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# Thermoregulation and microhabitat choice in the polymorphic asp viper (*Vipera aspis*)



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## ABSTRACT

In ectotherms, thermoregulation strongly depends on environmental conditions, as well as on intrinsic factors, such as skin colour. Indeed, due to its physical properties, melanin pigments allow melanistic morphs to benefit of a more efficient thermoregulation compared to non-melanistic ones. Despite thermal benefits of melanism have often been highlighted under experimental conditions, such field data remain scarce. In this study, we investigated the influence of colouration on body temperature and microhabitat choice in a montane population of colour polymorphic asp viper (*Vipera aspis*) characterized by a strong presence of melanism (64%). Results highlighted a difference in internal body temperature, but only within gravid females, with melanistic individuals having higher body temperatures compared to non-melanistic ones. No differences were found when considering both sexes. We also showed that melanistic and non-melanistic vipers were found in different microhabitat types, i.e. melanistic snakes used areas marked by a scarcer sun exposure and by higher vegetation cover compared to non-melanistic ones. This result has important implications. Indeed, besides providing a possible explanation for the lack of difference in body temperature (except for gravid females), it confirms that melanistic individuals can potentially use their efficient thermoregulation in order to inhabit less exposed and thermally unfavourable microhabitats.

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## 1. Introduction

Polymorphism plays a major role in survival and viability at intraspecific level. Genetic, phenotypic and behavioural diversity are the key to evolutionary success, ecological adaptations and ability to deal with environmental changes. Populations, in which individuals present phenotypic variations can indeed better colonize heterogeneous habitats, and cope with constraints imposed by the environment, parasites or diseases (Wilson et al., 2001; Forsman and Åberg, 2008a, 2008b; Forsman et al., 2008; Pizzatto and Dubey, 2012).

The occurrence of melanistic morphs is common in ectothermic vertebrates (Clusella-Trullas et al., 2007; Ducrest et al., 2014; Dubey and Roulin, 2014) and one of the most plausible and widely studied hypothesis highlights its advantage in terms of thermoregulation (Clusella-Trullas et al., 2007, 2009; Broennimann et al., 2014). Such advantage arise from the lower reflectance of darkly compared to lightly coloured integuments (Brakefield and

Willmer, 1985; Jong et al., 1996). In fact, as suggested by various experimental studies, such property allows melanistic individuals (under similar environmental conditions) to heat up faster, reach a higher temperature and maintain an optimal temperature for longer periods compared to non-melanistic ones (Crisp et al., 1979; Forsman, 1995; Tanaka, 2005, 2007). In turn, a thermal advantage can have a positive impact on several ecological factors. For example, some studies conducted on different snakes species highlighted a higher growth rate and/or larger body size, and better body conditions in melanistic individuals (Andr n and Nilson, 1981; Luiselli, 1995; Monney et al., 1996; Castella et al., 2013). Another benefit may be related to a major daily and seasonal activity, overall in cooler regions. In this regard, only the melanistic morphs of the Japanese striped snakes expose themselves during the early winter (Ota and Tanaka, 2002). However, in most field studies, no difference in body temperature was detected between melanistic and non-melanistic individuals (Crisp et al., 1979; Forsman, 1995; Tanaka, 2005, 2007; Clusella-Trullas et al., 2009; Geen and Johnston, 2014). This is understandable considering that, in natural conditions, benefits of a better thermoregulation may be buffered by behavioural differences between morphs or by the use of different habitat types, as

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e.g. melanistic morphs are often less cryptic to predators compared to non-melanistic ones (Andr n and Nilson, 1981; Forsman, 1995; W ster et al., 2004; Niskanen and Mappes, 2005).

Thus, by considering costs and benefits of melanism, it is possible to draw two major scenarios that can explain how melanistic individuals take advantage of their more efficient thermoregulation (resulting in e.g. higher maximum body temperature in similar environmental conditions). First, free ranging melanistic individuals might be characterized by a higher body temperature compared to non-melanistic ones, since they use their more efficient thermoregulatory capacity in order to increase their activity, growth rate, body size, or reproductive output. Second, there are no differences in body temperature between melanistic and non-melanistic morphs, since darker individuals might use thermoregulatory advantage to inhabit thermally unfavourable microhabitats (in which non-melanistic morphs could hardly live).

The asp viper (*V. aspis*) is an adequate system to study the evolution of colour polymorphism in ectothermic vertebrates. It exhibits intrapopulational colour polymorphism with the presence of melanistic and non-melanistic individuals in mountainous areas of central Europe, likely for thermoregulatory reasons (Supplementary online materials 3; Castella et al., 2013; Broennimann et al., 2014). In addition, it can be found in very heterogeneous habitat types (see e.g. Castella et al., 2013 and Supplementary online materials 3). In this study, we tested on a large asp viper (*V. aspis*) population, characterized by a strong presence of melanism (64%), if (i) melanistic vipers significantly differed from non-melanistic ones in term of internal body temperature and (ii) whether melanistic and non-melanistic individuals are distributed in different microhabitat types, hypothesizing that their potential thermoregulatory advantage might enable melanistic individuals to better deal with unfavourable environmental conditions.

## 2. Materials and methods

### 2.1. Studied area and sampling

All vipers included in the study were collected and measured in western Swiss Alps, more precisely in the district of Riviera-Pays-d'Enhaut (Canton de Vaud). The sampling sites were located on the southern slope of the valley (46.49°N, 7.09°E) between 870 and 1600 m asl. and spread out over a surface of approximately 1800 ha. Sampling was carried out between 2012 and 2014 from April to September and snakes were captured by hand (using a double pair of protective gloves). On a total of 608 observations of 392 different individuals (recapture mean =  $1.55 \pm 1.12$ ), 233 were found in open areas, 194 vipers in vegetation patches (> 4 m from the edge of forest or bush areas), and 181 at the transition between vegetation patches and open area (< 4 m from the edge of forest or bush areas). For each individual, sex and colouration (melanistic or non-melanistic) were determined and the following measures were recorded: time of capture (hour and minutes), altitude (m asl.), geographic coordinates, air temperature (°C), and snout-vent length (SVL in mm). Internal temperature (°C) was only recorded in 2014 with a cloacal probe (A313; Physitemp, NJ, USA) directly after individuals were captured to avoid potential bias. For females whose length exceeded 40 mm, the reproductive status (gravid or not gravid) was verified by palpation (Bonnet and Naulleau, 1996; Castella et al., 2013; Monney et al., 1996). Snakes were marked by scale clipping and a picture of the head of each individual was taken, in order to efficiently identify recaptures.

### 2.2. Computed environmental predictors

With the purpose to define the asp viper microhabitat in the studied area, three types of environmental predictors were considered: topographic (slope in degrees), bioclimatic (solar radiation in kWh/m<sup>2</sup>), and the Normalized Difference Vegetation Index (NDVI). The fourth environmental predictor corresponded to the altitude and was calculated in the field. In order to spatially compute slope and solar radiation, digital elevation models (DEMs) with a resolution of 2 m were used. These DEMs were subsequently computed by aggregating a 1 m DEM from Swisstopo (Pradervand et al., 2013). Slope (2 m resolution) was calculated using the spatial analyst tool in ArcGIS 10 with a 3 × 3 pixel moving window (Pradervand et al., 2013). Solar radiation (2 m) was calculated for each pixel and every day of year. The entire area has been used as input in order to compute, using DEM, the direct diffused and reflected solar radiation. Local exposure and shading topography have also been considered for computing, using the spatial analyst tool in ArcGIS 10 (Pradervand et al., 2013). Solar radiation and slope values for each pixel (corresponding to the coordinates of a capture event) were obtained from ArcGIS raster data. In the statistical analysis, solar radiation was used as the average of days included in the period between April and September. Finally, it is important to remember that solar radiation is a potential value, which, in the case of a forest or a surface with strong plant productivity, is calculated at the canopy level and not on the soil as in open area. This means that there is a slight overestimation of the solar radiation for captures carried out in points marked by a strong vegetation density. Finally, NDVI corresponds to an annual average of the vegetal biomass productivity and its index ranges from -1 to +1. Highly positive values (> 0.5) represent surfaces with important vegetation density. Low positive values represent shrub and grassland (approximately 0.2–0.4). Values close to zero (-0.1 to 0.1) mainly highlight barren or rocky areas, while values lower than -0.1 characterize a complete lack of vegetation (Carlson and Ripley, 1997). NDVI rasters with a resolution of 2 × 2 m<sup>2</sup> were obtained from red and infrared aerial photographs (Swissimage FCIR, Swisstopo). Values were subsequently calculated using the following formula (Wang et al., 2003), implemented in ArcGIS 10:  $VI = \frac{(NIR - RED)}{(NIR + RED)}$

### 2.3. Statistical analysis

#### 2.3.1. PCA analysis for environmental predictors

Because some environmental predictors selected for both thermoregulation and microhabitat models (NDVI, altitude, solar radiation and slope) were partly correlated (involving collinearity problems), we summarized the information contained in these variables in a principal component analysis (PCA) using R software (version 3.1.1). The PCA axes, used later in both analyses (i.e. thermoregulation and microhabitat choice), were selected based on two criteria: eigenvalues higher than 1 and proportion of explained variance exceeding 10% (Quinn and Keough, 2002; Online supplementary material 3).

#### 2.3.2. Generalized linear mixed model (GLMM) selection

For all GLMMs used in this study, we proceeded as follows: (1) we build the model with all pairwise interactions and a random structure to control independency (relative to recapture), (2) we checked assumptions of the model (homoscedasticity and normality of residuals), (3) we applied a backward selection based on *F*-statistic with associated *p*-values and (4) we validated the final model thanks to model assumptions. When heteroscedasticity issues were noticed, we corrected the model with variance structures available in the "lme" function (package "nlme",

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