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Buffered microclimate determines the presence of *Salamandra corsica*

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Abstract Numerous amphibian species occupy microhabitats with buffered thermal and moisture conditions, typically under forest canopies. Here, we assessed whether the insular endemic *Salamandra corsica* also uses this type of habitat, which could have important implications for its conservation. We used data loggers to record the air temperature and air humidity at 4 h intervals over a period of 2 years, at 13 stations with a confirmed presence of *S. corsica*. These data were compared with those recorded at Corsican weather stations and those generated by a climate model (WorldClim 2). The weather station data showed significant deviations from the probe data, by an average of -1.26 °C (minimum temperature), $+2.61$ °C (maximum temperature), and -0.04% (relative humidity). Similarly, the WorldClim 2 data showed significant deviations from the probe data, by an average of -2.49 °C (minimum temperature) and $+1.69$ °C (maximum temperature). These discrepancies reflect the use of densely vegetated and topographically complex habitats by *S. corsica*, which reduce temperature fluctuations. Overall, our results highlight the importance of natural vegetal cover in the conservation of populations of this endemic salamander.

Keywords Fire salamander · Island endemic · Microclimate · Probe · Threatened species

Introduction

Macroclimatic models are commonly used in investigating the patterns of niche occupancy and diversification of ectothermic vertebrates (Guisan and Hofer 2003; Pyron and Burbrink 2012). This approach has the advantage of using global databases, which allow ecological hypotheses to be evaluated while including a large number of species in a broad environmental framework. However, these databases characterize the environment at a coarse scale and do not capture the small-scale variations in temperature/moisture associated with fine landscape gradients (Anderson et al. 2007; Shoo et al. 2011; Scheffers et al. 2014). For this reason, such broad-scale models may be unsuitable in testing the environmental conditions that control the occurrence of forest species (Frey et al. 2016).

This limitation also hampers studies of terrestrial salamanders because many salamander species are associated with a narrow range of environmental conditions, often involving a dense cover of vegetation (Crawford and Semlitsch 2007). This is because salamanders have permeable skins and are at risk of dehydration if environmental moisture decreases rapidly (Grover 2000). For this reason, the presence and abundance of salamanders are strongly determined by fine gradients in environmental temperature and humidity (Grant et al. 2018; Gade and Peterman 2019).

In the present study, we evaluated whether the occurrence of *Salamandra corsica* is associated with thermally buffered environments. This salamander is endemic to the island of Corsica, where it is distributed throughout most of the island (Delaugerre and Cheylan 1992). Whether this species

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occupies buffered microhabitats may have repercussions for its conservation and management, particularly in those populations that occur in peripheral areas and are exposed to high climate seasonality, as at Cap Corse in northern Corsica (Lanza et al. 2007). Previous research revealed that broad-scale models fail to predict the presence of this salamander at the edges of its distribution (Escoriza and Hernandez 2019). The authors of that study hypothesized that broad-scale data fail to describe the actual conditions of the microhabitats occupied by this species. We tested this hypothesis by using data loggers to characterize the microenvironmental conditions (air temperature and humidity) at sites inhabited by the salamander and then compared these datasets with those recorded at weather stations and generated by climate models.

Materials and methods

Study region

The study region was the island of Corsica (8722 km²). This island has a rugged terrain, and 39% of its surface exceeds elevations of 600 m. The mountains affect the climate, which varies from warm coastal to subalpine variants of the Mediterranean group (*Csa–Csb–Csc*; Köppen classification) to alpine/subarctic (*Dsc–Dfc*; Köppen classification) in the high mountains (Rome and Giorgetti 2007).

Data collection

Before this study, we undertook several surveys to determine the habitat use by *S. corsica* (Escoriza and Hernandez 2019). We selected 13 sites with species presence, covering most of its distributional and elevational ranges (175–1705 m; $x=629$ m) (Fig. 1). The probes were placed at ground level, at the precise points at which an adult *S. corsica* was previously located (± 1 m), with the sensor facing north. Temperature (°C) and relative air humidity (%) were measured with an onset HOBO U23 Pro-V2 data logger (accuracy ± 0.21 °C/ $\pm 2.5\%$). The probes continuously recorded the temperature and relative humidity (RH) at 4 h intervals between December 2016 and September 2018. Comparisons were made between the environmental data collected on-site and those recorded at 13 weather stations located throughout Corsica (Fig. 1), provided by the Climate Forecast System Reanalysis dataset (CFSR) and the European Climate Assessment and Dataset project (ECAD; <https://www.ecad.eu/>). These stations are located at elevations of 5–1302 masl ($x=458$ m), covering an elevation range that did not differ significantly from that of the probes (Mann–Whitney test $U=61$, $P=0.238$).

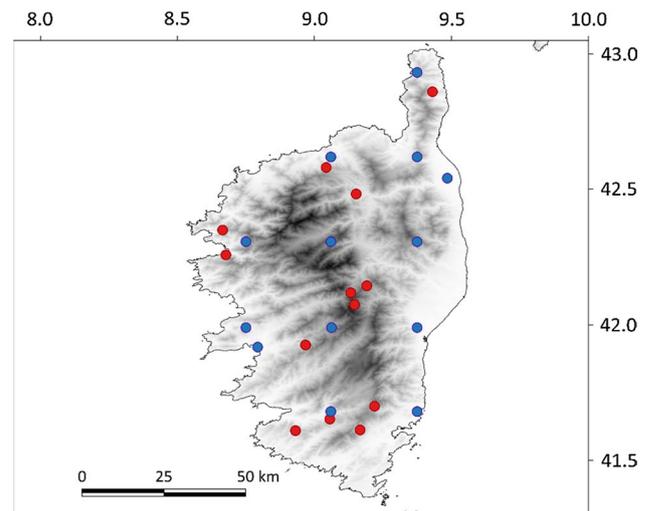


Fig. 1 Map of the study region. Red circles: presence sites of *Salamandra corsica*; blue circles: weather stations

The weather station data provided the daily maximum and minimum temperatures and the daily average RH in the periods 1979–2014 (CFSR) and 1949–2019 (ECAD). We also calculated an index of climatic variability. To do this, we calculated the weekly standard deviation of temperature and RH, and these values were scaled in percentiles. The values were combined for both variables and scaled between 0 and 100: a value of 100 indicated maximum variability relative to the other weather stations. The data-logger data were also compared with data generated from a coarse-resolution database, WorldClim 2 (Fick and Hijmans 2017). This provided the average monthly values for the maximum and minimum temperatures in the period 1970–2000, with a spatial resolution of ~ 1 km pixel⁻¹ (Fick and Hijmans 2017).

Data analysis

The data recorded by data loggers were visualized using R (R Core Development Team 2019). The daily values were plotted, and trend lines generated using a general additive model were added. To identify significant differences among sites, we used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on a Euclidean distance matrix of the normalized predictor variables. Univariate differences were evaluated with ANOVA.

The differences between the series of data recorded by data loggers and at the weather stations were evaluated for the daily values obtained during 1 year. We used the data for a consecutive 12-month period randomly selected between December 2016 and November 2018 (data loggers) and a single year for the weather stations. PERMANOVA was used to determine the multivariate

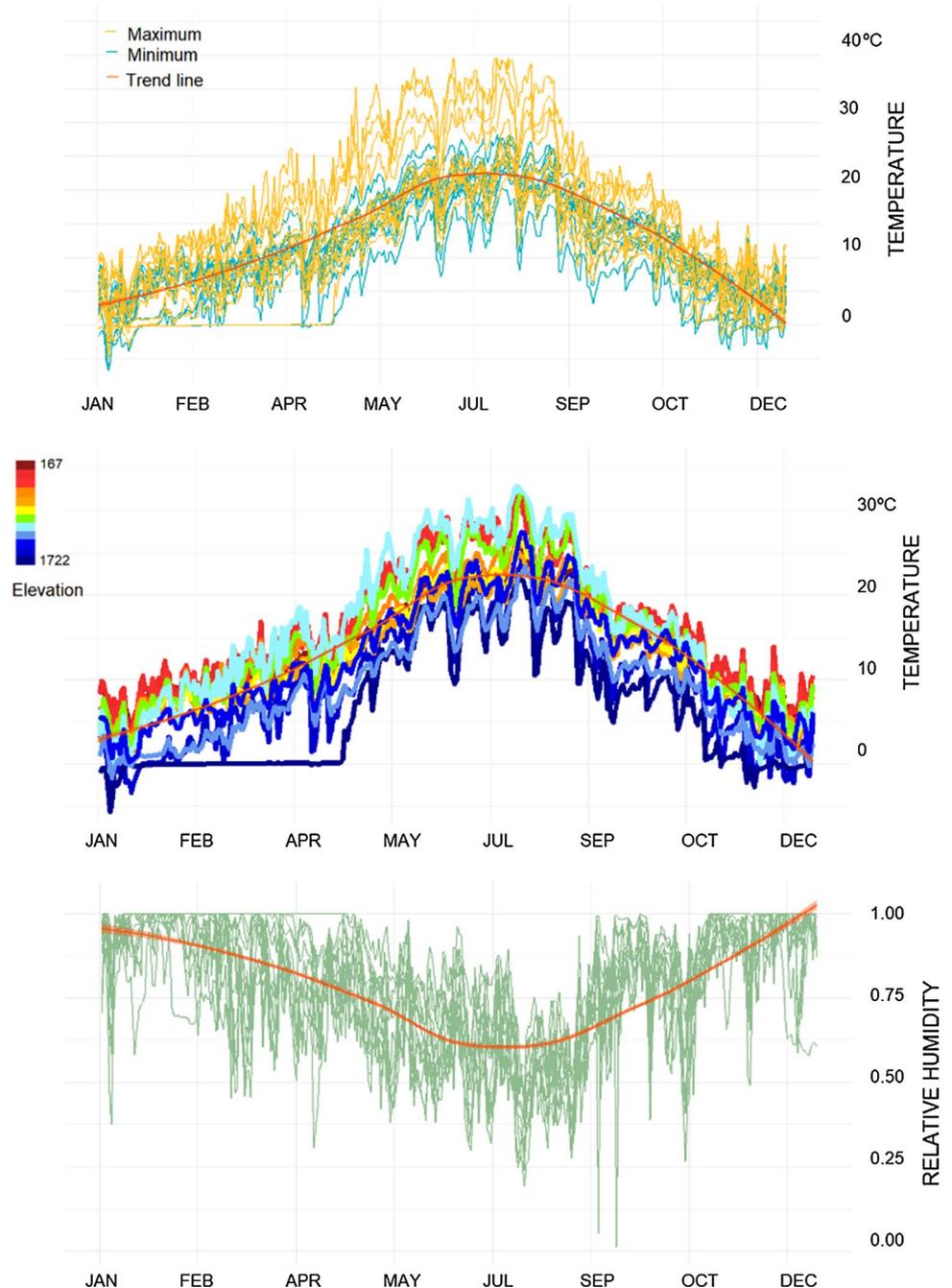
differences between the probe and weather station data. Student's *t* test was used to assess univariate differences.

We also compared the probe data with the WorldClim 2 data for the same sites. We evaluated whether both series of monthly data were correlated by calculating Pearson's *r*, and a paired *t* test was used to assess the statistical differences. These analyses were performed in the R environment.

Results

The data generated at the 13 sites of *S. corsica* presence showed an average annual temperature of 13.62 ± 0.11 °C (mean \pm standard error), a mean annual minimum temperature of 11.70 ± 0.09 °C, and a mean annual maximum temperature of 15.53 ± 0.13 °C (Fig. 2). The mean annual relative humidity was $0.79 \pm 0.003\%$ (Fig. 2). The site at which the minimum temperatures were registered was *Source de Pizzolo* (beech forest; 1722 masl), which had a mean annual temperature of 6.40 ± 0.38 °C, a mean annual

Fig. 2 Plot of temperatures (°C) and relative humidity (%), of the presence sites of *Salamandra corsica*, with a trend line estimated by a general additive model. From top to bottom: plot 1, minimum and maximum temperatures; plot 2, average temperatures, as a function of the elevation gradient; plot 3, relative humidity



minimum temperature of 5.34 ± 0.34 °C, and a mean annual maximum temperature of 7.45 ± 0.43 °C (Fig. 2). The mean annual relative humidity was $0.85 \pm 0.01\%$ (Fig. 2). The site at which the maximum temperatures were registered was *Girolata* (Mediterranean maquia; 215 masl), which had a mean annual temperature of 16.42 ± 0.37 °C, a mean annual minimum temperature of 13.55 ± 0.32 °C, and a mean annual maximum temperature of 19.29 ± 0.42 °C (Fig. 2). The mean annual relative humidity was $0.69 \pm 0.009\%$ (Fig. 2). The stations showed statistically significant differences in both the whole set of variables (PERMANOVA, pseudo- $F = 101.1$, $P = 0.0001$) and individual variables (Table 1).

The results of PERMANOVA showed significant differences between the probe data and weather station data (pseudo- $F = 184.4$, $P = 0.0001$). The differences were also significant when the three variables (minimum and maximum temperature, and RH) were evaluated separately (Table 2). The mean differences were $+1.26$ °C (i.e., the minimum temperature was 1.26 °C higher in the probe data), -2.61 °C (maximum temperature), and $+0.04\%$ (RH). The climatic variability was smaller in the probe data than in the weather station data, and this difference was also significant (Table 2).

The probe data showed a significant correlation with the climate model data, although the strength of this correlation

Table 1 Comparison of the data registered by the probes in the presence-sites of *Salamandra corsica*, using ANOVA tests

	Statistics	
Mean minimum temperature	<i>df</i>	12
	<i>F</i>	75.07
	<i>P</i>	8.07×10^{-170}
Mean maximum temperature	<i>df</i>	12
	<i>F</i>	119.0
	<i>P</i>	4.94×10^{-262}
Mean relative humidity	<i>df</i>	12
	<i>F</i>	39.1
	<i>P</i>	1.52×10^{-88}

Table 2 Comparison of the data (mean and standard error) recorded daily by the presence-sites probes and the weather stations in a period of 1 year, using Student's *t*-tests

	Probes	Weather stations	Statistics	
Mean minimum temperature	11.70 ± 0.09	10.44 ± 0.09	<i>t</i>	9.37
			<i>P</i>	9.04×10^{-21}
Mean maximum temperature	15.53 ± 0.13	18.15 ± 0.11	<i>t</i>	-15.75
			<i>P</i>	3.50×10^{-55}
Mean relative humidity	0.79 ± 0.003	0.75 ± 0.002	<i>t</i>	12.79
			<i>P</i>	3.79×10^{-37}
Climate variability	46.09 ± 0.97	55.43 ± 0.82	<i>t</i>	-7.35
			<i>P</i>	3.32×10^{-13}

Temperature, °C; relative humidity, %

Table 3 Comparison of the data (mean and standard error is showed) generated by the presence-sites probes and WorldClim 2, using Student's *t*-tests for paired samples

	Probe	WorldClim 2	Statistics	
Mean minimum temperature	11.18 ± 0.53	8.69 ± 0.52	<i>t</i>	-5.83
			<i>P</i>	3.09×10^{-8}
Mean maximum temperature	14.92 ± 0.68	16.61 ± 0.49	<i>t</i>	4.02
			<i>P</i>	9.15×10^{-5}

Temperature, °C

varied widely between the minimum temperature ($r = 0.360$) and the maximum temperature ($r = 0.792$). The comparison based on a paired *t* test showed significant differences (Table 3). The mean differences were $+2.49$ °C (minimum temperature) and -1.69 °C (maximum temperature) (Table 3).

Discussion

Statistical tests indicated that the climate models overestimated the thermal range at the sites occupied by *S. corsica*. This suggests that geographic information system (GIS) data are a weak surrogate for the actual environmental niches of *S. corsica* and should be used with caution when drawing ecological conclusions about this species.

Our analysis also showed significant differences between the probe data and the weather station data. The stations are installed according to a protocol that is used to standardize their measurements. To do this, they are usually situated several meters above ground level and in open places, far from buildings and trees that would interfere with wind flow (Anderson and Ingram 1989). For this reason, these stations characterize environments that are not buffered by vegetation or topographic barriers. Our in situ probes recorded a data series with lower thermal oscillations and higher moisture

than those recorded at the weather stations, thereby supporting our initial hypothesis.

All these results indicate that *S. corsica* occupies environmentally buffered habitats, as previously suggested (Escoriza and Hernandez 2019). The probe data also detected the important variability between sites, which was dependent on the elevational gradient, indicating that *S. corsica* is not a narrow thermal specialist. During the surveys, we detected diurnal, crepuscular, and nocturnal activity among adult *S. corsica* in a temperature range of 4.8–22.0 °C and at RH exceeding 68.7% (Escoriza and Hernandez, unpublished data). These observations, combined with the probe data, suggest that the periods of activity of this species are concentrated from mid spring to early autumn at high elevations (above 1000 m) and during autumn–spring at lower elevations. The presence of larvae in streams and springs between late October and late May at mid and low altitudes indicates that reproduction occurs mainly in the autumn and spring, as in other species of Mediterranean salamanders (Caldonazzi and Tripepi 2006; Escoriza and Ben Hassine 2014). The temperature decline/humidity increase during September–October could trigger the onset of reproductive activity at low elevations.

The use of buffered habitats may prolong the period of surface activity of *S. corsica* in both the cold and warm seasons of the year and reduce its risk of exposure to lethal extreme temperatures (Hutchison 1961). Surface activity is critical for salamanders because it is associated with foraging, mating, and larval deposition (Lanza et al. 2007). Our results suggest that the conservation of patches of dense natural vegetation, particularly riparian formations in the maquia belt, will be important for the long-term preservation of this endemic island salamander.

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