Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

Melanism, body condition and elevational distribution in the asp viper

B. Castella[1]*, J. Golay[1]*, J.-C. Monney[2], P. Golay[1], K. Mebert[3] & S. Dubey[1]

1 Department of Ecology and Evolution, Biophore Bld, University of Lausanne, Lausanne, Switzerland
2 karch (Centre de coordination pour la protection des amphibiens et des reptiles de Suisse), Neuchâtel, Switzerland
3 Siebeneichenstrasse 31, Merenschwand, Switzerland

Keywords
coloration; crypsis; melanism; montane species; reptile.

Correspondence
Sylvain Dubey, Department of Ecology and Evolution, Biophore Bld, University of Lausanne, 1015 Lausanne, Switzerland.
Tel: +4121 692 4204; Fax: +4121 692 4165
Email: sylvain.dubey@unil.ch

*Briseïs Castella and Joaquim Golay contributed equally to this work.

Dedication
We dedicate this paper to our highly esteemed co-author Jean-Claude Monney who passed away in December 2012. For this reason, we express our deep thanks for his collaboration on the ecology and evolution of the asp viper that began many years ago. We will never forget him.

Editor: Mark-Oliver Rödel

Received 22 January 2013; revised 3 March 2013; accepted 4 March 2013

doi:10.1111/jzo.12037

Abstract

Alternative morphotypes can confer important selective advantages in different habitats, whereas they can be penalized in other circumstances. In ectotherms, such as reptiles, the body colour can have direct effects on numerous aspects of their existence, such as thermoregulation or prey–predator interactions. Darker melanic individuals show lower skin reflectance and consequently heat up more rapidly and maintain optimal body temperatures more easily than lighter coloured individuals. As a consequence, melanistic individuals of diurnal species in cool areas may exhibit higher body condition, growth rate, survival and fecundity than lighter coloured individuals. Such advantages of dark coloration may be counterbalanced by a lower crypsis to predators and a decreased foraging efficiency. We investigated, in two montane populations of asp vipers *Vipera aspis*, the relationship between (1) colour polymorphism and body condition and length and (2) the coloration of individuals and their elevational distribution. We showed significant relationships between (1) the coloration, body condition and sex of individuals; (2) sexes and reproductive state and morph frequency; and (3) colour morphs that were distributed following an elevational gradient. Hence, colour polymorphism plays an important role in the ecology and evolution of the asp viper and is maintained through differential selective pressures.

Introduction

The presence of multiple colour morphs may promote the ecological success of populations and species (Forsman & Åberg, 2008a,b), because it may broaden the range of environmental conditions under which individuals are able to survive and maintain reproductive populations (e.g. Forsman *et al.*, 2008; Caesar, Karlsson & Forsman, 2010; Pizzatto & Dubey, 2012). Hence, a morphotype can gain a strong selective advantage in a specific habitat or under certain environmental conditions, whereas it can be penalized in other circumstances. Consequently, different phenotypes may represent equally fit alternative strategies (Galeotti, Rubolini & Dunn, 2003; Roulin, 2009), and the frequency of morphotypes may not be stable through time and space (e.g. Roulin, Burri & Antoniazza, 2011).

Within a species or a population, patterns of phenotypic variation (e.g. body shape and coloration) can be strongly impacted by the ways in which those differences reflect variations in fitness of individuals (see e.g. Olsson *et al.*, 2002; Du, Ji & Shine, 2005; Stuart-Smith *et al.*, 2008; Dubey *et al.*, 2009; Dubey, Chevalley & Shine, 2011). For example, body colour can have direct effects on numerous aspects of an ectotherm's life history, such as thermoregulation and prey–predator interactions (i.e. camouflage, aposematism or mimicry; Roulin, 2004; Protas & Patel, 2008; Rosenblum *et al.*, 2010).

In ectotherms, at similar temperatures, intensity of solar radiation and wind speed, darker individuals heat up more rapidly due to lower skin reflectance, and consequently maintain optimal body temperatures more easily than do lighter coloured individuals (De Jong, Gussekloo & Brakefield, 1996; Clusella-Trullas, van Wyk & Spotila, 2007). As a conse-

Figure 1 Melanistic (a) and normal (patterned) (b) asp vipers *Vipera aspis* from the Swiss Prealps (Canton of Vaud).

quence, melanistic individuals of diurnal species in cool areas [high elevation and latitude, or forested (shady) areas] exhibit better locomotor performances, longer activity periods, higher growth, body condition, survival and fecundity than do lighter coloured individuals (Huey & Kingsolver, 1989; Luiselli, 1992; Capulla & Luiselli, 1994; Clusella-Trullas *et al.*, 2007). For the same reasons, melanistic coloration confers advantages in forested (shady) areas (Monney, 1996; Tanaka, 2005, 2007, 2009). However, such benefits of dark coloration may be counterbalanced by reduced crypsis to predators and hence a higher predation rate (e.g. Gibson & Falls, 1979; Andrén & Nilson, 1981). High predation risk may also lead in increased physiological stress and in decreased foraging efficiency, which can in turn negatively impact body condition (e.g. Perez-Tris, Diaz & Telleria, 2004; San-José, Gonzales-Jimena & Fitze, 2008).

Interactions between an organism's colour and the local environment are also very important for ambush-foraging ectotherms that rely upon background colour matching or disruptive coloration to evade detection by potential prey. Hence, colour traits in these species are subject to complex multifunctional optimizations between, for example, efficient thermoregulation and ability to ambush prey successfully (Ayers & Shine, 1997; Shine *et al.*, 1998). Thus, an adequate model system in which to explore this problem would be an ectothermic ambush-foraging species exhibiting intra-populational colour polymorphism. The asp viper *Vipera aspis* fulfils all these criteria; it is distributed along a wide elevational gradient over its range (central and western Europe), from sea level to more than 2000 m asl (above sea level) (Meyer, Zumbach & Schmidt, 2009), and individuals and populations differ strongly in coloration. In Switzerland, only the patterned (cryptic) morph is present below 700 m asl, whereas melanistic individuals (non-cryptic) are common in some, but not all, mid- and high-elevation sites (Fig. 1). In Switzerland and in Italy, non-melanistic *V. aspis* tend to be longer than their melanistic conspecifics, despite a trend for higher growth rates in melanistic snakes (Monney, Luiselli & Capula, 1996). This pattern is likely explained by a lower predation rate in cryptically patterned snakes, allowing them to reach a higher mean age (and hence a larger body length) than melanistic snakes (Monney *et al.*, 1996). Nevertheless, the body condition in relation to colour polymorphism was not investigated, precluding further conclusions.

In the present study, we investigated, in two colour polymorphic montane populations (Swiss Prealps) of asp vipers *V. aspis*, the relationship between (1) colour polymorphism and body condition and length; (2) sexes, reproductive state and morph frequency; and (3) the coloration of individuals and their elevational distribution, in order to better evaluate the advantage of being melanistic in montane areas.

Methods

Sampling

In spring 2012 (late April to mid-June), we captured by hand (with protective gloves) 128 different asp vipers (62 females and 66 males) in a population from the Swiss Prealps of the Canton of Vaud (on a mountain range with a mainly south-east exposure; latitude 46.4913°, longitude 7.0859°) between 1160 and 1587 m asl. A total of 56 females ($N_{\text{melanistic}} = 37$; $N_{\text{patterned}} = 19$; 66% of melanistic individuals) and 50 males ($N_{\text{melanistic}} = 38$; $N_{\text{patterned}} = 12$; 76% melanistic individuals) measured > 40 cm in snout-vent length (SVL) and were considered as adult (see Bonnet & Naulleau, 1996; Monney, 1996; Monney *et al.*, 1996). About 77% of individuals were found in lightly forested areas (or at no more than 10 m from a patch of trees) with a high proportion of maple trees and masses of fallen rocks. Because the treeline started roughly between 1400 and 1600 m asl, the proportion of individuals living in or next to the forest decreased with the elevation (pers. obs.).

In addition, we included in our analyses the individuals collected from 1988 to 1993 (6 years) in the Bernese Oberland (a prealpine locality situated 17 km southeast of our site and displaying a south to southeast exposure; latitude 46.3914°, longitude 7.2562°) by Monney *et al.* (1996). In contrast with our site, it is characterized by a very open habitat. Consequently, snakes at the Bernese site were mainly found in fully open areas instead of lightly forested (shady) areas (pers. obs.). The dataset based on 400 observations of 153 different snakes [87 females ($N_{\text{melanistic}} = 32$; $N_{\text{patterned}} = 55$; 37% of melanistic individuals) and 66 males ($N_{\text{melanistic}} = 25$; $N_{\text{patterned}} = 41$; 38% of melanistic individuals)] includes body mass, length, sex and colour morph of individuals, as well as the elevation of capture site (from 1384 to 1960 m) and date of capture.

The body mass (measured with a Pesola spring scale only if no recent trophic activity was detected, i.e. in absence of prey in the digestive tract), total length and tail length were recorded for each snake; moreover, snakes were sexed by eversion of the hemipenes as, for example, in Dubey *et al.* (2008) and marked by scale clipping. Ovulation normally occurs between the end of May and early June (Saint Girons & Duguy, 1992). Knowing that gestation lasts for 2–3 months, parturition occurs from late August to late September or even October at high elevation (Meyer *et al.*, 2009). During the gestation period, gravid females usually stop feeding, in contrast to non-gravid females.

Statistical analyses

We were unable to combine the two datasets, because data were collected in 2012 in the Canton of Vaud and from 1988 to 1993 in the Bernese Oberland; consequently, the analyses were performed separately for both populations.

We calculated the body condition of individuals based on the residual values of linear regressions with body mass (log transformed) and body length (log-transformed SVL) as response and explanatory variables, respectively (see e.g. Shine & Madsen, 1997). We estimated the body condition of (1) non-gravid females and males together; (2) both gravid and non-gravid females; and (3) gravid females.

We first performed linear mixed models, considering the body condition of adult individuals (excluding gravid females) as response variable and the sex, colour morph, date of capture and elevation as explanatory variables (only significant variables and interactions were kept in the analyses). Then, the same analyses were performed in females considering their reproductive state (Canton of Vaud, $n = 21$; Bernese Oberland, $n = 73$; determined by palpation of the ovarian follicles; see Monney *et al.*, 1996); consequently, only individuals captured just after the ovulation period were considered. Finally, we performed the same analyses, but strictly in gravid females. Because data were recorded at several occasions for some individuals during the field season, we considered the identity of individuals as a random effect (as well as the year for the dataset from Monney *et al.*, 1996) in the analyses to avoid pseudoreplications. Similarly, we performed linear mixed models, considering the body length of adult individuals (log-transformed SVL) as response variable.

Second, we tested for a difference in the proportion of gravid females in melanistic versus patterned snakes, with a chi-squared test.

Third, we tested [with linear model (LM) or generalized linear model (GLM)] whether the colour morph and the gender of individuals influenced their elevational distribution in the Canton of Vaud and Bernese Oberland populations, respectively. When more than one elevation was available for the same individual, we estimated its mean elevation in order to avoid pseudoreplication.

Statistical analyses were performed with JMP 8.0 and SAS v9.2 (SAS Institute, Cary, NC, USA).

Results

Body condition

In the Canton of Vaud, our linear mixed model revealed a significant interaction between coloration and sex ($F_{1,77.91} = 3.77$, $P = 0.0557$; date of capture and elevation were not significant alone nor in interaction with the other variables; all P-values ≥ 0.12; see Table 1), with a higher body condition in melanistic than in patterned females and no apparent differences in males (Fig. 2a).

In Bernese Oberland, only the date of capture had a significant effect on the body condition of individuals ($F_{1,198.1} = 4.47$, $P = 0.0357$), with body condition increasing through the season (likely due to an increase of prey availability) (see Table 1; Fig. 2b). Elevation, coloration, and sex were not significant alone nor in interaction with other variables, and date of capture was not significant in interaction with other variables (all P-values ≥ 0.09).

Within females of the Canton of Vaud, our LM including the reproductive state of individuals revealed significant effects of the colour morph ($F_{1,56} = 4.74$, $P = 0.034$) as well as of the reproductive state on the body condition of females ($F_{1,56} = 11.19$, $P = 0.002$; date of capture and elevation were not significant alone nor in interaction with the other variables, and coloration and reproductive state were not significant in interaction; all P-values ≥ 0.08; Table 1) with gravid females showing better body conditions than non-gravid females, and melanistic females higher body condition than patterned females (Fig. 2c).

In the Bernese Oberland, our linear mixed model revealed significant effects of the reproductive state on the body condition of individuals ($F_{1,126.4} = 13.67$, $P = 0.0003$; Table 1), with gravid females showing better body condition than non-gravid females, as well as of the date of capture, the body condition slightly increasing through the season ($F_{1,126.7} = 4.31$, $P = 0.04$; coloration and elevation were not significant alone nor in interaction with the other variables, and date of capture and reproductive state were not significant in interaction; all P-values ≥ 0.09; Table 1; Fig. 2d).

In gravid females at both sites, we found no significant effect of the different variables alone nor in interaction on the body condition (all P-values ≥ 0.10).

Table 1 Results of the linear and linear mixed models in (i) the Canton of Vaud and (ii) the Bernese Oberland for the body condition in (a) males and non-gravid females and (b) females considering their reproductive state (in bold, variables and interactions included in the final models; in italic, non-significant variables or interactions excluded from the final models), and (c) body length.

	d.f.	*F*-value	*P*-value
(i) Canton of Vaud			
(a) Response variable: Body condition in males and non-gravid females			
Sex	**79.91**	**0.00**	**0.973**
Coloration	**79.91**	**1.75**	**0.189**
Sex*coloration	**79.91**	**3.77**	**0.058**
Date	44.06	0.90	0.348
Elevation	76.17	0.40	0.527
Coloration*elevation	75.44	2.44	0.123
Elevation*sex	75.5	1.06	0.307
Elevation*date	75.87	1.34	0.251
Date*sex	61.79	0.65	0.423
Date*coloration	72.84	0.26	0.614
(b) Response variable: Body condition in females			
Reproductive state	**1**	**11.19**	**0.002**
Coloration	**1**	**4.74**	**0.034**
Altitude	1	2.86	0.10
Date	1	1.78	0.19
Elevation*coloration	1	2.94	0.09
Date*elevation	1	0.70	0.41
Reproductive state*date	1	0.22	0.64
Date*coloration	1	0.26	0.61
Reproductive state*coloration	1	0.11	0.74
Reproductive state*elevation	1	0.00	0.98
(c) Response variable: Body length (log-transformed SVL)			
Sex	**105.9**	**6.24**	**0.014**
Date	**44.78**	**1.81**	**0.19**
Sex*date	**44.78**	**4.90**	**0.0319**
Melanism	104.6	0.45	0.50
Elevation	101.5	0.03	0.86
Elevation*melanism	98.66	1.86	0.18
Sex*melanism	99.89	1.54	0.22
Date*coloration	99	1.08	0.30
Sex*elevation	96.45	0.48	0.49
Date*elevation	96.75	0.76	0.39
(ii) Bernese Oberland			
(a) Response variable: Body condition in males and non-gravid females			
Date	**198.1**	**4.47**	**0.036**
Elevation	166.6	2.57	0.111
Coloration	69.67	2.51	0.118
Sex	88.55	0.75	0.388
Sex*elevation	160.4	2.94	0.089
Elevation*coloration	165.2	1.03	0.312
Coloration*date	195	0.12	0.731
Sex*date	227.4	0.04	0.848
Sex*coloration	83.09	0.00	0.995
(b) Response variable: Body condition in females			
Date	**126.7**	**4.31**	**0.04**
Reproductive state	**126.4**	**13.67**	**0.0003**
Elevation	102.2	0.40	0.53
Coloration	29.15	0.11	0.75
Elevation*reproductive state	118.7	3.01	0.09
Reproductive state*coloration	125	1.63	0.20
Elevation*coloration	111.9	0.21	0.65
Reproductive state*date	123	0.07	0.79
Coloration*date	121.1	0.07	0.79
(c) Response variable: Body length (log-transformed SVL)			
Elevation	**305.4**	**2.45**	**0.12**
Melanism	**147.6**	**1.64**	**0.20**
Elevation*melanism	**304.9**	**11.44**	**0.0008**
Date	197	3.05	0.08
Sex	146.1	0.18	0.67
Sex*date	203.7	1.21	0.27
Coloration*date	195.5	0.78	0.38
Sex*altitude	217	0.08	0.78
Sex*melanism	143.7	0.08	0.77

SVL, snout-vent length.

SVL

In the Canton of Vaud, our linear mixed model revealed a significant effect of sex ($F_{1,105.9} = 6.24$, $P = 0.014$) and of the interaction between sex and date of capture ($F_{1,44.78} = 4.90$, $P = 0.0319$; date of capture was not significant alone; see Table 1), with body length of captured females slightly decreasing through the season, but not in males. Elevation and coloration were not significant alone nor in interaction with other variables, and date of capture and sex were not significant in interaction with other variables (all P-values ≥ 0.18). In the Bernese Oberland, we revealed a significant interaction between coloration and elevation ($F_{1,304.9} = 11.44$, $P = 0.0008$; these variables, as well as date of capture and sex, were not significant alone nor in interaction with other variables; all P-values ≥ 0.08) with body length increasing with the elevation in patterned individuals and decreasing in melanistic individuals.

Proportion of colour morphs

In both populations, we found no significant differences in the proportion of colour morphs between sexes (Canton of Vaud: 66% and 76% of melanistic individuals in females and males, respectively; chi-squared test: $\chi^2 = 1.26$, $P = 0.26$; Bernese Oberland: 37% and 38% of melanistic individuals in females and males, respectively; chi-squared test: $\chi^2 = 0.02$, $P = 0.89$).

The proportion of gravid melanistic females (49%) was significantly higher than in the patterned snakes in the Canton of Vaud (21%; chi-squared test: $\chi^2 = 4.218$, $P = 0.04$), whereas in Bernese Oberland, we found no significant difference between colour morphs or between years (81% and 73% of gravid patterned and melanistic snakes, respectively; coloration: $\chi^2 = 1.73$, $P = 0.19$; year: $\chi^2 = 1.40$, $P = 0.24$).

Distribution of colour morphs

In the Canton of Vaud, patterned snakes were found at higher elevation than melanistic snakes, independent of their gender (LM; melanistic: mean elevation = 1328 m asl, patterned: mean elevation = 1392 m asl; coloration: $F_{2,103} = 6.73$, $P = 0.018$; sex: $F_{1,101} = 1.22$, $P = 0.2719$; sex*interaction: $F_{1,101} = 0.13$, $P = 0.7224$; Fig. 3).

In Bernese Oberland, the same pattern was observed (Fig. 3), but the difference was stronger in females than in males (GLM with a Poisson distribution; melanistic females: mean elevation = 1519 m, patterned females: mean elevation = 1555 m asl; melanistic males: mean elevation = 1523 m, patterned males: mean elevation = 1525 m asl; coloration: $F_{1,149} = 7.57$, $P = 0.0067$; sex: $F_{1,149} = 3.76$, $P = 0.0545$; sex*interaction: $F_{1,149} = 6.51$, $P = 0.0117$).

Discussion

Our study, focusing on two asp viper populations from the Swiss Prealps, shows that the body conditions of the two colour morphs differed between sexes and sites. Indeed, in Bernese Oberland (characterized by a low level of melanism),

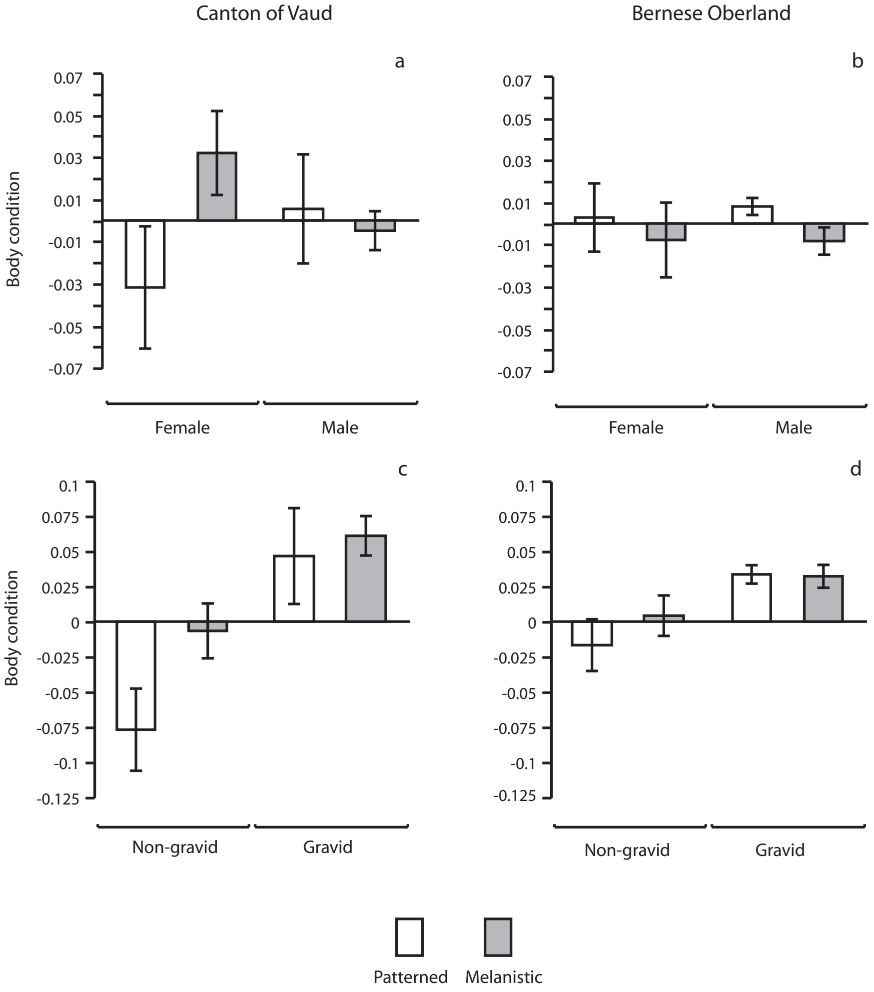

Figure 2 Relationship between body condition and sex and colour morph (a and c) and female reproductive state and colour morph (b and d) in the Canton of Vaud and Bernese Oberland, respectively (mean with standard error).

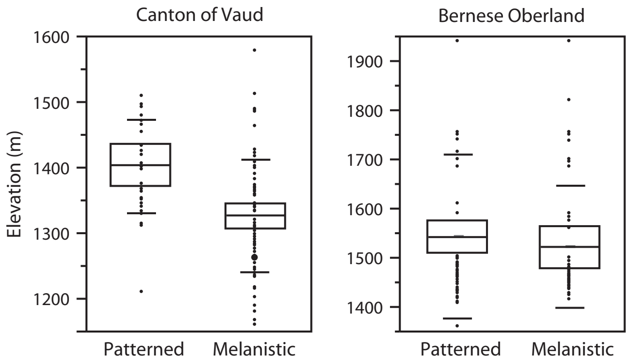

Figure 3 Elevational distribution (mean with standard error and 95% standard deviation) of colour morphs (patterned and melanistic) in the Canton of Vaud and the Bernese Oberland.

no differences in body condition were found between patterned and melanistic individuals, whereas in the Canton of Vaud (characterized by a high level of melanism) melanistic individuals showed better body condition than did patterned individuals. Consequently, the difference in coloration frequency may reflect different selective advantages of being melanistic (or not) in these two populations, and hence might be context dependent and associated with the presence of particular predators, vegetation types and/or climatic conditions. Individuals displaying different colorations may be adapted to different environments and thus represent equally fit alternative strategies in adequate environments (Galeotti *et al.*, 2003; Roulin, 2009). However, given that our study focused on only two populations, we were not able to test this hypothesis.

Interestingly, in males from the Canton of Vaud, differences in body condition were not apparent (Fig. 2a), which suggests that melanism may play a more important role for females than for males in this particular population. Females of this viviparous species usually have an annual reproductive cycle in southern Europe, but in some cold or montane areas (such as our study areas), populations display a tri- or even quadrennial cycle (e.g. Naulleau & Bonnet, 1996), meaning 4 years is necessary for a female to build up enough resources for breeding (Monney, 1996), contrary to males, that can reproduce annually and do not need to build important fat body reserves (Aubret *et al.*, 2002). Moreover, efficient thermoregulation is essential for females living in such areas, and melanism is likely to play a stronger role in females than in males.

In addition, this phenomenon could be explained by a higher rate of predation in melanistic males compared to patterned ones due to a lower crypticity. Since males are actively searching for females during the breeding season (from April to May), and are therefore forced to move away from their shelter and between forested patches (Monney, 1996), their chance of being predated is greater than for females, a pattern that has been shown for numerous species (Christe, Keller & Roulin, 2006). These behavioural differences between sexes coupled to the lower crypticity of melanistic individuals could be linked to the absence of a positive relationship between melanism and body condition in males from the Canton of Vaud. Indeed, high predation risk may lead in decreased foraging efficiency, which can in turn negatively impact body condition (e.g. Perez-Tris *et al.*, 2004; San-José *et al.*, 2008).

Similarly, in adders *Vipera berus*, patterned males had a higher survival rate than melanistic males, but the reverse was true in females, which was interpreted as a difference in sexual behaviour, with an increase of predation intensity in melanistic males but not in females (Forsman, 1995a,b).

In both populations, no clear effect of coloration was apparent on the body condition of gravid females (Fig. 2c,d), a pattern that could be explained by the fact that females (independent of their coloration) are capital breeders and therefore need to accumulate substantial fat reserves and reach a particular threshold to induce a vitellogenic process (Naulleau & Bonnet, 1996; Aubret *et al.*, 2002; Bonnet, 2011). Consequently, the variation in body condition of gravid females is expected to be lower than in other individuals of both sexes. Interestingly, the proportion of gravid patterned females (21%) compared to melanistic ones (49%) differs in the Canton of Vaud, whereas no significant differences between morphs were present in the Bernese population (patterned: 81%, melanistic: 73%), again suggesting an advantage of being melanistic in a particular area or year. However, long-term monitoring of populations is needed to see if such patterns are stable through time.

Despite significant relationships between colour polymorphism and body conditions in the asp viper, we cannot exclude that indirect effects (dependent or independent of environmental conditions) due to possible pleiotropic mechanisms (or linked genes) could at least partly affect our results. For example, a few studies found associations between colour polymorphism, immunocompetence, developmental rate and resistance to food depletion in vertebrates (e.g. see Roulin *et al.*, 2004; Ducrest, Keller & Roulin, 2008; Dreiss *et al.*, 2010). If comparable effects were found in the asp viper, they could partly explain the strong differences observed between our two populations in terms of body condition relative to colour morphotypes, which could indicate that environmental conditions play an important role in the expression of particular phenotypes in this species.

In our two montane polymorphic populations, colour morphs were distributed following an elevational gradient, with the proportion of melanistic individuals decreasing with the elevation (Fig. 3). Similarly, the body length (SVL) of melanistic individuals was decreasing with the elevation in the Bernese Oberland (the opposite was true for patterned individuals). This suggests an advantage of melanism at mid-elevation, where forested (shady and cool) areas are the predominant habitat types, compared with higher elevation sites, which are situated above the treeline and receive more solar radiation. This phenomenon, largely attributable to the more efficient thermoregulatory capacity of melanistic (non-cryptic) individuals in shady areas, might also be due to higher predation rate on melanistic individuals inhabiting open areas (without tree cover protection), where raptors such as buzzards are common (see e.g. Monney, 1996; Monney *et al.*, 1996; Tanaka, 2005, 2007).

In a more general context, recent studies on colour polymorphic populations of the Japanese four-lined rat snake *Elaphe quadrivirgata* found that, in the laboratory, the melanistic morph reached its optimal body temperature faster than the striped one. In the wild, striped individuals showed greater thermoregulatory effort than melanistic snakes by using scarce thermally favourable microhabitats such as forest gaps, whereas melanistic individuals rarely used such exposed open habitats (Tanaka, 2005, 2007, 2009). Consequently, striped individuals may do as well as melanistic ones in the wild due to behavioural differences between morphs (e.g. Tanaka, 2005, 2007, 2009). Nevertheless, in the absence of sunny forest gaps, melanistic individuals may be more efficient. The same conclusion was reached by Forsman (1995a,b) who showed that melanistic *V. berus* heat faster and reach slightly higher body temperature. Additionally, in large-sized garter snakes *Thamnophis sirtalis*, the coloration affected equilibrium temperature, melanistic snakes maintaining higher temperatures than striped ones (Gibson & Falls, 1979; Bittner, King & Kerfin, 2002). Obviously, melanistic coloration in snakes confers thermoregulatory advantages in cold or forested areas.

In conclusion, the perpetuation of intra-population colour polymorphism in Swiss alpine asp viper populations is likely to be due (1) to different selective pressures acting on males and females, as has been shown in *V. berus* by Forsman (1995a,b), and (2) to the thermoregulatory advantage of being melanistic in cool and forested (shady) areas (lacking predators such as raptors), as has been hypothesized for the Japanese four-lined rat snake (Tanaka, 2005, 2007, 2009). Hence, the advantage of melanism might be context dependent.

Future studies should include a larger number of populations exhibiting colour polymorphism. Furthermore, they should also focus on the survival of individuals and the variation of the reproductive output of females, based on their coloration in association with different environmental conditions during pregnancy, as well as on the genetic components of colour polymorphism, in order to draw a more complete picture of the evolution and the persistence of such polymorphism in vipers.

Acknowledgements

We thank the Swiss National Science Foundation (SNSF) for funding; Michaël Corboz, Arnaud Gaigher, Sylvain Ursenbacher and Nicolas Rodrigues for their help in the field; and Charlene Ruppli, Matt Greenlees, Philippe Christe and Alexandre Roulin for helpful comments. The samples were collected with the authorizations of the 'Conservation de la Faune du Canton de Vaud' (No. 1586) and of the 'Office vétérinaire cantonal' (No. 2291).

References

Andrén, C. & Nilson, G. (1981). Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. *Biol. J. Linn. Soc.* **15**, 235–246.

Aubret, F., Bonnet, X., Shine, R. & Lourdais, O. (2002). Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). *Horm. Behav.* **42**, 135–147.

Ayers, D.Y. & Shine, R. (1997). Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Ecology* **11**, 342–347.

Bittner, T.D., King, R.B. & Kerfin, J.M. (2002). Effects of body size and melanism on the thermal biology of garter snakes (*Thamnophis sirtalis*). *Copeia* **2002**, 477–482.

Bonnet, X. (2011). The evolution of semelparity. In *Reproductive biology and phylogeny of snakes*: 645–672. Aldridge, R.D. & Sever, D.M. (Eds). Reproductive Biology and Phylogeny Series. Enfield: Science Publishers.

Bonnet, X. & Naulleau, G. (1996). Catchability in snakes: consequences for estimates of breeding frequency. *Can. J. Zool.* **74**, 233–239.

Caesar, S., Karlsson, M. & Forsman, A. (2010). Diversity and relatedness enhance survival in colour polymorphic grasshoppers. *PLoS ONE* **5**, e10880.

Capulla, M. & Luiselli, L. (1994). Reproductive strategies in alpine adders, *Vipera berus* – the black females bear more often. *Acta Oecol.* **15**, 207–214.

Christe, P., Keller, L. & Roulin, A. (2006). The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos* **114**, 381–394.

Clusella-Trullas, S., van Wyk, J.H. & Spotila, J.R. (2007). Thermal melanism in ectotherms. *J. Therm. Biol.* **32**, 235–245.

De Jong, P.W., Gussekloo, S.W.S. & Brakefield, P.M. (1996). Differences in thermal balance, body temperature and activity between non-melanic and melanic two-spot ladybird beetles (*Adalia bipunctata*) under controlled conditions. *J. Exp. Biol.* **199**, 2655–2666.

Dreiss, A., Henry, I., Ruppli, C., Almasi, B. & Roulin, A. (2010). Darker eumelanic barn owls better withstand food depletion through resistance to food deprivation and lower appetite. *Oecologia* **164**, 65–71.

Du, W.G., Ji, X. & Shine, R. (2005). Does body volume constrain reproductive output in lizards? *Biol. Lett.* **1**, 98–100.

Dubey, S., Brown, G.P., Madsen, T. & Shine, R. (2008). Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Mol. Ecol.* **17**, 3506–3514.

Dubey, S., Brown, G.P., Madsen, T. & Shine, R. (2009). Sexual selection favours large body size in males of a tropical snake (*Stegonotus cucullatus,* Colubridae). *Anim. Behav.* **77**, 177–182.

Dubey, S., Chevalley, M. & Shine, R. (2011). Sexual dimorphism and sexual selection in a montane scincid lizard (*Eulamprus leuraensis*). *Aust. Ecol.* **36**, 68–75.

Ducrest, A.L., Keller, L. & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.* **23**, 502–510.

Forsman, A. (1995*a*). Heating rates and body temperature variation in melanistic and zigzag *Vipera berus*: does colour make a difference? *Ann. Zool. Fennici* **32**, 365–374.

Forsman, A. (1995*b*). Opposing fitness consequences of colour pattern in male and female snakes. *J. Evol. Biol.* **8**, 53–70.

Forsman, A. & Åberg, V. (2008*a*). Associations of variable coloration with niche breadth and conservation status among Australian reptiles. *Ecology* **89**, 1201–1207.

Forsman, A. & Åberg, V. (2008*b*). Variable coloration is associated with more northerly geographic range limits and larger range sizes in North American lizards and snakes. *Evol. Ecol. Res.* **10**, 1025–1036.

Forsman, A., Ahnesjo, J., Caesar, S. & Karlsson, M. (2008). A model of ecological and evolutionary consequences of color polymorphism. *Ecology* **89**, 34–40.

Galeotti, P., Rubolini, D. & Dunn, P.O. (2003). Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* **16**, 635–646.

Gibson, A.R. & Falls, B. (1979). Thermal biology of the common garter snake *Thamnophis sirtalis* L. II. The effects of melanism. *Oecologia* **43**, 99–109.

Huey, R.B. & Kingsolver, J.G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* **4**, 131–135.

Luiselli, L. (1992). Reproductive success in melanistic adders: a new hypothesis and some considerations on Andren and Nilson's (1981) suggestions. *Oikos* **64**, 601–604.

Meyer, A., Zumbach, S. & Schmidt, B. (2009). *Les amphibiens et les reptiles de Suisse*. Bern: Haupt Verlag.

Monney, J.C. (1996). *Biologie comparée de* Vipera aspis *L. et de* Vipera berus *L. (Reptilia, Ophidia, Viperidae) dans une station des Préalpes bernoises*. PhD thesis, University of Neuchâtel, Switzerland. 179.

Monney, J.C., Luiselli, L. & Capula, M. (1996). Body size and melanism in *Vipera aspis* in the Swiss Prealps and central Italy and comparison with different Alpine populations of *Vipera berus*. *Rev. Suisse Zool.* **103**, 81–100.

Naulleau, G. & Bonnet, X. (1996). Body condition threshold for breeding in a viviparous snake. *Oecologia* **107**, 301–306.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* **56**, 1538–1542.

Perez-Tris, J., Diaz, J.A. & Telleria, J.L. (2004). Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? *Anim. Behav.* **67**, 511–521.

Pizzatto, L. & Dubey, S. (2012). Colour-polymorphic snake species are older. *Biol. J. Linn. Soc.* **107**, 207–218.

Protas, M.E. & Patel, N.H. (2008). Evolution of coloration patterns. *Annu. Rev. Cell. Dev. Biol.* **24**, 425–446.

Rosenblum, E.B., Rompler, H., Schoneberg, T. & Hoekstra, H.E. (2010). Molecular and functional basis of phenotypic convergence in white lizards at White Sands. *Proc. Natl. Acad. Sci. USA* **107**, 2113–2117.

Roulin, A. (2004). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biol. Rev.* **79**, 815–848.

Roulin, A. (2009). Covariation between eumelanic pigmentation and body mass only under specific conditions. *Naturwissenschaften* **96**, 375–382.

Roulin, A., Bize, P., Ravussin, P.A. & Broch, L. (2004). Genetic and environmental effects on the covariation between colour polymorphism and a life-history trait. *Evol. Ecol. Res* **6**, 1253–1260.

Roulin, A., Burri, R. & Antoniazza, S. (2011). Owl melanin-based plumage redness is more frequent near than away from the equator: implications on the effect of climate change on biodiversity. *Biol. J. Linn. Soc.* **102**, 573–582.

Saint Girons, H. & Duguy, R. (1992). Evolution de la masse corporelle et de la masse relative des corps gras, des ovaires et des oeufs au cours des cycles reproducteurs chez *Vipera aspis*. *Amphib-reptil.* **13**, 351–364.

San-José, L.M., Gonzales-Jimena, V. & Fitze, P. (2008). Frequency and phenotypic differences of melanistic and normally colored common lizards, *Lacerta* (*Zootoca*) *vivipara* of the Southern Pyrenees (Spain). *Herpetol. Rev.* **39**, 422–425.

Shine, R., Ambariyanto, Harlow, P. & Mumpuni (1998). Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*. *Oecologia* **116**, 113–119.

Shine, R. & Madsen, T. (1997). Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. *Ecology* **78**, 1078–1086.

Stuart-Smith, J.F., Stuart-Smith, R.D., Swain, R. & Wapstra, E. (2008). Size dimorphism in *Rankinia* [*Tympanocryptis*] *diemensis* (Family Agamidae): sex-specific patterns and geographic variation. *Biol. J. Linn. Soc.* **94**, 699–709.

Tanaka, K. (2005). Thermal aspects of melanistic and striped morphs of the snake *Elaphe quadrivirgata*. *Zool. Sci.* **22**, 1173–1179.

Tanaka, K. (2007). Thermal biology of a colour-dimorphic snake, *Elaphe quadrivirgata*, in a montane forest: do melanistic snakes enjoy thermal advantages? *Biol. J. Linn. Soc.* **92**, 309–322.

Tanaka, K. (2009). Some like it cool? Intermorph comparison of preferred body temperature in a colour-dimorphic snake. *Anim. Biol. Leiden Neth.* **59**, 31–39.