The warmer, the yellower? Colour patterns of fire salamanders across different scales in the face of rising temperatures

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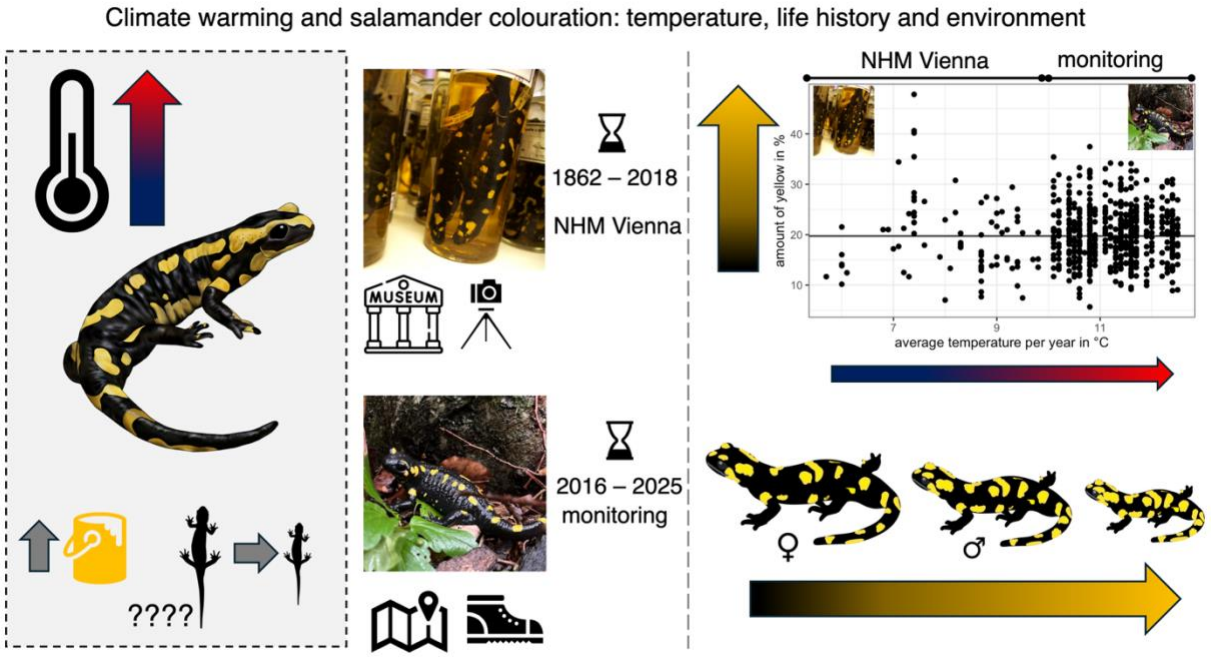
Abstract

The unprecedented increase in global temperatures might lead to phenotypical changes in many species to account for increased thermoregulatory processes. This could be due to increased selection pressures on traits such as colouration or body size. Using specimens from the Natural History Museum in Vienna for a long-term series and recent data from an ongoing fire salamander monitoring programme as a short-term series, we test the hypotheses that increasing temperatures over time are associated with reduced amount of black colouration of fire salamanders (yellower individuals), smaller body size and relatively longer limbs. We found no relationship between environmental temperature and proportion of yellow and black colouration at either time scale. In the long-term dataset, differences in colouration were only explained by location, whereas in the short-term dataset it was best predicted by body size, body condition and sex, with females being larger, heavier and less yellow than males. Likewise, we did not detect any decrease in body size or differences in limb length over time. The size and sex related patterns we observed are consistent with ontogenetic colour change and with potentially greater predation pressure on the smaller, more mobile males. Therefore, we conclude that yellow colouration is more pronounced during early life stages, strengthening the aposematic signal when individuals are most vulnerable towards predation. Yellow colouration is further influenced by resource availability during early life, individual age, predator community composition and natural selection, factors which cannot be resolved with our museum based and recent dataset.

Keywords: Allens rule, Bergmanns rule, Bogert effect, aposematism, thermal melanism

Graphical Abstract:



1. Introduction

The past few decades have shown a sharp rise in average temperatures. The period between 2011 and 2020 was ~1.09°C warmer than that between 1850 and 1900, and current projections under different scenarios indicate that temperatures will continue to rise in the coming years (IPCC 2023). This increase in global temperatures has affected, and will affect, the physiology, morphology, life history and behaviour of life on Earth (Abrahms et al. 2023, Bennet et al. 2021, Cavicchioli et al. 2019, Dillon et al. 2010, Masoero et al. 2024). Ectotherms are particularly vulnerable to temperature fluctuations because their own body temperature depends on that of their environment, and the steep temperature increases our planet is experiencing may lead them to reach their critical thermal maximum (Deutsch et al. 2008, Jørgensen et al. 2022, Pottier et al. 2025, Ruthsatz et al. 2024, Ujszegi et al. 2022). Therefore, adaptive genetic changes, migration or behavioural adjustments are necessary for ectotherms to avoid unfavourable temperatures and heat stress (Fuller et al. 2010, Muñoz 2022, Sunday et al. 2014).

Thermoregulation plays a pivotal role in the body's response to rising temperatures (Seebacher 2009, Muñoz 2022). One morphological feature crucial for thermoregulation is colouration. Dark colours absorb heat and are therefore more prevalent at higher latitudes and elevation, while lighter colours reflect radiation and are thus more common at lower latitudes and elevations. This phenomenon is known as Bogert's rule (Bogert 1949, Clusella-Trullas et al. 2007, 2008). Data from 41% of known anuran species provide support for

Bogert's rule, showing that frog colouration tends to become darker in colder regions, with thermoregulation being one of the main drivers of this pattern in temperate regions (Laumeier et al. 2023). A darker colouration also provides better protection against UVBs and the main pigments involved with the expression of dark colouration, melanins, are known to enhance immunocompetence (Laumeier et al. 2023, Mackintosh 2001, Roulin 2014).

Other morphological features, such as body size and limb length relative to body length, are also key for thermoregulation. Longer limbs help raise the body above the surface and dissipate heat, which has led to the formulation of Allen's Rule, a macroecological pattern whereby individuals in warmer climates have longer limbs relative to their body size than their counterparts from colder regions (Allen 1877). Likewise, species in colder climates are expected to be larger than those in warmer regions, a phenomenon known as Bergmann's Rule (Bergmann 1847). While both Allen's and Bergmann's rules have their origins in biogeography, they can also be used to predict potential responses to global warming (Tian & Benton 2020). Therefore, under the current global upward trends in temperature, one could expect a decrease in body size and an increase in limb length in relation to body length. While these trends have been observed in multiple taxa, ectotherms and endotherms alike (Alhajeri et al. 2020, Gardner et al. 2011, McQueen et al. 2024, Sheridan & Bickford 2011), the validity of these 'rules' is still under debate, as small-scale microhabitat conditions might be more relevant predictors (Goldenberg et al. 2022). This is particularly true for

amphibians, whose responses to warming temperatures appear to be less predictable than for other taxa (Adams & Church 2008, Alho et al. 2008, Ashton 2002, Guo et al. 2024, Liu et al. 2025).

Evolutionary changes require time and can only be observed over long periods, which limits our possibilities of detecting them. The collections available at Natural History Museums preserve the history of species over long periods of time, allowing us to have a glimpse of the past, and to access valuable information for predicting future changes in response to environmental pressures (Pyke & Ehrlich 2010, Sanders et al. 2023). Museum collections have aided the discovery of colour changes in ground beetles in urban habitats (Keinath et al. 2020), the detection of disease origins (Chytridiomycosis in frogs; Weldon et al. 2004), and changes in plant phenology (Vitasse et al. 2022), among others.

Ectotherm species displaying large areas of melanisation, large body sizes and short limbs in relation to their body length can be particularly vulnerable under increasing temperatures. Such is the case with the fire salamander (*Salamandra salamandra*), a widespread amphibian with the largest size among European urodeles (Sillero et al. 2014), short and sturdy limbs, and a characteristic bright, contrasting colouration featuring yellow (or orange/red) markings of various shapes and sizes on a black background (see Fig. 1A). Higher proportions of yellow (and thus lower proportions of black) have been found to elicit fewer predation attempts by avian predators (Caspers et al. 2020), highlighting potential trade-offs between antipredator protection and thermoregulation as previously found in other taxa

(Hegna et al. 2013, Lindstedt et al. 2009). Therefore, major changes in the proportion of black and yellow may directly affect fire salamanders' survival and ability to regulate their temperature in a warming world. Here, using museum specimens collected in Austria between 1862 and 2018, and individuals sampled in the field between 2016 and 2025, we tested the hypothesis that fire salamanders are becoming less black (yellower) over time in response to increasing temperatures. In agreement with Allen's and Bergmann's rules, we further hypothesise that fire salamanders are evolving longer limbs and smaller body sizes over time.

2. Methods

2.1 Data collection

2.1.1 Study species

The European fire salamander is widespread in Europe (Sillero et al. 2014) and inhabits mixed deciduous forests (Kovar et al. 2024). Its characteristic black and yellow (or orange/red) colouration (see Fig. 1A) becomes apparent upon metamorphosis (Sánchez et al. 2018) and is coupled with noxious chemical defences (i.e., it is aposematic; Knepper et al. 2019, Lüddecke et al. 2018, Poulton 1890, Sillero et al. 2014). The yellow markings are visible to avian and snake predators even under dim light conditions (Aguilar et al. 2023, Sánchez et al. 2019), and previous studies have shown that they are, at least to some extent, resource-dependent (Barzaghi et al. 2022, Caspers et al. 2020) and influenced by their background's albedo during development (Sánchez et al. 2019). Furthermore, the unique

127 individual colour pattern can be used to identify individuals, as the pattern does not change
128 much during adulthood (Balogová et al 2016, Wisniewski & Wisniewski 1998). While the
129 function of their colouration is believed to be mainly deterring predators, other hypotheses
130 are frequently discussed, e.g. males are more yellow than females (Balogová & Uhrin 2015,
131 Mühlenhaupt et al. 2025, Preißler et al. 2019), which could be related to sexual selection.
132 However, no behavioural studies exist that investigated mate choice in that species. Another
133 frequently discussed hypothesis is thermoregulatory function, although fire salamanders are
134 mainly active during dawn and during the night over most of their geographic range
135 (Thiesmeier 2004). We often observe them active during the day if the weather conditions
136 are favourable (mainly wet and with temperatures between 5 and 10°C; Catenazzi 2016).
137 Their peak activity times are spring (March-May when females deposit larvae into streams)
138 and autumn (Sept-Nov, when males are more active to search mating opportunities), with
139 this bimodal activity flattening to unimodal in higher elevations (Kovar et al. 2024).
140 Additionally, their larvae develop in small first or second order streams (and sometimes
141 ponds; Steinfartz et al. 2007) and are susceptible to increased temperatures as they develop
142 their colouration. Increasing temperatures could therefore influence the development of
143 larvae.

144 *2.1.2 Museum specimens*

145 We photographed the dorsal pattern of 92 adult fire salamanders (*Salamandra salamandra*
146 *salamandra*) from the herpetological collection of the Natural History Museum in Vienna,

147 Austria (hereon NHMW). The specimens were collected between 5 and 161 years ago (mean
148 ± SD = 70.14 ± 33.05 years) at 50 locations, primarily in central and eastern Austria (mean ±
149 SD = 1.84 ± 1.88 individuals per location; range = 1–10 individuals per location, Fig. 1B).
150 While the collection has a much larger number of specimens, we selected only those whose
151 dorsal patterns could be reliably photographed. The ethanol and formaldehyde used to
152 preserve amphibians dissolves the colour pigments in the skin (Juszczyk 1952), making it
153 impossible to characterise colouration beyond the pattern, i.e. proportions of yellow and
154 black. The other criteria to include specimens was a concise label with an approximate
155 location and year of collection. Most individuals had only broad location information, e.g.
156 the city nearby, or a district. We used Google Maps to get as close as possible to the actual
157 locations and extracted the coordinates in WGS84.

158 Photographs were taken with a Canon EOS 1200D camera (ISO 200, RAW, F4.5, 1/15,
159 standard), next to graph paper for scale. Due to the preservation, some of the salamanders
160 were crooked and it was therefore impossible to take a photograph from the whole dorsum.
161 We made sure to obtain the best view of their dorsum from the remaining specimens,
162 allowing for subsequent image processing. The images were analysed using the software
163 Image J (Schneider et al. 2012). First, we measured the snout-vent length (SVL) of the
164 salamanders with the *straight* tool, using the mm-paper for calibration. We then selected
165 the dorsal area (excluding the tail and limbs) with help of the polygon selection tool. Images
166 were converted to RGB-stacks, and the “red” image stack was used for further analyses. All

the patches were delimited and all instances caused by reflection on the skin were corrected with the black brush tool. The "Auto Threshold" function was used and bright outliers with a radius over 10 pixels and thresholds over 10 were removed. Finally, we analyse all particles from 50 to Infinity pixel² size, with circularity ranging from 0 to 1. We extracted the total proportion of yellow colouration on the dorsum (%), the number of patches (number) and the mean area of patches in mm² (area). The proportion of black colouration was calculated by subtracting the area with yellow colouration from the total dorsal area.

2.1.3 Historical temperatures

We connected QGIS (QGIS Development Team 2024) to the Geosphere Austria data hub (https://data.hub.geosphere.at/dataset/histalp-v1-1y) using the Austria weather API plugin (Matzl 2024). Then, we mapped the approximate locations of the museum specimens included in the study and identified the closest weather station for which temperature data was available (Fig. 1B). We extracted the average annual temperature data for the 12 closest weather stations in the years of salamander collection. Additionally, we used the elevation of the weather stations as a proxy for the elevation at which the salamanders were found to test for a correlation between elevation and proportion of yellow colouration. The elevation range of the weather stations is 209 m to 855 m. We used the HISTALP homogenised long-term dataset (Auer et al. 2007) for the temperature database. This approach aimed to minimise the inherent uncertainty in museum data collection in cases where exact locations were unavailable.

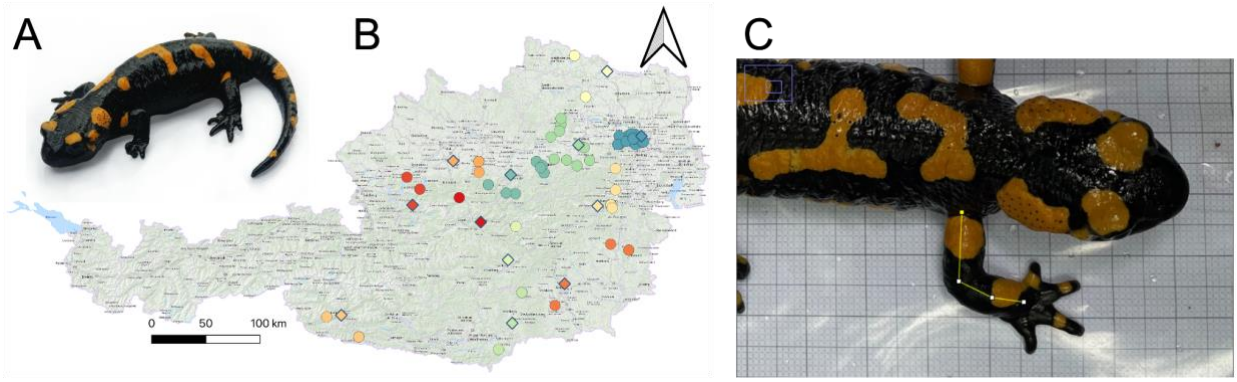


Fig. 1. (A) Fire salamander (*Salamandra salamandra*) in the Vienna Woods with typical dorsal pattern (Photo: Kristin R. Szydlik) and (B) approximate locations of fire salamanders from the herpetological collection (round dots) and the closest weather station (diamonds). Each colour corresponds to a fire salamander location and the respective weather station as the source for annual temperature data and elevation. Source map: Geoland Basemap Austria (http://open.data.gv.at). (C) Example of how the limb measurements were obtained using the program Image J and the "segmented line" tool (Photo: Kristin R. Szydlik).

2.1.4 Field sampling

Since 2016, the Vienna Zoo has led a salamander monitoring program in which photographs of fire salamanders have been taken in three locations in the Viennese part of the Biosphere Reserve Vienna Woods: Neuwaldegg, Waldandacht and Moosgraben. Up to 50 individuals were sampled per year in each locality, all of which were weighed and photographed on

graph paper for further measurement of body size and limb length. Limb length was measured as the length from the axilla to the wrist (Fig. 1C).

For our colour pattern analyses we randomly chose up to 20 individuals, 10 females and 10 males, from each location and year (total n = 555, females = 270, males = 285). The images were analysed using the software Image J (Schneider at el. 2012). The size of each individual was measured on a photo after calibrating using the reference lines on the graph paper. To minimise optical distortion, four reference lines were used to set the mean number of pixels per centimetre as the scale (two horizontal and two vertical lines, one at each end of the salamander). Then, we measured the snout-vent length (SVL) of the salamanders along the spine using the "segmented line" tool. Using the "polygon selection" tool we selected the dorsal area (excluding the tail and the limbs). If the photo was taken from a different angle than 90°, we excluded the flanks to account for differences in body shape (e.g. bloated individuals). The images were then converted into RGB-stacks, and the red image stack was used for further analyses. All reflections on the skin were corrected using the black brush tool. We used the "Auto Threshold" function to remove bright outliers with a radius over 10 pixels and thresholds over 10. Finally, we analysed all particles with an area from 50 to Infinity pixel² size and with circularity ranging from 0 to 1. We extracted the total proportion of yellow colouration on the dorsum (%), the number of patches (number) and the mean area of patches in mm² (area).

We calculated body condition using the Scaled Mass Index (Peig & Green 2009), but we used a non-linear power function to calculate the scaling exponent instead of the standard major axis regression (Brodeur et al. 2020). This reduced the correlation between Scaled Mass Index and SVL (Brodeur et al. 2020). The scaling exponent was 2.29 and the mean SVL of salamanders was 11.3 cm.

2.1.5 Recent temperature

The recent temperature data were extracted with the Austria weather API plugin (Matzl 2024) to connect QGIS to the Geosphere Austria data hub. We used the historical time series Spartacus v2.1 as base for the temperature data (https://data.hub.geosphere.at/dataset/spartacus-v2-1y-1km) and extracted yearly annual mean temperature for the years 2016 – 2025. The 1 km grid cell was based on sample location, Neuwaldegg (N 48.249014, E 16.264597), Waldandacht (N 48.214128, E 16.202622) and Moosgraben (N 48.227256, E 16.258833, all WGS84).

2.2 Statistics

The NHMW specimens were grouped based on the location of the nearest weather station. In the case of samples from Styria, they were grouped based on biome similarities and elevation. This approach was adopted to minimise the number of singletons in the data (Fig. S1, Appendix A) and to account for differences in elevation, given that exact locations could not be identified.

We used pairwise Pearson correlations to check for autocorrelation among the variables. We then used the variance inflation factor from the *car* package (version 3.1–3; Fox & Weisberg 2019) to reduce the number of autocorrelated variables in our models. The full linear model used to analyse the (log-transformed) proportion of yellow colouration in the museum's dataset included mean annual temperature, scaled snout-vent length (SVL) in cm, weather station and year of collection as predictors. The full linear model used to analyse the proportion of yellow colouration (log-transformed) in the recent dataset included mean annual temperature, scaled snout-vent length (SVL) in cm, location, body condition, sex, and year of collection. The dredge function (MuMIN, version 1.48.11; Barton 2025) was used for backward selection to determine the optimal model based on the Akaike information criterion for small samples (AICc) (Burnham et al. 2011). We calculated relative limb length as the residuals from linear models of limb length as a function of body size, with values above 0 indicating that the limbs are longer than expected based on the model. All analyses were conducted using R (version 4.4.1, R Core Team 2024) in the RStudio environment (version 2024.9.1.394, Posit Team 2024). The packages *ggplot2* (version 3.5.1, Wickham 2016) and *gridExtra* (version 2.3, Augie 2017) were used for visualisation; *dplyr* (version 1.1.4, Wickham et al. 2023) for data manipulation; *DHARMa* (version 0.4.7, Hartig 2024) for model validation; and *GGally* (version 2.4.0, Schloerke et al. 2025) for visual data exploration (correlation matrix). The R script for conducting the analyses has been made available alongside the data (Dittrich et al. 2026).

3. Results

3.1 Museum specimens

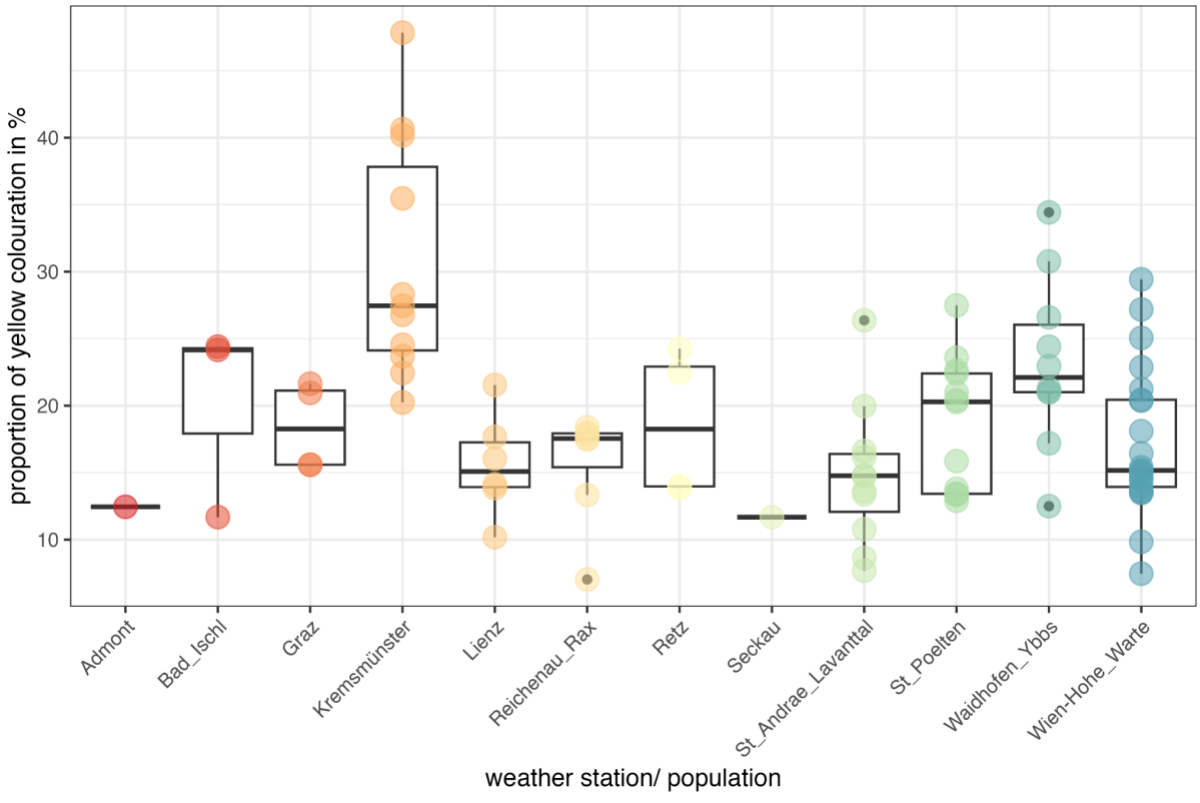
The NHMW dataset included 92 individuals (35 females, 55 males and two individuals of unknown sex). There was a difference in body size between the sexes, with females being slightly larger on average (female SVL = 97.33 ± 7.75 mm; male SVL = 92.8 ± 8.06 mm; t-test, $t = 2.65$, $p < 0.01$). We could not detect a difference between females and males in the proportion of yellow colouration. The body size of all individuals shows a trend to increase over time (Pearson's $r = 0.2$, $p = 0.054$, n = 92), which might be due to a couple of specimens (Fig. S2, Appendix A) as the linear model shows a poor support ($t = 1.95$, $p = 0.054$, *adj.* $R^2 = 0.03$).

Variables quantifying dorsal colour patterns exhibited strong correlations with one another. For instance, the average patch size is strongly and positively correlated with the overall proportion of yellow (Pearson's $r = 0.84$, $p < 0.001$, n = 92). Conversely, the number of yellow patches is negatively correlated with the average patch size (Pearson's $r = -0.63$, $p < 0.001$, n = 92). In other words, salamanders with more patches on their dorsal area had smaller patches. Consequently, there was also a negative correlation between the number of patches and the proportion of yellow (Pearson's $r = -0.46$, $p < 0.001$, n = 92). Due to these inherent correlations, we only used the proportion of yellow as the response variable.

The annual mean temperature and elevation of weather stations showed a strong negative correlation (Pearson's $r = -0.79$, $p < 0.001$, n = 12, Fig. S3, Appendix A). Therefore, we used

284 either annual mean temperature or elevation as a variable in our models to reduce
285 autocorrelation.

286 The automated model selection process to predict the proportion of yellow colouration
287 indicated that location (i.e., weather station) was the best predictor of colouration
288 differences, regardless of mean annual temperature, SVL, year or elevation ($p < 0.001$, *adj.*
289 $R^2 = 0.31$; Fig. 2). When we ran the model with elevation as a predictor variable, the
290 automated model selection gave two models with the same AICc and weights that included
291 location and elevation as predictors. Using the model average function, we found that only
292 location (the same final model as above) showed a significant effect, not elevation.



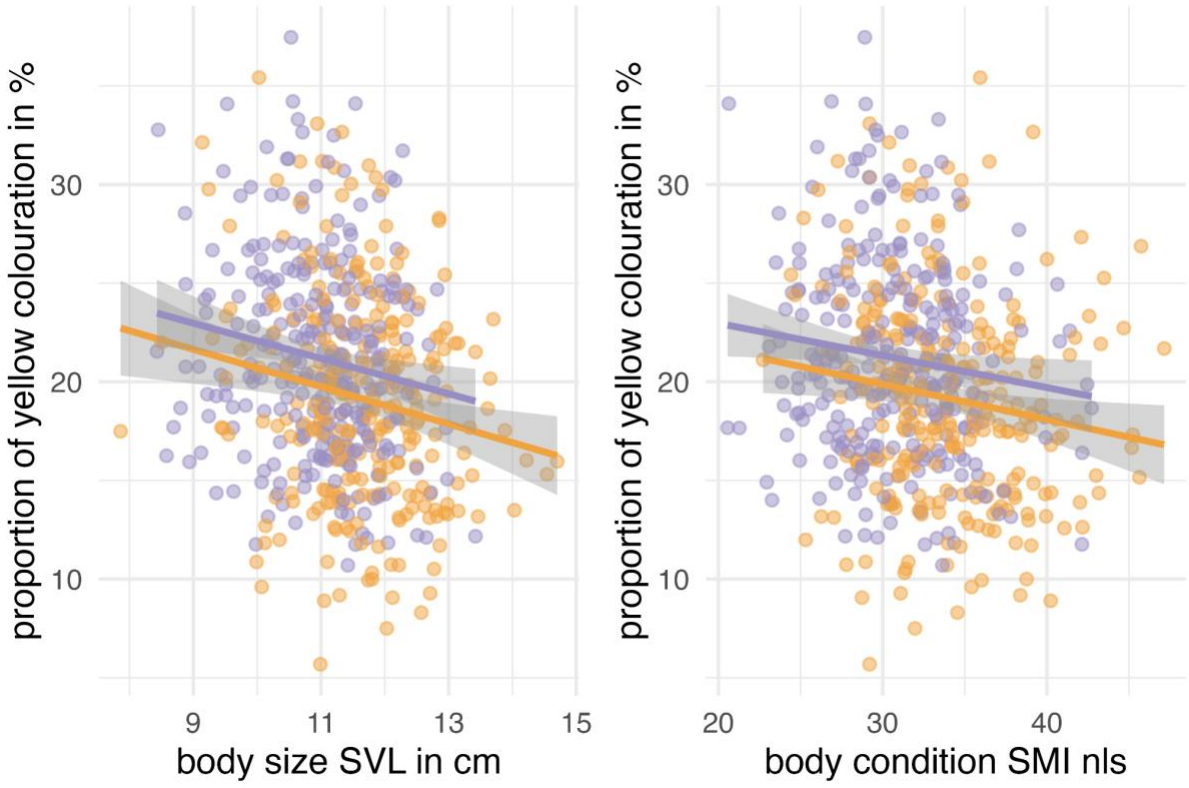
293

Fig. 2. Given is the proportion of yellow colouration on the dorsum in percent for each individual (dots). Colours represent the locations on the map given in Fig 1B. The salamanders in the collection have been grouped to the nearest weather station as a proxy for population (boxplots with median, and whiskers showing the 1.5 interquartile range).

3.2 Field sampling

We observed sex differences in body size (all Welsh two sample t-test; $t = 7.91$, $p < 0.001$), body condition ($t = 9.05$, $p < 0.001$), and proportion of yellow colouration ($t = -4.65$, $p < 0.001$). Females were larger, heavier and less yellow than males. The body size increases slightly over time (Pearson's $r = 0.1$, $p = 0.016$, n = 553, Fig. S4, Appendix A), but the linear model shows a poor support ($t = 2.41$, $p = 0.016$, *adj.* $R^2 = 0.009$). The body size shows no trend with temperature per se. The proportion of yellow colouration on the dorsal area varied considerably within the dataset, ranging from 5.7% to 37.5% (mean ± SD: 20.2 ± 5.3%), and correlated positively with mean patch size (Pearson's $r = 0.69$, $p < 0.001$, n = 553) and negatively with patch number (Pearson's $r = -0.23$, $p < 0.001$, n = 553). Therefore, the number of patches and the mean patch size show a strong negative correlation (Pearson's $r = -0.62$, $p < 0.001$, n = 553): the more patches, the smaller the mean size of the patches. This is the same pattern observed in the historical dataset.

313 The best linear model for explaining variability in the proportion of yellow colouration
314 included body size, body condition, and sex as informative variables. Larger, heavier females
315 displaying lower proportions of yellow colouration ($p < 0.001$, *adj.* $R^2 = 0.09$, Fig. 3, model
316 details in Appendix A). We observed an increase in mean annual temperature in all three
317 locations over the ten-year period, with Waldandacht being the warmest location (Fig. S5,
318 Appendix A). However, temperature was not retained as an informative variable in any
319 model.
320



321

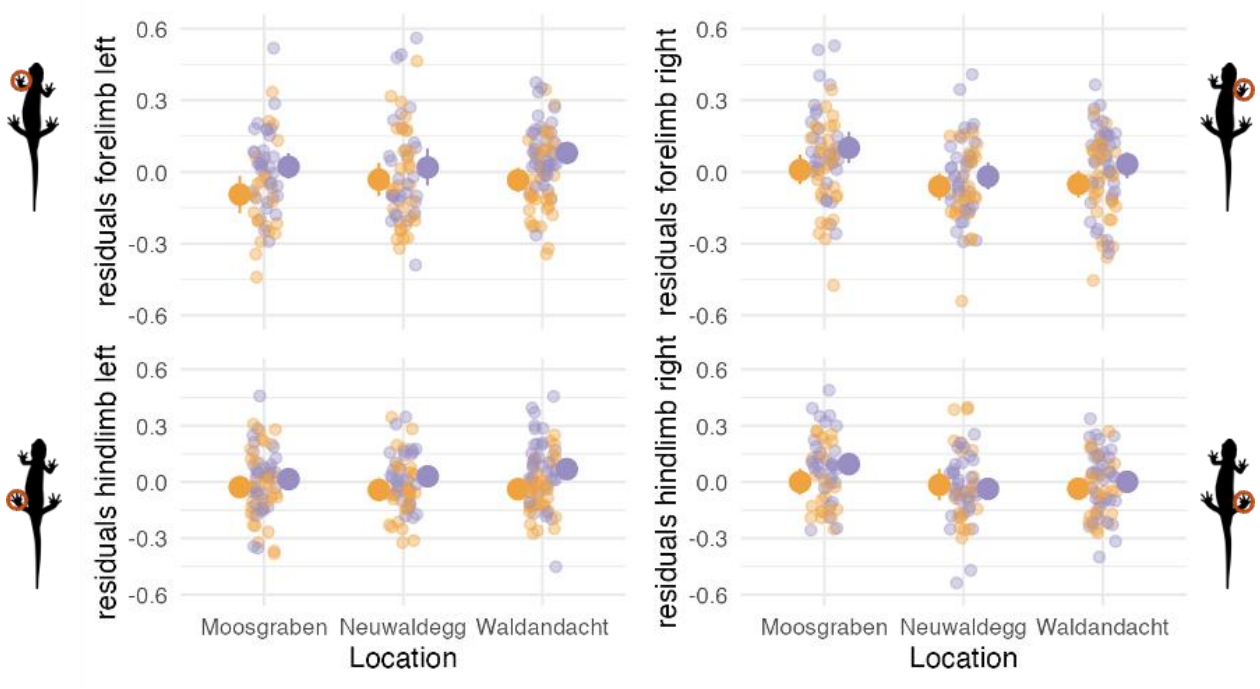
322 **Fig. 3.** Linear model of body size (SVL) in cm (left) and body condition as Scaled Mass Index
323 (right) from a non-linear regression on proportion of yellow colouration of salamanders

dorsum (orange = female, purple = male). The grey shading corresponds to the 95% confidence interval. Both variables were retained in the best models to explain the proportion of yellow colouration on the dorsal area of the salamanders (n = 555).

3.3 Limb length in relation to body size

Due to differences in the angles at which the photos were taken or blurred pictures due to the motion of salamanders, we were unable to measure all four limbs of each individual. Therefore, we have a maximum of two measurements per individual. We measured the right and left forelimbs of 200 and 196 individuals, respectively. Likewise, we measured the right and left hindlimbs of 181 and 204 individuals, respectively.

We found a significant effect of sex in all models, with males having comparably longer limbs than females (forelimb left, $t = 3.93$, $p < 0.001$; forelimb right, $t = 2.78$, $p < 0.01$; hindlimb left, $t = 2.92$, $p < 0.01$), except for the right hindlimb (Fig. 4; detailed models in Appendix A). Annual mean temperature was not retained as an informative variable in any of the models.



340

341 **Fig. 4.** The residuals of the left and right forelimbs (upper panels) and the hindlimbs length
342 (lower panels) are related to SVL. They are separated by sex (orange = females; purple =
343 males) and location, where males mostly show positive residuals (longer limbs in relation to
344 body size). The small circles represent individual values, and the larger circles represent
345 mean values with bootstrapped 95% confidence intervals per sex and location.

346

347 **4. Discussion**

348 Museum collections and long-term series sampling have been recognised as meaningful
349 sources of information to investigate phenotypic changes in response to climate change
350 (Koskenpato et al. 2023, MacLean et al. 2019, Ożgo et al. 2017, Sanders et al. 2023, Zipkin
351 & Williams 2025). Contrary to our expectations, we observed neither a reduction in body
352 size nor an increase in proportion of yellow colouration over time at any of the time scales

353 studied. Hence, we found no support for Bergmann's rule in either time scale. Moreover,
354 we did not observe increases in limb length over time in the recent dataset, thereby failing
355 to support Allen's rule. Instead, we found that body size did only slightly increase over time
356 at both time scales, and that the proportion of yellow colouration was best explained by
357 location in the historical dataset, and by body size, body condition and sex in the recent
358 dataset, regardless of annual mean temperature for the year of collection.
359
360 **4.1 Museum data**
361 *4.1.1 Colouration*
362 We found no evidence that temperature influenced the proportion of yellow colouration of
363 fire salamanders from the NHMW herpetological collection across the years studied. In fact,
364 we could not detect any trend in the proportion of yellow over time. Instead, and consistent
365 with Bogert's rule, location was the best predictor of the yellow proportion, which might
366 be related to local and elevational differences (less yellow at higher elevations, although not
367 significant in our model). Other confounding factors that could contribute to differences in
368 the proportion of yellow among locations are resource availability (Barzaghi et al. 2022,
369 Caspers et al. 2020), thermal microhabitats (Sears & Angilletta 2015) and/or predator
370 communities (Hagnier & Dittrich et al. 2025, Rönkä et al. 2020, Valkonen et al. 2012).
371 However, several limitations prevent us from drawing any evidence-based conclusions
372 about the true effects of location. First, the sample size used for the analyses is too small
373 considering the time span. Second, because the exact locations of where the specimens were

found are unknown, we approximated each locality to a 20 km radius around the location mentioned on the specimen label or in the collection books. Due to the topography of many mountain valleys, significant elevational differences exist on a small spatial scale. This is why we used weather stations as a proxy for elevation; however, the true elevation of the specimens may differ considerably. This could explain why we do not observe a significant influence of elevation on the proportion of yellow, despite a trend in the data.

Food availability during larval development has been shown to affect the proportion of yellow in post metamorphic individuals in some studies (Caspers et al. 2020), but not in others which, instead, show an effect on yellow colouration hue and saturation (Barzaghi et al. 2022). These contradictory but complementary findings point at yellow colouration as a plastic trait. This environmental plasticity makes it more difficult to attribute adaptive effects based on natural or sexual selection, particularly given that heritability of yellow colouration between parents and their offspring appears weak, based on neutral genomic markers (Sánchez et al. 2019, Burgeon et al. 2020). Nevertheless, differential expression of colour genes is associated with colour morphs (Burgon et al. 2020) and might be influenced by epitranscriptomic RNA-methylation (Strowbridge et al. 2026), indicating a multimolecular mechanism of colour variation, potentially influenced by environmental effects, besides pure genetic heritability. Given the nature of museum data, it is practically impossible to estimate the availability of resources during early life stages of the sampled individuals if their exact locations are unknown. Landsat data or historical information

394 could offer a rough proxy of resource availability at the time of collection, but this approach
395 requires further investigation.
396 Historical habitat characteristics could also improve predictions of habitat heterogeneity
397 which is a key buffer against thermal stress (Angilletta 2009, Suggit et al. 2011). Variable
398 thermal environments could mitigate thermal heat stress by providing suitable
399 microhabitats (Sears & Angilletta 2015). Through such thermoregulatory behaviour,
400 organisms can reduce evolutionary pressures by seeking out thermally preferred
401 microhabitats, decreasing the potential evolutionary rate, known as the Bogert effect
402 (Muñoz 2022). If salamanders can thermoregulate through behavioural adaptations in a
403 suitable heterogeneous habitat, the selective pressure to adapt morphologically would be
404 greatly reduced, providing an alternative explanation for the lack of any relationship
405 between temperature and proportion of yellow over time. This could also be true for the
406 lack of changes in body size (Bergmann's rule) and limb length (Allen's rule) we
407 hypothesised.
408 Geographic variation in colour patterns may reflect differences in the composition of
409 predator communities among localities, with predators exerting stronger selection on
410 certain colour patterns in one location than in others (Nokelainen et al. 2014, Rönkä et al.
411 2020, Valkonen et al. 2012). Such differences in predation pressure are shaped by habitat
412 characteristics themselves (Van Tran & Nishikawa 2023). Fire salamanders, for example,
413 have been suggested to experience higher predation pressure in forest patches with greater
414 tree diversity and evenness (Hagnier & Dittrich et al. 2025), although this selective pressure

415 is unlikely to act uniformly across life stages. While adult fire salamanders appear well
416 protected from predators, with only a few known bird and mammal predators (e.g., birds of
417 prey: Bustamante 1985; Łaciak 2022; rats: Velo-Antón 2024; wild boars: Thiesmeier &
418 Grossenbacher 2004), juveniles seem to be more vulnerable (Thiesmeier 2004). Rats,
419 chickens and ducks have all been reported to prey on them (Horter & Greven 1981), likely
420 because metamorphs are very conspicuously displaying a large proportion of yellow
421 colouration, but not necessarily a large amount of toxins (Preißler et al. 2019, Sánchez et al.
422 2019, Burgon et al. 2020).
423
424 *4.1.2 Caveats of using museum specimens*
425 Although museum collections have proven valuable to investigate the effects of global
426 change (Sanders et al. 2023), offering spatio-temporal biodiversity records of a depth
427 unavailable from other sources, they come with inherent caveats such as poor spatial and
428 temporal resolutions that vary with the species and historical collection efforts. In our case,
429 many localities were represented by single observations which we assigned to the next
430 available weather station. This may not accurately reflect temperatures at specific locations,
431 but it allows us to model the data with a consistent and reliable bias across all samples. This
432 underscores the importance of metadata in museum collections, a resource with great
433 potential and ongoing refinements (Hedrick et al. 2020, Schindel & Cook 2018, Skevakis et
434 al. 2014). A further source of error is collector bias: because more conspicuous individuals
435 are easier to detect, sampling may have favoured individuals with a larger proportion of

436 yellow. The individuals from Kremsmünster, for example, were the most yellow, with
437 values well above average, and contributed substantially to the significant effect of location
438 in our dataset.
439 Beyond sampling, the preservation and storage of specimens introduce their own challenges
440 (Pierson et al. 2020). Preservation treatments have been shown to induce the shrinkage or
441 enlargement of specimens in different magnitudes depending on the time elapsed since
442 fixation, reducing the accuracy of morphological measurements (Lee 1982). Studies on
443 anurans, for example, have shown a shrinkage of nearly 6%, with larger species suffering
444 greater absolute shrinkage than smaller ones (Deichman et al. 2009). Preservation also alters
445 colouration, as fixatives lead to a loss of natural colours present in the living animals
446 (Juszczyk 1952). This makes it impossible to assess whether there are changes in the colours
447 themselves over time. However, because fire salamanders bear characteristic yellow
448 markings on a black background, the proportions of both colours can be calculated despite
449 the dull appearance of the preserved specimens.
450 A more fundamental limitation concerns timing. Because yellow colouration develops early
451 in life, shortly before metamorphosis (Sánchez et al. 2018), the temperatures experienced
452 during development may matter more than the temperature experienced at the time when
453 the animal was found. However, the true age of the preserved specimens cannot be reliably
454 determined. Some studies suggest that averaging temperatures over the 5-8 years prior to
455 the year of collection is more informative and avoids the influence of temperature extreme

456 years (Mühlenhaupt et al. 2025). Even so, we expect this bias to remain stable, and the
457 overall warming trend should still be represented in our dataset.
458
459 **4.2 Field data**
460 *4.2.1 Body size, condition and sex*
461 We found no evidence that temperature affected the proportion of yellow colouration of
462 fire salamanders sampled over the last 10 years, consistent with the broader absence of
463 empirical support for "thermal melanism" in this species (Burgon et al. 2020, Mühlenhaupt
464 et al. 2025). Instead, the best predictors of yellow proportion in our recent dataset were
465 body size, body condition and sex. Females were larger and in better body condition but
466 displayed a significantly smaller proportion of yellow. This sexual dimorphism echoes
467 previous studies (Bálogova & Uhrin 2015, Preißler et al. 2019, Mühlenhaupt el al. 2025,
468 Alarcón-Ríos et al. 2026), in which males consistently show a larger proportion of yellow
469 than females. Likewise, and confirming previous findings, (Barzaghi et al. 2022, Caspers et
470 al. 2020), larger individuals of both sexes had lower proportions of yellow.
471 These sex and size related patterns are likely intertwined. Fire salamander colour patterns
472 change during ontogeny, particularly in the first year after metamorphosis, as markings
473 shrink in area and/or split into two or more (Wisniewski & Wisniewski 1998, Balogová et
474 al. 2016, K. Szydlik's own observation). This could gradually reduce the proportion of yellow
475 towards adulthood. Because body size serves as a proxy for age in this continuously growing
476 species (Barzaghi et al. 2022), and yellow proportion decreases with body size, the apparent

477 sex specific patterns observed may stem partly from body size *per se*, given that males are
478 usually smaller than females (Labus et al. 2013).
479 Differences in mobility and predation risk may further reinforce this pattern, although
480 through contrasting routes in each sex. Males are smaller and lighter, but are also more
481 mobile when searching for mates during their main activity peaks in spring and summer
482 (Kovar et al. 2024) and occupy larger home ranges (Burgstaller et al. 2021). This higher
483 activity increases their exposure to potential predators, making a larger proportion of yellow
484 advantageous as a warning signal (Caspers et al. 2020), a pattern observed in other
485 aposematic species, where the more mobile and presumably more vulnerable sex is the more
486 conspicuously coloured (Rojas & Endler 2013; Rojas et al. 2026). Females, by contrast,
487 become highly visible when depositing their larvae in streams, as the background changes
488 from mainly leaf-coloured soils to bare rocks or sand of first-order streams. Yet, their narrow
489 home ranges, situated close to water (Burgstaller et al. 2021), keep their overall mobility,
490 and thus their predation exposure, to a minimum.
491
492 *4.2.2 Limb length*
493 Males also had longer limbs than females, a common pattern observed in this species and
494 family (Altunışık 2017, Labus et al. 2013, Reinhard et al. 2015). This dimorphism likely
495 reflects the demands of male reproductive behaviour. Males engage in rival combats with
496 other males (Altunışık 2017), perform "scouting" behaviour by pushing up on their
497 forelimbs to survey their surroundings from a higher position, and they wrap their forelimbs

around the females´ legs during courtship (ventral amplexus, Arnold 1987). Such behaviourally driven selection on the forelimbs is consistent with broader evidence that male locomotor and grasping traits are often under stronger selection to increase relative to body size, enabling males to outcompete rivals (Howard & Kluge 1985, Petrović et al. 2017, Altunışık 2017). As with the proportion of yellow, we found no evidence of an increase in limb length with rising temperature, and therefore no support for Allen's rule in this case.

5. Conclusion

Our findings do not support the hypothesis that rising temperatures have influenced the amount of yellow/black colouration in fire salamanders over time. Additionally, individual size did not decrease as postulated in our initial hypothesis. Instead, the proportion of yellow was best predicted by location in the historical dataset, and by size, body condition and sex in the recent dataset. Males display more yellow than the larger females, a pattern likely shaped by ontogenetic colour change and sex differences in mobility and predation risk. Future work integrating fine-scale historical data on resources, microhabitats and predator communities will be key to disentangle the plastic, behavioural and selective pressures underlying colour variation in fire salamanders.

Ethical statement

All handling of animals was in accordance with the Austrian animal welfare Act (Tierschutzgesetzt). Permits for handling the live salamanders were granted by Magistrat

519 der Stadt Wien, Umweltschutzabteilung (MA 22) to Doris Preininger (permit N. MA 22 -
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521
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529
530 **Author contributions (CRediT)** – Conceptualisation: BR, CD; Data curation: AKKJ, CD,
531 KRS, DP; Formal analysis: CD, KRS; Investigation: AKKJ, CD, DP; Methodology: CD, BR,
532 KRS; Resources: DP, BR; Supervision: CD, BR; Visualization: CD; Writing – original draft:
533 CD, BR; Writing – review and editing: All authors.
534
535 **Data and Code availability**: All data and R code was uploaded to a Zenodo repository in
536 order to re-run all analysis. The DOI is 10.5281/zenodo.21258587
537
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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Declaration of generative AI use

During the preparation of this work CD used Claude Opus 4.8 (adaptive) to improve the structure of the discussion and clarity of writing. After using this tool/service, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

Appendix A: Supplementary material

Historic dataset (NHM Vienna)

Proportion of yellow colouration over time in the NHM dataset. We see many singletons per location and year, no clear pattern regarding the proportion of yellow over time. In order to be able to run models, we summarized locations per nearest weather station (n = 12).

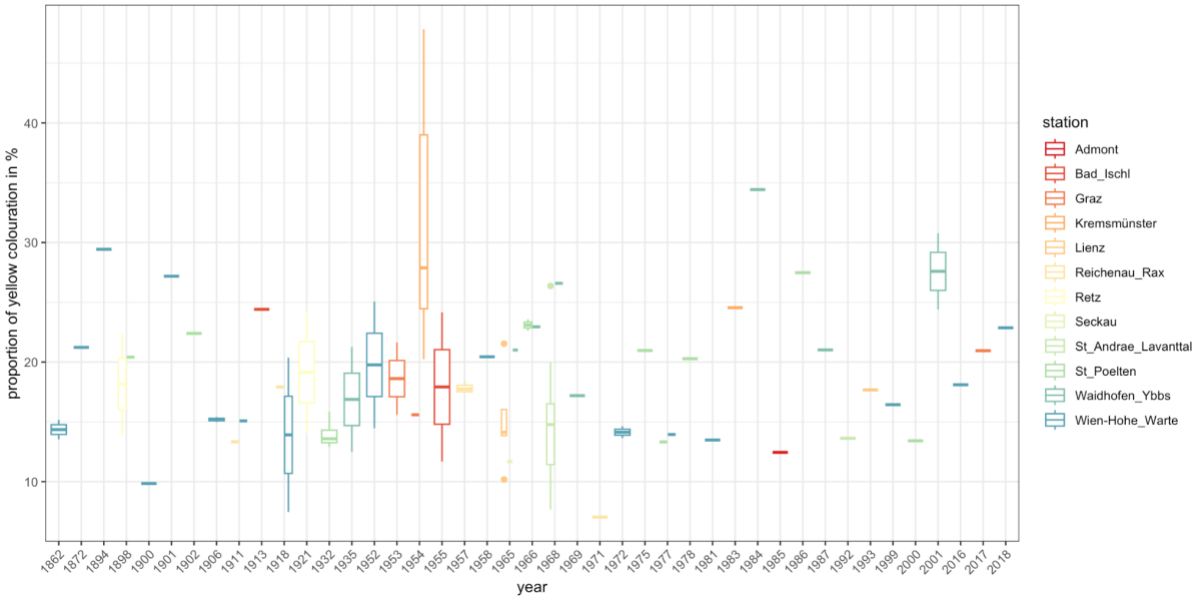
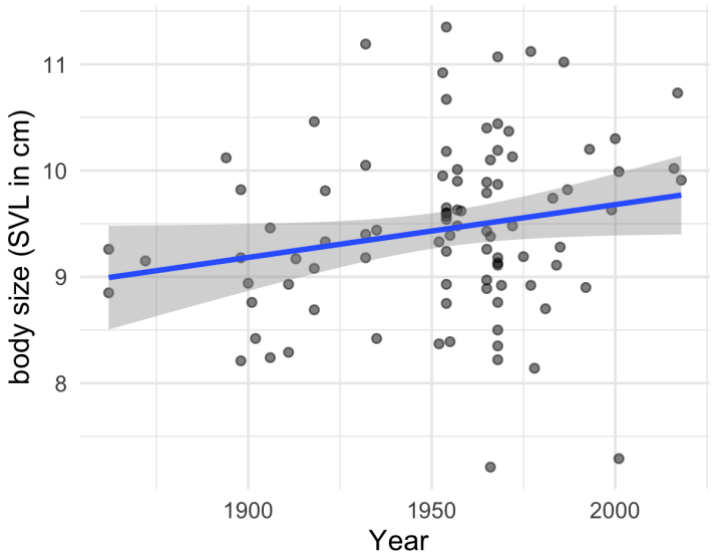


Fig. S1. Proportion of yellow colouration in % (y-axis) and year of collection (x-axis). Colouration based on weather stations presented in Fig. 1B.

Body size

Changes in body size of specimens in the collection over time (Pearson, $r = 0.2$, $p = 0.054$, n = 92), linear model ($t = 1.95$, $p = 0.054$, *adj.* $R^2 = 0.03$).



574

575 **Fig. S2.** Body size (SVL cm) over time (year as an integer). There is a trend towards bigger

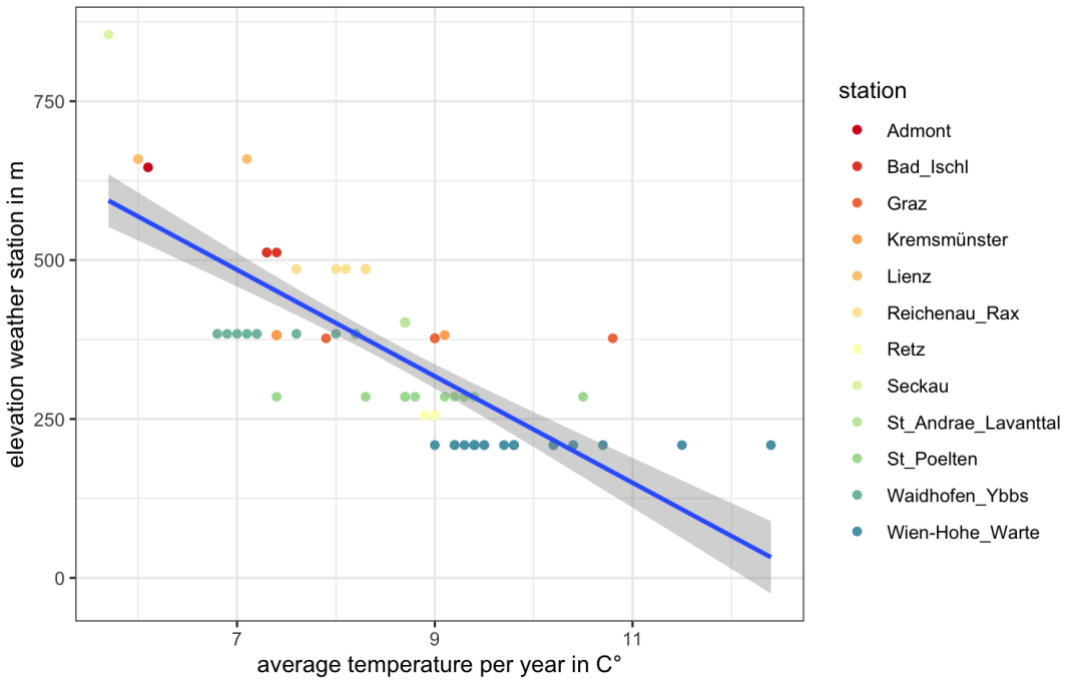
576 body size in the collected specimens.

577

578 **Environmental correlations**

579 Elevation of weather stations and average mean annual temperature when salamanders

580 have been collected. Strong correlation of both variables Pearson, $r = -0.79$, $p < 0.001$.



581

Fig. S3. Weather station data from the HistAlp dataset, dots represent temperature data from that station at a given year (when salamanders have been collected). The x-axis gives annual mean temperature in °C, y-axis the elevation in metres above NN. Colours for each station (n=12) according to Fig 1B and linear model regression line in blue.

Recent dataset (2016 - 2025, three locations in the Biosphere reserve Wienerwald)

Body size increase over time

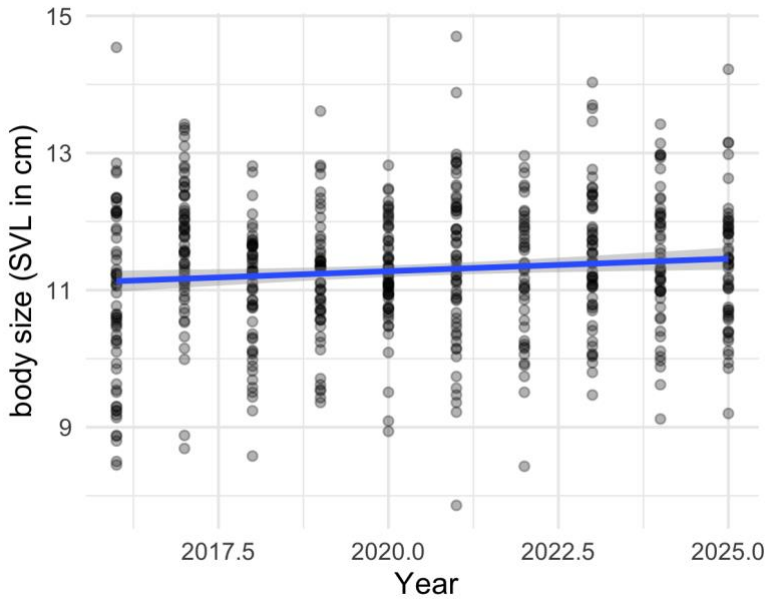


Fig. S4 Body size in SVL (cm) over time (Year as integer variable). Slight increase of body size over time (Pearson, $r = 0.1$, $p = 0.017$, n = 553), but poor model support for a linear model (estimate = 0.037, $p = 0.016$, $r^2 = 0.009$).

Temperature data

Recent data set

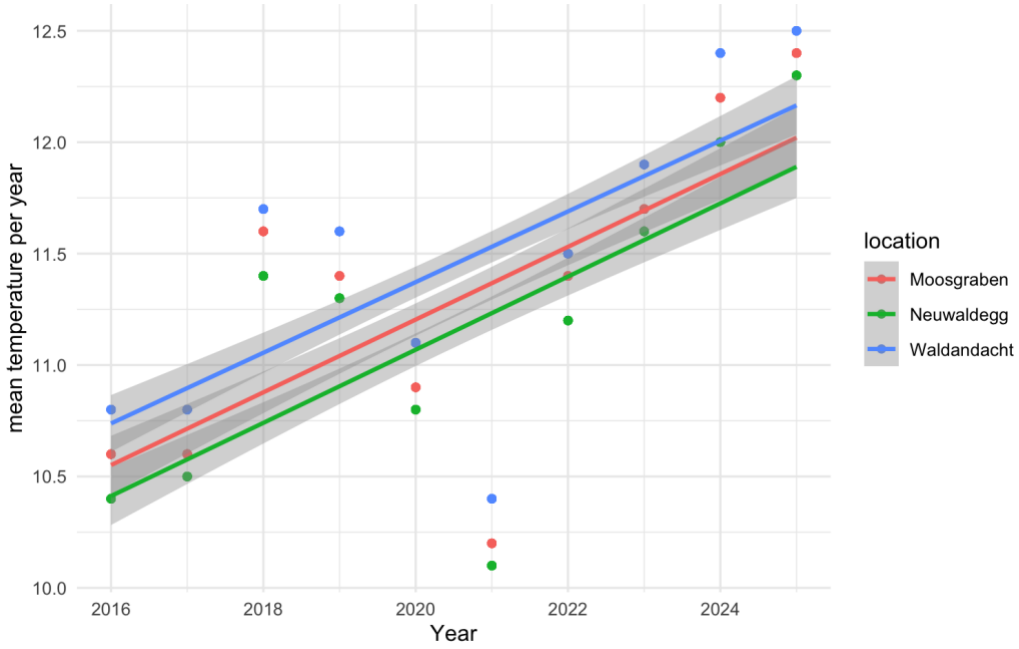


Fig. S5 Mean temperature per year for the three locations in the Biosphere reserve Vienna Woods where salamanders have been sampled. Increase in temperature over time

Detailed output of the best model predicting the proportion of yellow colouration in the recent data set

1. Model of proportion of yellow, recent data

Full model: lm(log(perc_yellow) ~ Temp_annual_mean + SVL_cm + location + year_f + sex + smi_nls, data = rec)

Best model: lm(formula = log(perc_yellow) ~ location + SVL_cm + sex + smi_nls + 1, data = rec)

Residuals: Min 1Q Median 3Q Max

-1.2796 -0.1695 0.0212 0.1786 0.6137

Coefficients: Estimate Std. Error t value Pr(>|t|)

(Intercept) 3.745054 0.178112 21.026 < 2e-16 ***

SVL_cm -0.046789 0.011625 -4.025 6.51e-05 ***

smi_nls -0.009022 0.002682 -3.364 0.000823 ***

sexM 0.054976 0.025401 2.164 0.030873 *

locationNeuwaldegg 0.001994 0.027311 0.073 0.941826

locationWaldandacht 0.049206 0.027347 1.799 0.072524 .

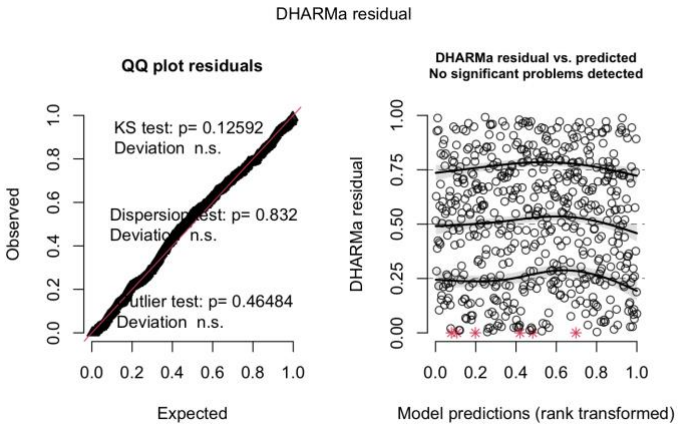
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.2605 on 549 degrees of freedom

Multiple R-squared: 0.09752, Adjusted R-squared: 0.0893

F-statistic: 11.86 on 5 and 549 DF, p-value: 6.456e-11

Model validation with DHARMa



Detailed output of the best models predicting the limb length in the recent data set

2. Limb length

Models for limb length, separated by limb

Fore limb right: Final model and validation

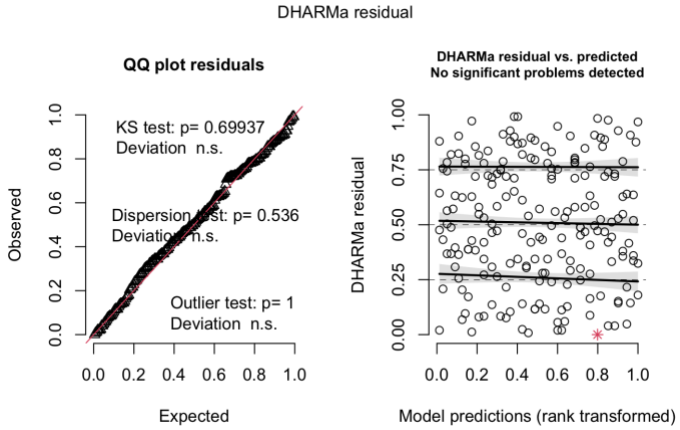
lm(formula = m1$residuals ~ sex + year_f + location, data = df_fl_right)

Residuals: Min 1Q Median 3Q Max

-0.65275 -0.09955 0.00460 0.12386 0.45430

```
Coefficients:    Estimate Std. Error t value Pr(>|t|)
(Intercept)      -0.012613   0.056798  -0.222  0.82450
sexM              0.070718   0.025449   2.779  0.00601 **
year_f2017        0.153899   0.070871   2.172  0.03115 *
year_f2018       -0.007535   0.063745  -0.118  0.90604
year_f2019       -0.008849   0.065878  -0.134  0.89329
year_f2020        0.001908   0.062915   0.030  0.97584
year_f2021        0.009628   0.065396   0.147  0.88311
year_f2022        0.004368   0.065208   0.067  0.94667
year_f2023        0.039337   0.065372   0.602  0.54808
year_f2024        0.016369   0.064054   0.256  0.79857
year_f2025       -0.021728   0.062848  -0.346  0.72994
locationNeuwaldegg  -0.077270   0.031756  -2.433  0.01590 *
locationWaldandacht -0.038601   0.031233  -1.236  0.21805
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.1783 on 187 degrees of freedom
Multiple R-squared:  0.1148,    Adjusted R-squared:  0.05794
F-statistic:  2.02 on 12 and 187 DF,  p-value: 0.02457
```

Model Validation with DHARMa



Fore limb left

lm(formula = m2$residuals ~ sex + year_f, data = df_fl_left)

Residuals: Min 1Q Median 3Q Max

-0.35112 -0.11949 -0.00132 0.11279 0.39148

Coefficients: Estimate Std. Error t value Pr(>|t|)

(Intercept)	0.08280	0.03466	2.389	0.017898 *
sexM	0.09419	0.02397	3.929	0.000120 ***
Year_f2017	-0.04051	0.05014	-0.808	0.420191
Year_f2018	-0.14678	0.05176	-2.836	0.005082 **
Year_f2019	-0.27085	0.05176	-5.233	4.5e-07 ***
Year_f2020	-0.14951	0.04599	-3.251	0.001366 **
Year_f2021	-0.12009	0.04868	-2.467	0.014537 *
Year_f2022	-0.12278	0.06414	-1.914	0.057131 .
Year_f2023	-0.17252	0.04607	-3.745	0.000241 ***
Year_f2024	-0.18567	0.05172	-3.590	0.000424 ***
Year_f2025	-0.16654	0.05086	-3.275	0.001263 **

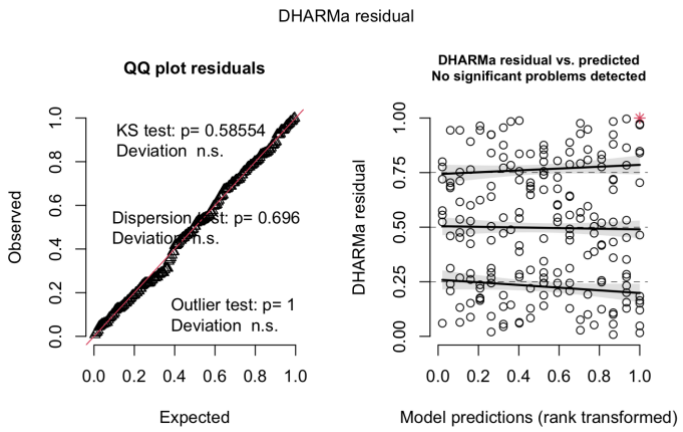
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.1658 on 185 degrees of freedom

Multiple R-squared: 0.2246, Adjusted R-squared: 0.1827

F-statistic: 5.359 on 10 and 185 DF, p-value: 6.078e-07

Model Validation with DHARMa



688

689

690 **Hind limb left**

691 lm(formula = m4$residuals ~ sex, data = df_hl_left)

692 Residuals: Min 1Q Median 3Q Max

693 -0.65230 -0.09464 -0.00558 0.10297 0.43100

694

695 Coefficients: Estimate Std. Error t value Pr(>|t|)

696 (Intercept) -0.03555 0.01700 -2.091 0.03775 *

697 sexM 0.06906 0.02369 2.915 0.00396 **

698 ---

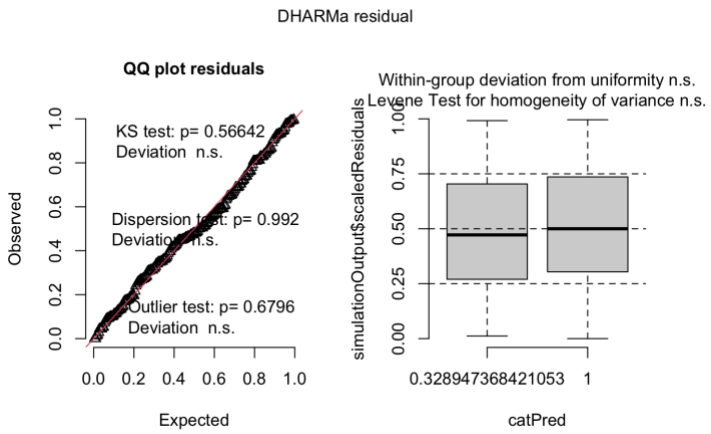
699 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

700 Residual standard error: 0.1691 on 202 degrees of freedom

701 Multiple R-squared: 0.04037, Adjusted R-squared: 0.03562

702 F-statistic: 8.497 on 1 and 202 DF, p-value: 0.003958

703 Model Validation with DHARMa



704

705

706 **Hind limb right**

707 lm(formula = m3$residuals ~ location, data = df_hl_right)

708

709 Residuals: Min 1Q Median 3Q Max

710 -0.67904 -0.13056 -0.00057 0.12221 0.45075

711

712 Coefficients: Estimate Std. Error t value Pr(>|t|)

713 (Intercept) 0.04446 0.02439 1.823 0.0700 .

714 locationNeuwaldegg -0.07219 0.03419 -2.111 0.0361 *

715 locationWaldandacht -0.05826 0.03341 -1.744 0.0829 .

716 ---

717 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

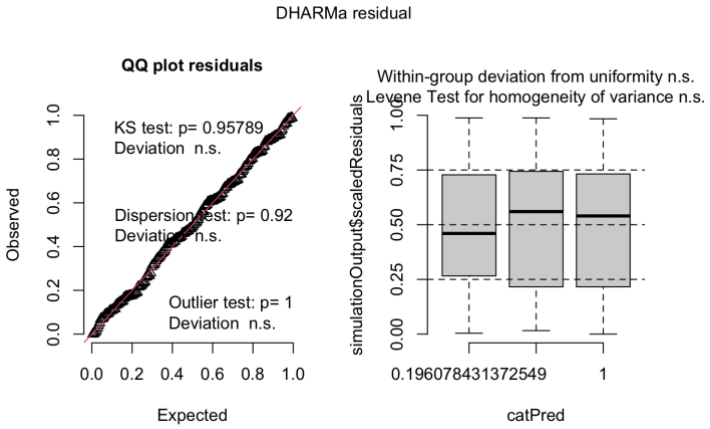
718 Residual standard error: 0.1841 on 178 degrees of freedom

719 Multiple R-squared: 0.02747, Adjusted R-squared: 0.01654

720 F-statistic: 2.514 on 2 and 178 DF, p-value: 0.08382

721

722 Model Validation with DHARMa



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728 **References**

729 Abrahms, B., Carter, N.H., Clark-Wolf, T.J., Gaynor, K.M., Johansson, E. McInturff, A.,

730 Nisi, A.C., Rafiq, K., West. L. (2023). Climate change as a global amplifier of human–

731 wildlife conflict. *Nat. Clim. Chang.* 13: 224–234. https://doi.org/10.1038/s41558-023-

732 01608-5

733 Adams D.C., Church J.O. (2008). Amphibians do not follow Bergmann's rule. *Evolution*,

734 62(2):413–420. https://doi.org/10.1111/j.1558-5646.2007.00297.x

735 Aguilar, P., Pérez i de Lanuza, G., Martínez-Gil, H., Dajčman, U., Simčič, T., Pinho, C.,

736 Žagar, A., Megía-Palma, R. (2024). Color morphs of the fire salamander are

737 discriminated at night by conspecifics and predators. *J. Zool.,* 322:141–155.

738 https://doi.org/10.1111/jzo.13131

739 Alarcón-Ríos, L., Saabi González, M., Velo-Antón, G. (2026). Melanism in salamanders:
740 effects of insularity, sex and size on dorsal colouration in *Salamandra salamandra*. *J.*
741 *Zool*. https://doi.org/10.1111/jzo.70133
742 Alho, J.S., Herczeg, G., Laugen, A.T., Räsänen, K., Laurila, A., Merilä, J. (2011). Allen's
743 rule revisited: quantitative genetics of extremity length in the common frog along a
744 latitudinal gradient. *J. Evol. Biol.,* 24:59–70. https://doi.org/10.1111/j.1420-
745 9101.2010.02141.x
746 Allen, J.A. (1877). The influence of physical conditions in the genesis of species. *Radical*
747 *review*, 1:108–140.
748 Angilletta, M.J. (2009). Thermal adaptation: a theoretical and empirical synthesis. Oxford
749 University Press, Oxford. pp. 289.
750 https://doi.org/10.1093/acprof:oso/9780198570875.001.1
751 Arnold, S.J. (1987). The comparative ethology of courtship in salamandrid salamanders. 1.
752 Salamandra and Chioglossa. *Ethology*, 74(2):133–145. https://doi.org/10.1111/j.1439-
753 0310.1987.tb00926.x
754 Ashton K.G. (2002). Do amphibians follow Bergmann's rule? *Can. J. Zool.*, 80(4): 708–
755 716. https://doi.org/10.1139/z02-049
756 Alhajeri, B.H., Fourcade, Y., Upham, N.S., Alhaddad, H. (2020). A global test of Allen's
757 rule in rodents. *Global Ecol. Biogeogr.,* 29:2248–2260. https://doi.org/10.1111/geb.13198

Altunışık, A. (2017). Sexual size and shape dimorphism in the Near Eastern fire salamander, *Salamandra infraimmaculata* (Caudata: Salamandridae). *Animal Biology*, 67(1):29–40. https://doi.org/10.1163/15707563-00002519

Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., Schöner, W., Ungersböck, M., Matulla, C., Briffa, K., Jones, P., Efthymiadis, D., Brunetti, M., Nanni, T., Maugeri, M., Mercalli, L., Mestre, O., Moisselin, J.-M., Begert, M., Müller-Westermeier, G., Kveton, V., Bochnicek, O., Stastny, P., Lapin, M., Szalai, S., Szentimrey, T., Cegnar, T., Dolinar, M., Gajic-Capka, M., Zaninovic, K., Majstorovic, Z., Nieplova, E. (2007). HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *Int. J. Climatol.*, 27:17–46. https://doi.org/10.1002/joc.1377

Auguie, B. (2017). gridExtra: Miscellaneous Functions for "Grid" Graphics. R package, version 2.3, https://CRAN.R-project.org/package=gridExtra.

Balogová, M., Uhrin, M. (2015). Sex-biased dorsal spotted patterns in the fire salamander (*Salamandra salamandra*). *Salamandra*, 51(1):12–18.

Balogová, M., Kyselová, M., Uhrin, M. (2016). Changes in dorsal spot pattern in adult *Salamandra salamandra* (Linneaeus, 1758). *Herpetozoa*, 28:167–171.

Bartoń, K. (2025). MuMIn: Multi-Model Inference. R package version 1.48.11, https://CRAN.R-project.org/package=MuMIn.

777 Barzaghi, B., Melotto, A., Cogliati, P., Manenti, R., Ficetola, G.F. (2022). Factors
778 determining the dorsal coloration pattern of aposematic salamanders. *Sci. Rep.*,
779 12(1):17090. https://doi.org/10.1038/s41598-022-19466-0
780 Bennett, J.M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R.,
781 Araújo, M.B., Algar, A.C., Clusella-Trullas, S., Hawkins, B.A., Keith, S.A., Kühn, I.,
782 Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., Olalla-Tárraga, M.A. (2021).
783 The evolution of critical thermal limits of life on Earth. *Nat. Commun.* 12:1198.
784 https://doi.org/10.1038/s41467-021-21263-8
785 Bergmann C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer
786 Grösse. *Göttinger Studien,* 3:595–708.
787 Bogert, C.M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution*,
788 3(3):195–211. https://doi.org/10.2307/2405558
789 Brodeur, J.C., Damonte, M.J., Candioti, J.V., Poliserpi, M.B., D'Andrea, M.F., Bahl, M.F.
790 (2020). Frog body condition: Basic assumptions, comparison of methods and
791 characterization of natural variability with field data from *Leptodactylus latrans*. *Ecol.*
792 *Indic.*, 112:106098. https://doi.org/10.1016/j.ecolind.2020.106098
793 Burgon, J.D., Vieites, D.R., Jacobs, A., Weidt, S.K., Gunter, H.M., Steinfartz, S., Burgess,
794 K., Mable, B.K., Elmer, K.R. (2020). Functional colour genes and signals of selection in
795 colour-polymorphic salamanders. *Mol. Ecol.*, 29:1284–1299.
796 https://doi.org/10.1111/mec.15411

797 Burgstaller S., Leeb, C, Ringler, M., Gollmann G. (2021). Demography and spatial activity
798 of fire salamanders, *Salamandra salamandra* (Linnaeus, 1758), in two contrasting
799 habitats in the Vienna Woods. *Herpetozoa*, 34:23–34.
800 Burnham, K. P., Anderson, D. R., Huyvaert, K. P. (2011). AIC model selection and
801 multimodel inference in behavioral ecology: Some background, observations, and
802 comparisons. *Behav. Ecol. Sociobiol.*, 65(1):23–35. https://doi.org/10.1007/s00265-010-
803 1029-6
804 Bustamante, J. (1985). Alimentación del ratonero común (*Buteo buteo*, L. 1758) en el norte
805 de España. *Doñana, Acta Vertebrata*, 12:51–62.
806 Caspers, B.A., Krause, E.T., Hermanski, I., Wiesbrock, C., Kastrup, F.W., Steinfartz, S.
807 (2020). Developmental costs of yellow colouration in fire salamanders and experiments
808 to test the efficiency of yellow as a warning colouration. *Amphibia-Reptilia*, *41*(3):373–
809 385. https://doi.org/10.1163/15685381-bja10006
810 Catenazzi, A. (2016). Ecological implications of metabolic compensation at low
811 temperatures in salamanders. *PeerJ,* 4:e2072. https://doi.org/10.7717/peerj.2072
812 Cavicchioli, R., Ripple, W.J., Timmis, K.N. *et al.* (2019). Scientists' warning to humanity:
813 microorganisms and climate change. *Nat. Rev. Microbiol.,* 17:569–586.
814 https://doi.org/10.1038/s41579-019-0222-5
815 Clusella-Trullas, S., van Wyk, J.H., Spotila, J.R. (2007). Thermal melanism in
816 ectotherms. *J. Therm. Biol.*, 32(5):235–245.
817 https://doi.org/10.1016/j.jtherbio.2007.01.013

Clusella-Trullas, S., Terblanche, J.S., Blackburn, T.M., Chown, S.L. (2008). Testing the Thermal Melanism Hypothesis: A Macrophysiological Approach. *Funct. Ecol.*, 22(2):232–238. http://www.jstor.org/stable/20142796

Dittrich, C., Szydlik, K.R., Jokinen, A-K.K., Preininger, D., Rojas, B. (2026). Data and Code: The warmer, the yellower? Colour patterns of fire salamanders across different temporal scales in the face of global rising temperatures. Zenodo, version V1. https://doi.org/10.5281/zenodo.21258587

Deichmann, J.L., Boundy, J., Williamson, G.B. (2009). Anuran artifacts of preservation: 27 years later. *Phyllomedusa,* 8:51–58. https://doi.org/10.11606/issn.2316-9079.v8i1p51-58

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor,C.K., Haak, D.C., Martin, P.R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.,* 105(18):6668–6672. https://doi.org/10.1073/pnas.0709472105

Dillon, M., Wang, G., Huey, R. (2010). Global metabolic impacts of recent climate warming. *Nature,* 467:704–706. https://doi.org/10.1038/nature09407

Fox, J., Weisberg, S. (2019). An R Companion to Applied Regression. Third edition. Sage, Thousand Oaks CA. https://www.john-fox.ca/Companion/.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R. S., Mitchell, D., Maloney, S. K. (2010). Physiological Mechanisms in Coping with Climate Change. *Physiol. Biochem. Zool.: Ecol. Evol. Approaches*, 83(5):713–720. https://doi.org/10.1086/652242

839 Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., Heinsohn, R. (2011). Declining body
840 size: a third universal response to warming?. *Trends in Ecol. Evol.*, 26(6):285–291.
841 https://doi.org/10.1016/j.tree.2011.03.005
842 Goldenberg, J., Bisschop, K., D'Alba, L., Shawkey, M.D. (2022). The link between body
843 size, colouration and thermoregulation and their integration into ecogeographical rules:
844 a critical appraisal in light of climate change. *Oikos*, e09152.
845 https://doi.org/10.1111/oik.09152
846 Guo, Q., Qian, H., Liu, P., Zhang, J. (2024). Bergmann's rule in global terrestrial
847 vertebrates. *Biol. J. Linn. Soc.*, 143(2):blae092.
848 https://doi.org/10.1093/biolinnean/blae092
849 Hagnier, D., Dittrich, C., van den Bos, M., Rojas, B. (2025). Habitat alteration impacts
850 predation risk in an aposematic amphibian. *J. Zool.*, 327: 60–72.
851 https://doi.org/10.1111/jzo.70036
852 Hartig, F. (2024). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
853 Regression Models. R package version 0.4.7, https://CRAN.R-
854 project.org/package=DHARMa.
855 Hedrick, B.P., Heberling, J.M., Meineke, E.K., Turner, K.G., Grassa, C.J., Park, D.S.,
856 Kennedy, J, Clarke, J.A., Cook, J.A., Blackburn, D.C., Edwards, S.V., Davis, C.C. (2020).
857 Digitization and the Future of Natural History Collections. *BioScience*, 70(3):243–251.
858 https://doi.org/10.1093/biosci/biz163

859 Hegna, R.H., Nokelainen, O., Hegna, J.R., Mappes J. (2013). To quiver or to shiver:
860 increased melanization benefits thermoregulation, but reduces warning signal efficacy
861 in the wood tiger moth. *Proc. R. Soc. B*, 280:20122812.
862 http://dx.doi.org/10.1098/rspb.2012.2812
863 Horter, M., Greven, H. (1981). Zur relativen Genießbarkeit juveniler Feuersalamander,
864 *Salamandra salamandra* (L.) (Amphibia, Urodela). *Amphibia-Reptilia*, 2:15–21.
865 https://doi.org/10.1163/156853881X00258
866 Howard, R.D., Kluge, A.G. (1985). Proximate mechanisms of sexual selection in wood
867 frogs. *Evolution*, *39*(2):260–277. https://doi.org/10.1111/j.1558-5646.1985.tb05665.x
868 IPCC (2023). *Climate Change 2023: Synthesis Report. Contribution of Working Groups I,*
869 *II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate*
870 *Change* [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland,
871 184 pp., doi: 10.59327/IPCC/AR6-9789291691647.
872 Jørgensen, L.B., Ørsted, M., Malte, H., Wang, T., Overgaard, J. (2022). Extreme escalation
873 of heat failure rates in ectotherms with global warming. *Nature,* 611:93–98.
874 https://doi.org/10.1038/s41586-022-05334-4
875 Juszczyk, W. (1952). The preservation of natural colors in skin preparations of certain
876 Amphibia. *Copeia,* 1952:33–38. https://doi.org/10.2307/1437621
877 Keinath, S., Frisch, J., Müller, J., Mayer, F., Rödel, M.O. (2020). Spatio-temporal color
878 differences between urban and rural populations of a ground beetle during the last 100
879 years. *Front. Ecol. Evol.*, 7:525. https://doi.org/10.3389/fevo.2019.00525

880 Knepper, J., Lüddecke, T., Preißler, K., Vences, M., Schulz, S. (2019). Isolation and
881 identification of alkaloids from poisons of fire salamanders (*Salamandra salamandra*).
882 *J. Nat. Prod.*, 82:1319–1324. https://doi.org/10.1021/acs.jnatprod.9b00065
883 Koskenpato, K., Lehikoinen, A., Morosinotto, C., Gunko, R., Karell, P. (2023). Regional
884 variation in climate change alters the range-wide distribution of colour polymorphism
885 in a wild bird. *Ecol. Evol.,* 13:e10311. https://doi.org/10.1002/ece3.10311
886 Kovar, R., Brabec, M., Moravec, P., Husak, T. (2024). Fire salamander, *Salamandra*
887 *salamandra*, niche selection in central European conditions. *Salamandra*, 60:129–146.
888 Labus, N., Cvijanović, M., Vukov, T. (2013). Sexual size and shape dimorphism in
889 *Salamandra salamandra* (Amphibia, Caudata, Salamandridae) from the central Balkans.
890 *Archives Biol. Sci.*, 65(3):969–975. https://doi.org/10.2298/ABS1303969L
891 Łaciak, M. (2022). Aposematism as a trap? A case of heavy predation on a poisonous
892 salamander. *Front. Ecol. Environ.*, 20:588. https://doi.org/10.1002/fee.2580
893 Laumeier, R., Brändle, M., Rödel, M.O., Brunzel, S., Brandl, R., Pinkert, S. (2023). The
894 global importance and interplay of colour-based protective and thermoregulatory
895 functions in frogs. *Nat. Commun.*, 14(1):8117. https://doi.org/10.1038/s41467-023-
896 43729-7
897 Lee, J.C. (1982). Accuracy and precision in anuran morphometrics: artifacts of
898 preservation. *Syst. Biol.,* 31:266–281. https://doi.org/10.1093/sysbio/31.3.266.

899 Lindstedt, C., Lindström, L., Mappes, J. (2009). Thermoregulation constrains effective
900 warning signal expression. *Evolution*, 63:469–478. https://doi.org/10.1111/j.1558-
901 5646.2008.00561.x
902 Liu, B.W., Yang, T., Shi, W.H., Yu, T.L. (2025). Altitudinal Variation in Body Size and Limb
903 Size Across Nine Populations of Male Minshan's Toads (*Bufo minshanicus*) to Test Allen's
904 Rule and Bergmann's Rule. *Herpetologica*, *81*(2):134–140.
905 https://doi.org/10.1655/Herpetologica-D-23-00061
906 Lüddecke, T., Schulz, S., Steinfartz, S., Vences, M. (2018). A salamander's toxic arsenal:
907 review of skin poison diversity and function in true salamanders, genus *Salamandra*. *Sci.*
908 *Nat.*, 105:1–16. https://doi.org/10.1007/s00114-018-1579-4
909 Mackintosh, J.A. (2001). The antimicrobial properties of melanocytes, melanosomes and
910 melanin and the evolution of black skin. *J. Theor. Biol.*, 211(2):101–113.
911 https://doi.org/10.1006/jtbi.2001.2331
912 MacLean, H.J., Nielsen, M.E., Kingsolver, J.G., Buckley, L.B. (2019). Using museum
913 specimens to track morphological shifts through climate change. *Phil. Trans. R. Soc., B*,
914 374:20170404. https://doi.org/10.1098/rstb.2017.0404
915 Masoero, G., Gencheva, K.G., Ioset, N., Bersier, L-F., Tettamanti. F., Bize, P. (2024).
916 Shrinking Alpine chamois: higher spring temperatures over the last 27 years in
917 Switzerland are linked to a 3 kg reduction in body mass of yearlings. *R. Soc. Open Sci.,*
918 11(3): 231295. https://doi.org/10.1098/rsos.231295

Matzl, A. 2024. Austria Weather API. Version 0.7. https://github.com/a-matz/austria_weather_api

McQueen, A., Klaassen, M., Tattersall, G.J., Ryding, S., Victorian Wader Study Group, Australasian Wader Studies Group, Atkinson, R., Jessop, R., Hassell, C.J., Christie, M., Fröhlich, A., Symonds, M.R.E. (2024). Shorebirds Are Shrinking and Shape-Shifting: Declining Body Size and Lengthening Bills in the Past Half-Century. *Ecol. Lett.*, 27:e14513. https://doi.org/10.1111/ele.14513

Mühlenhaupt, M., Hey, R., Starp, M., Anthes, N., Bachhausen, P., Bamann, T., Bleidißel, S., Bovensmann, E., Braunsdorf, J., Dehling, J.M., Ebert, S., Egle, H., Egle, K., Egle, S., Enderlein, H., Fischer, M. Gemeinhardt, L., Grond, S.G., Gundert, R.D., Krüger, O., Laux, L., Oswald, P., Schlindwein, X., Schmidt, M., Schulte, L., Schwalbe, R., Stipp, T., Veith, M., Wietbrok, F., Caspers, B. (2025). Citizen science data reveals widespread sexual dichromatism in the European fire salamander (*Salamandra salamandra*). *BMC Ecol. Evo.,* 25:122. https://doi.org/10.1186/s12862-025-02461-0

Muñoz, M.M. (2022). The Bogert effect, a factor in evolution. *Evolution*, 76(1):49–66. https://doi.org/10.1111/evo.14388

Najbar, A., Konowalik, A., Najbar, B., Ogielska, M. (2018). Yellow patterns polymorphism of the fire salamander *Salamandra salamandra* in Poland. *Acta Herpetol.*, 13(2):101–108. https://doi.org/10.13128/Acta_Herpetol-22886

938 Nokelainen, O., Valkonen, J., Lindstedt, C., Mappes, J. (2014). Changes in predator
939 community structure shifts the efficacy of two warning signals in Arctiid moths. *J. Anim.*
940 *Ecol.*, 83(3):598–605. http://www.jstor.org/stable/24034773
941 Ożgo, M., Liew, T.-S., Webster, N.B., Schilthuizen, M. (2017). Inferring microevolution
942 from museum collections and resampling: lessons learned from *Cepaea*. *PeerJ*, 5:e3938.
943 https://doi.org/10.7717/peerj.3938
944 Peig, J., Green, A.J. (2009). New perspectives for estimating body condition from
945 mass/length data: the scaled mass index as an alternative method. Oikos, 118:1883–
946 1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x
947 Petrović, T.G., Vukov, T.D., Kolarov, N.T. (2017). Sexual dimorphism in size and shape
948 of traits related to locomotion in nine anuran species from Serbia and Montenegro.
949 *Folia Zool.*, 66(1):11–21. https://doi.org/10.25225/fozo.v66.i1.a4.2017
950 Pierson, T.W. , Kieran, T.J., Clause, A.G., Castleberry, N.L. (2020). Preservation-induced
951 morphological change in salamanders and failed DNA extraction from a decades-old
952 museum specimen: implications for *Plethodon ainsworthi*. *J. Herpet.,* 54:137–143.
953 https://doi.org/10.1670/19-012
954 Preißler, K., Gippner, S., Lüddecke, T., Krause, E.T., Schulz, S., Vences, M., Steinfartz, S.
955 (2019). More yellow more toxic? Sex rather than alkaloid content is correlated with
956 yellow coloration in the fire salamander. *J. Zool.*, 308(4):293–300.
957 https://doi.org/10.1111/jzo.12676

958 Pottier, P., Kearney, M.R., Wu, N.C., Gunderson, A.R., Rej, J.E., Rivera-Villanueva, A.N.,
959 Pollo, P., Burke, S., Drobniak, S.M., Nakagawa, S. (2025). Vulnerability of amphibians
960 to global warming. Nature, 639:954–961. https://doi.org/10.1038/s41586-025-08665-0
961 Posit Team (2024). RStudio: Integrated Development Environment for R (Version
962 2024.9.1.394). Posit Software, PBC, Boston, MA. URL: http://www.rstudio.com/
963 Poulton, E.B. (1890). The colours of animals: their meaning and use, especially considered
964 in the case of insects. *The International Scientific Series Vol. 67*. D. Appleton and
965 Company, New York.
966 Pyke, G.H., Ehrlich, P.R. (2010). Biological collections and ecological/environmental
967 research: a review, some observations and a look to the future. *Biol. Rev.*, 85:247–266.
968 https://doi.org/10.1111/j.1469-185X.2009.00098.x
969 R Core Team (2024). R: A language and environment for statistical computing (Version
970 4.4.1). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-
971 project.org/
972 Reinhard, S., Renner, S., Kupfer, A. (2015). Sexual dimorphism and age of Mediterranean
973 salamanders. *Zoology*, *118*(1):19–26. https://doi.org/10.1016/j.zool.2014.08.002
974 Rönkä, K., Valkonen, J.K., Nokelainen, O., Rojas, B., Gordon, S., Burdfield-Steel, E., Mappes,
975 J. (2020). Geographic mosaic of selection by avian predators on hindwing warning colour
976 in a polymorphic aposematic moth. *Ecol. Lett.,* 23:1654–1663.
977 https://doi.org/10.1111/ele.13597

978 Rojas, B., Endler, J.A. (2013). Sexual dimorphism and intra-populational colour pattern
979 variation in the aposematic frog *Dendrobates tinctorius*. *Evol. Ecol.* 27:739–753.
980 https://doi.org/10.1007/s10682-013-9640-4
981 Rojas, B., Rojas-Montoya, M., Carvajal-Castro, J.D. (2026). Beyond protection from
982 predators: Correlates and additional benefits of aposematic signaling. In *Advances in the*
983 *Study of Behavior* (eds. J. Podos & S.D. Healy), 58:83–129, Academic Press.
984 https://doi.org/10.1016/bs.asb.2026.05.001
985 Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change.
986 *Global Change Biol.*, 20(11):3344–3350. https://doi.org/10.1111/gcb.12594
987 Ruthsatz, K., Dahlke, F., Alter, K., Wohlrab, S., Eterovick, P.C., Lyra, M.L., Gippner, S.,
988 Cooke, S.J., Peck, M.A. (2024). Acclimation capacity to global warming of amphibians
989 and freshwater fishes: Drivers, patterns, and data limitations. *Global Change Biol.*,
990 30:e17318. https://doi.org/10.1111/gcb.17318
991 QGIS Development Team (2024). QGIS Geographic Information System. Open Source
992 Geospatial Foundation Project. Version 3.34.15-Prizren. http://qgis.osgeo.org
993 Sánchez, E., Küpfer, E., Goedbloed, D. J., Nolte, A. W., Lüddecke, T., Schulz, S., Vences,
994 M., Steinfartz, S. (2018). Morphological and transcriptomic analyses reveal three
995 discrete categories of postembryonic development in the fire salamander, *Salamandra*
996 *salamandra*. *J. Exp. Zool. Part B*, 330:96–108. https://doi.org/10.1002/jez.b.22792
997 Sánchez, E., Pröhl, H., Lüddecke, T., Schulz, S., Steinfartz, S., Vences, M. (2019). The
998 conspicuous postmetamorphic coloration of fire salamanders, but not their toxicity, is

affected by larval background albedo. *J. Exp. Zool. Part B,* 332:26–35. https://doi.org/10.1002/jez.b.22845

Sanders, N.J., Cooper, N., Davis Rabosky, A.R., Gibson, D.J. (2023). Leveraging natural history collections to understand the impacts of global change. *J. Anim. Ecol.*, 92:232–236. https://doi.org/10.1111/1365-2656.13882

Schindel, D.E., Cook, J.A. (2018). The next generation of natural history collections. *PLoS Biol.,* 16(7): e2006125. https://doi.org/10.1371/journal.pbio.2006125

Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., Crowley, J. (2025). GGally: Extension to 'ggplot2'. R package version 2.4.0, https://CRAN.R-project.org/package=GGally.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods*, 9(7):671–675. https://doi.org/10.1038/nmeth.2089

Sears, M.W., Angilletta, M.J. (2015). Costs and Benefits of Thermoregulation Revisited: Both the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs. *Am. Nat.*, 185(4):E94-E102. https://doi.org/10.1086/680008

Seebacher, F. (2009). Responses to temperature variation: integration of thermoregulation and metabolism in vertebrates. *J. Exp. Biol.,* 212(18):2885–2891. https://doi.org/10.1242/jeb.024430

Sheridan, J., Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nat. Clim. Change,* 1:401–406. https://doi.org/10.1038/nclimate1259

1019 Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.A., Isailović, J.C.,
1020 Denoël, M., Ficetola, F.G., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P.,
1021 Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., Vences, M.
1022 (2014). Updated distribution and biogeography of amphibians and reptiles of Europe.
1023 *Amphibia-Reptilia*, *35*(1):1–31. https://doi.org/10.1163/15685381-00002935
1024 Skevakis, G., Makris, K., Kalokyri, V., Arapi, P., Christodoulakis, S. (2014). Metadata
1025 management, interoperability and Linked Data publishing support for Natural History
1026 Museums. *Int. J. Digit. Libr.* 14:127–140. https://doi.org/10.1007/s00799-014-0114-2
1027 Steinfartz, S., Weitere, M., Tautz, D. (2007). Tracing the first step to speciation: ecological
1028 and genetic differentiation of a salamander population in a small forest. *Mol. Ecol.*,
1029 16(21):4550–4561. https://doi.org/10.1111/j.1365-294X.2007.03490.x
1030 Strowbridge, N., Vieites, D.R., Ritchie, M.G., Elmer, K.R. (2026). Skin colour in
1031 salamanders is modulated by both epitranscriptomic methylation and gene expression.
1032 *Mol. Ecol.*, 35:e70302. https://doi.org/10.1111/mec.70302
1033 Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas,
1034 C.D. (2011). Habitat microclimates drive fine-scale variation in extreme temperatures.
1035 Oikos, 120:1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x
1036 Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey,
1037 R.B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior
1038 across latitude and elevation. *Proc. Natl. Acad. Sci. USA*, 111:5610–5615.
1039 http://dx.doi.org/10.1073/pnas.1316145111

1040 Tian, L., Benton, M.J. (2020). Predicting biotic responses to future climate warming with
1041 classic ecogeographic rules. *Curr. Biol.*, 30(13):R744–R749.
1042 https://doi.org/10.1016/j.cub.2020.06.003
1043 Thiesmeier B. (2004) Der Feuersalamander. Laurenti, Bielefeld, Germany.
1044 Thiesmeier, B., Grossenbacher, K. (2004). *Salamandra salamandra (Linnaeus, 1758)* -
1045 *Feuersalamander*. In: Handbuch der Reptilien und Amphibien Europas: Schwanzlurche
1046 IIB (pp. 1059–1132), Thiesmeier, B., Grossenbacher, K. (eds.) Aula-Verlag, Wiesbaden,
1047 Germany.
1048 Ujszegi, J., Bertalan, R., Ujhegyi, N., Verebélyi, V., Nemesházi, E., Mikó, Z., Kásler, A.,
1049 Herczeg, D., Szederkényi, M., Vili, N., Gál, Z., Hoffmann, O. I., Bókony, V., Hettyey, A.
1050 (2022). "Heat waves" experienced during larval life have species-specific consequences
1051 on life-history traits and sexual development in anuran amphibians. *Sci. Total Environ.*,
1052 835:155297. https://doi.org/10.1016/j.scitotenv.2022.155297
1053 Valkonen, J.K., Nokelainen, O., Niskanen, M., Kilpimaa, J., Bjorklund, M., Mappes, J.
1054 (2012). Variation in predator species abundance can cause variable selection pressure on
1055 warning signaling prey. *Ecol. Evol.*, 2:1971–1976. https://doi.org/10.1002/ece3.315
1056 Van Tran, D., Nishikawa, K. (2023). Clay model reveals the difference in day and night
1057 predation rates on Vietnam warty newt (Caudata: Salamandridae). *Curr. Herpetol.*,
1058 42:124–135. https://doi.org/10.5358/hsj.42.124

1059 Velo-Antón, G. (2024). When aposematism is not enough: Exotic *Rattus rattus* shows no
1060 mercy for carcasses of *Salamandra salamandra*in insular populations. *Ecol. Evol.*,
1061 14:e11229. https://doi.org/10.1002/ece3.11229
1062 Vitasse, Y., Baumgarten, F., Zohner, C.M., Rutishauser, T., Pietragalla, B., Gehrig, R., Dai,
1063 J., Wang, H., Aono, Y., Sparks, T.H. (2022). The great acceleration of plant phenological
1064 shifts. *Nat. Clim. Change,* 12:300–302. https://doi.org/10.1038/s41558-022-01283-y
1065 Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New
1066 York.
1067 Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D. (2023). dplyr: A Grammar
1068 of Data Manipulation. R package version 1.1.4, https://CRAN.R-
1069 project.org/package=dplyr
1070 Weldon, C., Du Preez, L.H., Hyatt, A.D., Muller, R., Speare, R. (2004). Origin of the
1071 amphibian chytrid fungus. *Emerg. Infect. Dis.*, 10(12):2100–2105.
1072 https://doi.org/10.3201/eid1012.030804
1073 Wisniewski, P.J., Wisniewski, L.M. (1998). Can a salamander change its spots?. *Bull. Br.*
1074 *Herpetol. Soc.*, (62):27–28.
1075 Zipkin, E.F., Williams, P.J. (2025). Revealing species responses to environmental change
1076 through long-term data and mechanistic frameworks. *J. Anim. Ecol.,* 94:2155–2158.
1077 https://doi.org/10.1111/1365-2656.70143