lambda}^2 V}, \quad (C3)$$

736 where  $\bar{\lambda}$  is the deterministic population growth rate of the mean kernel,  $\sigma_e^2$  is the environmental  
 737 variance (i.e., a consequence of between-year deviation from the mean kernel of the average  
 738 individual contribution to total reproductive value),  $\sigma_d^2$  is the demographic variance (i.e., a  
 739 consequence within-year deviation from the mean of the year of the individual contribution to total  
 740 reproductive value) and  $V$  is the total reproductive value (i.e., equivalent to population size when  
 741 the population reaches the stable distribution). We calculated  $\sigma_e^2$  by numeric simulations of the  
 742 growth rate, estimated  $\sigma_d^2$  from the slope of the regression of the mean exponential growth rate  
 743 against the inverse population size, and then simulated model (C2) with a diffusion approximation  
 744 of long-run growth rate following the numerical methods of Vindenes et al. (2011).

745 *Model parameterization*

746 Our female life cycle for the meadow viper counts individuals from the age of one year and  
 747 assumes annual reproduction followed by annual survival and body growth of juveniles, and the  
 748 annual survival, body growth and sexual maturation of immature individuals (until six years old,  
 749 equivalent to 7 age classes of immature individuals). Juvenile survival increases with offspring  
 750 mass at birth, which itself depends on offspring body size (snout-vent length, mm) that is influenced  
 751 by maternal body size and total clutch size. Maturation probability depends on both body size and  
 752 age of the female, and occurs around 4 to 6 years old. Once maturity is reached, females alternate  
 753 regularly breeding and non-breeding years (equivalent to two breeding classes of mature



## Climate warming and reproductive strategies in a viper

754 individuals) and their fecundity increases with body size. To calculate the number of viable  
 755 offspring produced by breeding females each year, we estimated fecundity (total clutch size), clutch  
 756 success (percentage of viable offspring within a clutch) and female sex ratio. This complex life  
 757 cycle was modelled with an IPM including both a continuous size structure and nine discrete  
 758 categories. The first seven discrete categories were age classes (from 0 to 6 years) for immature  
 759 individuals, and the two last discrete categories included the breeding and non-breeding states for  
 760 mature individuals. There is significant environmental variation for annual juvenile survival, body  
 761 size at birth and reproduction through clutch success. This life history is based on earlier results  
 762 (Baron et al., 2010a, Baron et al., 2013, Baron et al., 2010b) and results from the current study.

763 The IPM for this complex life cycle can be written like:

$$764 \quad n(y, t+1) = \int_Y k(y, x) \times n(x, t) \times dx, \quad (C4)$$

765 where  $n(y, t)$  is a vector of functions describing the size distribution in each class, and  $k$  is a  
 766 matrix of functions whose elements are kernel elements of a classical IPM for each transition between  
 767 classes. More precisely, we can write down the matrix  $k$  like:

$$768 \quad k(y, x) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & k_F & 0 \\ k_{0 \rightarrow 1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & k_{1 \rightarrow 2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & k_{2 \rightarrow 3} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & k_{3 \rightarrow 4} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & k_{4 \rightarrow 5} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & k_{5 \rightarrow 6} & 0 & 0 & 0 \\ k_{0 \rightarrow B} & k_{1 \rightarrow B} & k_{2 \rightarrow B} & k_{3 \rightarrow B} & k_{4 \rightarrow B} & k_{5 \rightarrow B} & k_{6 \rightarrow B} & k_{B \rightarrow B} & k_{NB \rightarrow B} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & k_{B \rightarrow NB} & k_{NB \rightarrow NB} \end{pmatrix} \quad (C5)$$

769 where elements of this matrix are listed below:

$$770 \quad k_{i \rightarrow j}(y, x) = (1 - \Pi_m(y, i+1)) \times f_{lm}(y, x) \times \phi_{lm}$$

Climate warming and reproductive strategies in a viper

771 
$$k_F(y, x) = \left[ \sum_{k=1}^{F_{max}} \Pi(F_0(x) = k) \times k \times f_F(y, x | F_0(x) = k) \right] \times p_{cs}(x) \times p_f \times \phi_0(m(y))$$

772 
$$k_{i \rightarrow B}(y, x) = \Pi_m(y, i + 1) \times f_i(y, x) \times \phi_{lm}$$

773 
$$k_{B \rightarrow B}(y, x) = P_{B \rightarrow B} \times f_B(y, x) \times \phi_A$$

774 
$$k_{NB \rightarrow B}(y, x) = P_{NB \rightarrow B} \times f_{NB}(y, x) \times \phi_A$$

775 
$$k_{B \rightarrow NB}(y, x) = P_{B \rightarrow NB} \times f_B(y, x) \times \phi_A$$

776 
$$k_{NB \rightarrow NB}(y, x) = P_{NB \rightarrow NB} \times f_{NB}(y, x) \times \phi_A$$

777

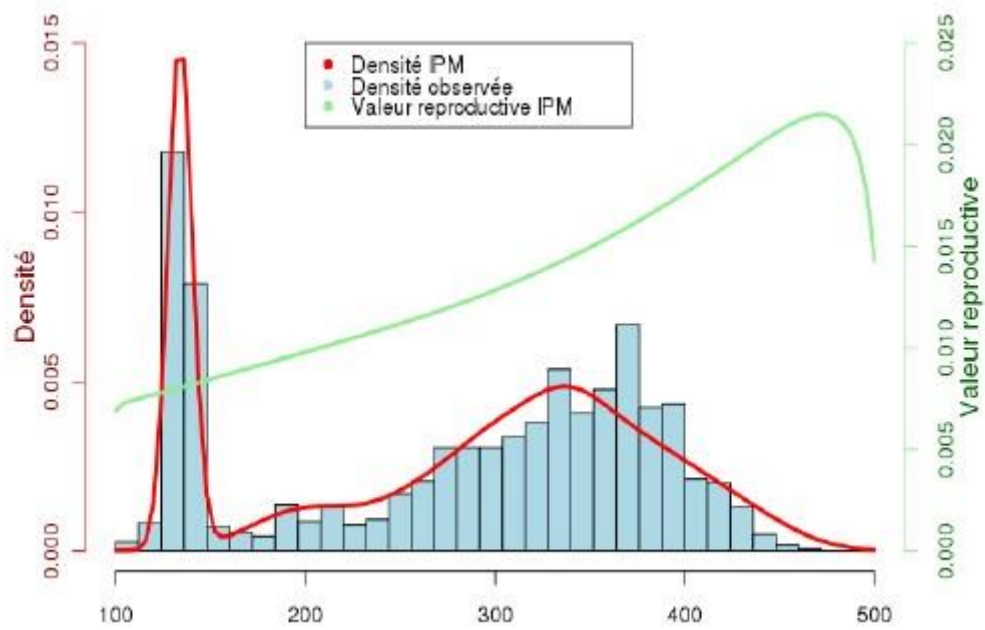
778 Parameters values for the different terms of these elements are provided in Table C1 averaging  
 779 across the two study sites. The stochastic model included inter-annual variation in clutch success, size  
 780 at birth and size growth of non-reproductive females (this study) as well as early juvenile survival  
 781 (Baron et al., 2010a, Baron et al., 2013, Baron et al., 2010b). The stochastic version was analysed  
 782 with an individual based model in Python whereas the deterministic version was fitted with Matlab.  
 783 Default parameter values of the deterministic model provided a good fit to the average size  
 784 distribution in the study population (see Figure C1)

785

786

Climate warming and reproductive strategies in a viper

787 **Figure C1.** Comparison between the size distribution predicted by the IPM and the observed size  
788 distribution in the pooled sample of females corrected for unequal capture probabilities. The two  
789 statistical distributions looked similar although the IPM tended to predict more of the small juvenile  
790 size classes and less of the old adults' size classes than observed ( $\chi^2$  test,  $P < 0.0001$ ).  
791



792  
793  
794

Climate warming and reproductive strategies in a viper

795 **Table C1:** Model parameters when size is estimated by snout-vent length (SVL, mm) for *Vipera ursinii*  
 796 *ursinii* at Mont Ventoux, France. The table provides the mean and error of the mean in the scale of the  
 797 statistical model used to estimate parameters, as well as inter-annual SD, statistical procedure / software and  
 798 kinds of distribution (glm: generalized linear model, lm: linear model, glmmPQL: generalized linear mixed  
 799 model with penalized quasi-likelihood, vglm: vector generalized linear model, lme: liner mixed model,  
 800 MARK CJS: Cormak-Jolly-Seber open population model including multi-state models).

<i>Trait</i>	<i>Scale</i>	<i>Estimate</i>	<i>SE</i>	<i>Inter-annual SD</i>	<i>Procedure</i>	<i>Distribution</i>
<b>Sexual maturation probability - <math>\Pi_m(y, i)</math></b>						
Intercept	Logit	-24.030	5.88	0	glm	Binomial
Slope age $i$	Logit	2.072	0.530	0		
Slope SVL $y$	Logit	0.050	0.017	0		
<b>Size of immature females at time <math>t + 1</math> - <math>f_{Im}(y, x)</math></b>						
Intercept	Identity	83.646	10.82	0	lm	Gaussian
Slope SVL $x$	Identity	0.8267	0.043	0		
Residual variance*	Power	321097	NA			
<b>Annual survival of immature females - <math>\phi_{Im}</math></b>						
Mean value	Logit	1.202	0.467	0	MARK CJS	Binomial
<b>Fecundity (total clutch size) - <math>F_0(x)</math></b>						
$\lambda$ - Mean value	elogit	-1.665	0.294	0	vglm	Generalised
$\Theta$ - Intercept	log	-1.090	0.285	0		Poisson
$\Theta$ - Slope SVL $x$	log	0.007	0.0007	0		
<b>Clutch success - <math>p_{cs}(x)</math></b>						
Intercept	Logit	3.662	1.822	1.139	glmmPQL	Binomial
Slope maternal SVL $x$	Logit	-0.024	0.323	0		
Residual variance	Logit	1.067	NA			
<b>Size at birth given fecundity - <math>f_F(y, x   F_0(x))</math></b>						
Intercept	Identity	116.895	4.14	4.064	lme	Gaussian
Slope maternal SVL $x$	Identity	0.0608	0.012	0		
Slope fecundity $F_0(x)$	Identity	-1.389	0.351	0		
Residual variance	Identity	6.143	NA			
<b>Female sex ratio - <math>p_f</math></b>						
Intercept	Logit	-0.044	0.1054		glm	Binomial

Climate warming and reproductive strategies in a viper

<b>Juvenile survival as a function of standardised body mass at birth - <math>\phi_0(m(y))</math></b>						
Intercept	Logit	-0.442	0.505	0.269	MARK CJS	Binomial
Slope body mass $m(y)$	Logit	0.837	0.539	0		
<b>Relationship between mass at birth and size at birth - <math>m(y)</math></b>						
Intercept	Identity	-3.393	0.276	0	lm	Gaussian
Slope size at birth $y$	Identity	0.047	0.002	0		
Residual variance	Identity	0.2933	NA			
<b>Transition from breeding to non-breeding state - <math>P_{B \rightarrow NB}</math></b>						
Mean value	Logit	3.200	0.524	0	MARK CJS	Binomial
<b>Size of breeding females at time <math>t + 1</math> - <math>f_B(y, x)</math></b>						
Intercept	Identity	21.559	14.76	0	lm	Gaussian
Slope SVL $x$	Identity	0.9514	0.039	0		
Residual variance	Identity	9.04	NA			
<b>Adult survival - <math>\phi_A</math></b>						
Mean value	Logit	0.789	0.116	0	MARK CJS	Binomial
<b>Transition from non-breeding to breeding state - <math>P_{NB \rightarrow B}</math></b>						
Mean value	Logit	1.756	0.391	0	MARK CJS	Binomial
<b>Size of non-breeding females at time <math>t + 1</math> - <math>f_{NB}(y, x)</math></b>						
Intercept	Identity	84.821	21.88	1.23	lm	Gaussian
Slope SVL $x$	Identity	0.8204	0.058	0		
Residual variance	Identity	11.43	NA			

801 \* Residual variance is modelled like a power function of predicted values (power exponent: -1.79)

802