Influence of climate on the presence of colour polymorphism in two montane reptile species

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The coloration of ectotherms plays an important role in thermoregulation processes. Dark individuals should heat up faster and be able to reach a higher body temperature than light individuals and should therefore have benefits in cool areas. In central Europe, montane local populations of adder (Vipera berus) and asp viper (Vipera aspis) exhibit a varying proportion of melanistic individuals. We tested whether the presence of melanistic V. aspis and V. berus could be explained by climatic conditions. We measured the climatic niche position and breadth of monomorphic (including strictly patterned individuals) and polymorphic local populations, calculated their niche overlap and tested for niche equivalency and similarity. In accordance with expectations, niche overlap between polymorphic local populations of both species is high, and even higher than that of polymorphic versus monomorphic montane local populations of V. aspis, suggesting a predominant role of melanism in determining the niche of ectothermic vertebrates. However, unexpectedly, the niche of polymorphic local populations of both species is narrower than that of monomorphic ones, indicating that colour polymorphism does not always enable the exploitation of a greater variability of resources, at least at the intraspecific level. Overall, our results suggest that melanism might be present only when the thermoregulatory benefit is higher than the cost of predation.

1. Introduction

The coloration of ectothermic vertebrates plays an important role in thermoregulation processes. According to the thermal melanism hypothesis [1], dark individuals, i.e. with a low skin reflectance, should heat up faster and should be able to reach a higher body temperature than light individuals, i.e. with a higher skin reflectance. As a consequence, darker conspecific animals should have benefits in cool habitats (montane or forested), such as longer activity periods, higher growth rate, better body condition, higher survival or increased reproductive output [2–6]. The thermal melanism hypothesis has been confirmed in ectothermic vertebrates at small scales (population level), but only for two reptile species, i.e. in the colour-polymorphic adder (Vipera berus) [3,7] and asp viper (Vipera aspis) [6], and at a large scale (species-distribution level) for heliothermic lizards [8]. The latter study found a positive relationship between the skin reflectance of 66 species and the sum of the annual solar radiation present at the sampled sites. These results, which remain even when accounting for phylogeny, indicate that individuals from locations receiving a lower amount of solar radiation are darker. However and despite the numerous advantages of being melanistic in cold conditions, dark coloration can be penalizing for organisms in some circumstances, such as when it results in a loss of crypsis or a change...
in aposematic signalling. In turn, dark coloration might result in an increased predation rate and stress [6,9].

Owing to the potential differences in thermal requirements between darkly and lightly coloured individuals, different colour morphs might be able to exploit different microhabitat types. This may allow colour-polymorphic populations to have wider niches and to be able to exploit a larger number of habitat types than monomorphic populations. The same is true for any type of polymorphism that enables an exploitation of different habitat types [10]. This assumption has been tested and confirmed at a large scale by comparing the climatic niche breadth of colour-polymorphic and monomorphic species of amphibians, reptiles and birds from North America and Australia [11–13]. However, these interspecific and higher taxonomic comparisons might be blurred by other physiological and morphological factors that could also have an effect on niche breadth. To the best of our knowledge, intraspecific comparisons of the niche breadth of polymorphic versus monomorphic populations are lacking.

The asp viper is distributed in western and central Europe from sea level to more than 2000 m a.s.l. in the Alps, whereas the adder is distributed from western Europe to eastern Asia and is one of the few reptile species reaching the arctic polar circle. Interestingly, both species are colour-polymorphic in central Europe, with the presence of a large proportion of melanistic individuals in some montane local populations, whereas other populations are strictly monomorphic with a complete absence of melanism (figure 1d). However, the presence of both monomorphic and polymorphic local populations in similar mountainous areas remains puzzling and suggests that additional factors might favour particular colour morphs. Indeed, despite this advantage, melanistic individuals might be less cryptic than patterned individuals or lack aposematic signalling, both anti-predatory strategies being non-exclusive [6,9]. For example, Andren & Nilson [7] revealed that melanistic males of V. berus were in better body condition than patterned ones, but that decoys of melanistic males were more often attacked than patterned ones in the study area.

The aim of this study is to test whether the presence of melanistic V. aspis and V. berus in particular mountainous areas of Switzerland can be explained by thermoregulatory advantages.

Figure 1. Niche characteristics in relation to colour morphs. Local populations of (a) Vipera aspis and (b) Vipera berus are shown in the climatic space of the PCA. Red dots indicate populations containing melanistic and patterned individuals (polymorphic). Blue dots show local populations strictly composed of patterned individuals (monomorphic). Solid and dashed lines indicate 100 and 50% most frequent climatic conditions available in Switzerland. (c) The correlation circle indicates that the first and second axes of the PCA mainly represent gradients of coldness and humidity, respectively. (d) Shows examples of colour patterns of melanistic and patterned V. berus (1 and 2, respectively) and for V. aspis (3 and 4, respectively). (Online version in colour.)
In particular, we hypothesized (i) that colour-polymorphic local populations should be constrained to colder habitats and (ii) that such local populations should have wider niches than monomorphic ones, because differently coloured individuals might be able to use different habitat types. In this respect, we measured the climatic niche position and breadth of monomorphic local populations (harbouring only patterned individuals) versus polymorphic local populations (containing a proportion of melanistic individuals). We further measured the niche overlap between these groups and tested for niche equivalency and similarity.

### 2. Material and methods

We collected data on the presence of colour patterns and melanism in 2033 individuals of *V. berus* and *V. aspis* throughout their distribution in Switzerland (electronic supplementary material, S1). A total of 53 and 94 local populations, with an average pairwise geographical distance of 126 ± 82 and 91 ± 49 km were sampled for the two species. Populations of *V. berus* ranged from 900 to 1970 m a.s.l. Seventeen local populations were polymorphic and 36 were monomorphic with strictly patterned individuals. For *V. aspis*, local populations ranged from 350 to 2300 m a.s.l. and 31 were polymorphic and 63 monomorphic with strictly patterned individuals. All *V. aspis* local populations at the lowland vegetation band (less than 750 m a.s.l., [15]) were patterned.

Local populations were characterized by retrieving environmental variables, relevant for the ecology of *Vipera*, from georeferenced grids at 100 m resolution [15]. Because vipers are heliothermic vertebrates that depend on adequate environmental conditions for an efficient thermoregulation [16], we included the following variables: site water balance (swb), annual number of days above 3°C (ddeg3), annual number of days with frost (sfroy), annual sum of precipitation (precy), average temperature during the summer (tave59), annual mean cloudiness (clou) and annual sum of solar radiation (srad) [17]. Following Broennimann et al. [18], we used a principal component analysis (PCA) to transform the climatic space of the seven climatic variables into a two-dimensional surface defined by the first and second principal components. The PCA was calibrated using environmental data at all sites in Switzerland at 100 m (i.e. background data). The scores of the occurrences of each species were then projected onto a 100 × 100 PCA grid of cells bounded by the minimum and maximum PMA values in the background data. A smoothed density of occurrence for each species in each cell of the PCA grid was then estimated using a kernel density function [18]. To calculate niche overlap, we chose the D metric [19], because it expresses an overall fit between niches over the full environmental space. The D metric varies from 0 (no overlap) to 1 (complete overlap). Tests of niche similarity and equivalency followed randomization tests as outlined by Broennimann et al. [18]. Rejection of niche equivalency means that the niches of native and non-native populations are not statistically equivalent, whereas a rejection of niche similarity indicates that niches are more similar than expected at random.

### 3. Results

Figure 1 shows the scores of the local populations along the first two PCA axes, which captured 75.3% of the variation. The first axis mainly represents a gradient of coldness (i.e. tave59 and ddeg3 are negatively correlated, whereas clou and sfroy are positively correlated with this axis; figure 1c), and the second axis mainly represents a gradient of humidity (i.e. swb and srad are positively and negatively correlated with this axis, respectively; figure 1c). Our results highlight that *V. aspis* local populations partially overlap climatically with *V. berus* local populations (overlap = 0.43; table 1) but are found in warmer and dryer conditions overall (figure 1 and table 2). The overlap between *V. aspis* and *V. berus* is even higher (0.66) when considering only montane and subalpine local populations of *V. aspis* (figure 1 and table 2).

When considering colour morphs, our results indicate that polymorphic local populations are found in colder conditions than monomorphic local populations both for *V. aspis* (mean on PCA axis 1 = 0.13 versus −1.88) and *V. berus* (mean on PCA axis 1 = 0.26 versus 0.49). Niche overlap between polymorphic populations of the two species (0.71) is higher than between polymorphic versus monomorphic local populations of *V. aspis* (0.33; 0.58 when considering only montane local populations) and *V. berus* (0.65; note that there are only montane populations of *V. berus* in Switzerland).

Finally, the variance of both the temperature and water availability axes of the PCA for the two species is larger in monomorphic local populations than in polymorphic ones (*V. berus*, axis 1: 0.44 versus 0.48, axis 2: 0.32 versus 0.57; *V. aspis*, axis 1: 0.93 versus 2.7, axis 2: 0.41 versus 1.57), even when strictly considering montane and subalpine local populations of *V. aspis* (axis 1: 0.73 versus 1.31, axis 2: 0.38 versus 0.77; table 2). This means that the niche width is larger in local populations that are monomorphic.

### 4. Discussion

Across both species, polymorphic local populations (i.e. including melanistic and patterned individuals) are restricted...
to cooler and wetter habitats, supporting the role of melanism in thermoregulation [5,8]. Interestingly, we found an important niche overlap between populations of both species that are polymorphic. This niche overlap is even higher than that of polymorphic versus monomorphic montane local populations of V. aspis, suggesting that the role of melanism in determining the niche of ectothermic vertebrates might supersede other species-specific characteristics.

Contrary to our expectations, the niche occupied by the polymorphic local populations of V. aspis and V. berus is not broader than the niche of monomorphic local populations (strictly composed of patterned individuals). It thus seems that the macro-ecological rule predicting that polymorphic species are able to exploit a greater variability of resources [11] may not always hold true at the intraspecific level. We cannot completely exclude, however, that our analysis missed an important ecological variable relating to characteristics of microhabitats that enable individuals to avoid predation.

Overall, our results on niche position and niche breadth highlight that very specific trade-offs between environmental conditions and local variation of predatory community might be required in order for dark coloration to be advantageous. Despite the clear thermoregulatory benefit of such coloration in cold habitats, predation pressure might prevent the successful establishment of melanistic individuals in local populations [6,9]. As a result, melanism might be present only when the thermoregulatory benefit is higher than the cost of the predation pressure. In this respect, it would be particularly interesting to study local populations strictly composed of melanistic individuals. However, to the best of our knowledge, such populations have never been documented in the literature for either species (see e.g. [20] for a review of the literature concerning V. berus; [6]).

Studying the effect of colour polymorphism on niche position and breadth could lead to different conclusions depending on the taxonomic scale at which the analyses are performed. Future studies should thus consider multiple scales, such as intra- and interpopulation-, and species-level. These multiple scales should be integrated with evolutionary drivers in order to understand how this polymorphism arose and what the impacts are on species’ ecology and their response to future environmental changes.

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References

14. Monney JC, Luiselli L, Capula M. 1996 Body size and melanism in Vipera aspis in the Swiss Prealps and central Italy and comparison with

Table 2. Niche characteristics of groups of local populations.

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