

A home for three: analysing ecological correlates of body traits in a triple contact zone of alpine vipers

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Abstract. The medium-sized vipers of the genus *Vipera* are mainly parapatric in Europe and only a few contact zones (syntopies) are known between two species. The partial syntopy of three viper species (*V. ammodytes*, *V. aspis*, and *V. berus*) is exceptional and has become known only from two neighbouring valleys in the southern Julian Pre-Alps along the Italian-Slovenian border (Valle Mea and Nadiza Valley). This unique situation puts forward questions concerning their co-existence, particularly when considering that natural hybrids are known among all three species. Our principal goals for this article were therefore to evaluate variation and integrity of key dorsal colour pattern and body size among *V. berus*, *V. ammodytes*, and *V. aspis* from Mount Stol, Nadiza Valley in Slovenia. We discuss these variations in the context of potential hybridization, interspecific competition, and local to regional synecological properties including diet, habitat, and climate. Despite the fact that a pre-study specimen showed intermediate colour pattern, suggesting a hybrid between *V. ammodytes* and *V. aspis*, no further intermediate specimens ($n > 100$) were detected based on external features. Comparison of body length and mass shows equal sizes between *V. ammodytes* and *V. aspis*, whereas *V. berus* is approximately 30% smaller. Furthermore, *V. berus* on Mount Stol is also much smaller and lacks melanism, unlike *V. berus* from a close population in Italy (< 15 km), where they are larger and melanism is relatively frequent. These local character expressions presumably are the result of environmental constraints at high elevations (> 1200 m asl.), such as a harsh climate of open, non-forested habitat and possibly a regionally different predation pressure and diet composition. At mid-elevation < 1200 m asl., syntopic *V. ammodytes* and *V. aspis* may compete for food, yet, the previously evaluated microhabitat differences appear sufficient to maintain species integrity for these two viper populations.

Keywords: syntopy, *Vipera ammodytes*, *V. aspis*, *V. berus*, snakes, Slovenia, body size, colour pattern.

Introduction

European vipers of the genus *Vipera* represent a monophyletic group of snakes (Garrigues et al. 2005) that are generally parapatric and separated by climatically distinct landscapes, but also locally, e.g., occupying different elevations or slopes in a valley (Saint Girons 1980). The species of this genus share relatively fixed ecological niches, including the preference for open warm and often rocky habitat and an adult diet predominantly based on small mammals, with young vipers frequently consuming lizards (Luiselli & Anibaldi 1991, Monney 1993, Naulleau 1997, Joger & Stümpel 2005). In the contact zones of these viper species, the overlap of their ecological niches increases the likelihood of interspecific competition,

and even promotes occasional hybridization among all three species (see refs. in Mebert et al. 2015). However, two sympatric (same area) viper species are separated mainly by local allotopy, using different macrohabitats (e.g. distinct slope, elevation, vegetation type, such as light forest or grassland: Monney et al. 1995, Luiselli 2006, Martinez-Freiria et al. 2009, 2010, 2008, Scali et al. 2011) or microhabitats (distinct habitat structures within a macrohabitat: Mebert et al. 2015). When such macrohabitats are adjacent and the transition is abrupt, individuals of both species come barely into contact (physical, visual, olfactory) with each other. However, when the transition between different macrohabitats is rather gradual, two viper species may find their own niches and are able to co-exist. For example, *V. aspis* and *V. berus* co-

occur in a small 70 ha area in the Swiss Alps (Monney et al. 1995), and similar examples are known from southwestern Europe (Saint-Girons 1980, Naulleau 1986, Brito & Crespo 2002). The same two species may share some microhabitats (syntopy), but use different mating periods and thermoregulatory strategies (Saint-Girons 1975, Monney 1995, Guillon et al. 2014). In this context, sympatric viperids are an exception among snakes in that they primarily partition available habitats and not only food (Luiselli 2006). Yet, all three "alpine" *Vipera* species (*ammodytes*, *aspis*, *berus*) show slightly different ecological preferences/tolerances, as *V. berus* occurs in areas that are comparatively cooler and more humid (mostly high-altitude or latitude regions), whereas *V. aspis* is found at less humid, warmer and lower altitudes/latitudes, whereas *V. ammodytes* occupies, even drier-warmer habitats (Saint-Girons 1975, Joger & Stümpel 2005, Scali et al. 2011, Guillon et al. 2014, Mebert et al. 2015). Indeed, contact zone studies between *V. aspis* and *V. berus* in lowland France showed interspecific differences related to climate adaptations, as *V. berus* digests prey at lower temperatures, faster at equal temperatures, and is capable of maintaining higher temperatures for longer periods in constraining weather than *V. aspis*, and even more so than *V. ammodytes* (Naulleau 1983, Lourdaïs et al. 2013).

Overall, the co-occurrence of two *Vipera* species is relatively uncommon in Europe, whereas the co-existence of more than two viper species is virtually unknown/rare. Jelic et al. (2013) indicated such a triple species contact between *V. berus* and *V. ammodytes* with the much smaller and ecologically divergent *V. ursinii* (meadow inhabitant, predominantly insectivorous) in Bosnia and Herzegovina. However, true syntopy has not been confirmed in this case, yet. For medium-sized vipers, a three-species contact zone was also expected in the Iberian Peninsula among *V. seoanei*, *V. aspis* and *V. latastei* (Duguy et al. 1979), but a closer look did not reveal a true syntopy between all three species (Martinez-Freiria et al. 2006, 2010). Elsewhere in Europe, the existence of three-species contact zones of medium-sized, congeneric vipers (hence, excluding *V. ursinii*) is virtually non-existing or appears to be extremely rare. Dalla Torre (1912) indicated localities of sympatry for *V. berus*, *V. aspis* and *V. ammodytes* south of Bolzano in Trentino-Alto Adige, Italy, but without referencing exact and reliable data sources. Such collection localities likely represent lumping stations for

snakes sampled by locals for a head price. Finally, no such triple contact zone has been confirmed to this day, even though the region of Bolzano is herpetofaunistically well investigated. It remains an open question, whether land use change (agriculture, plantation, urbanization, irrigation) over the last century since Dalla Torre's account (1912) may have eradicated potential contact zones or promoted even new ones (e.g., Bagnoli et al. 2014). Until recently, the only reliable but scarce report for the partial co-existence of *V. ammodytes*, *aspis*, and *berus* comes from Valle Mea (Alta Val Torre) in the Julian Pre-Alps near the Italian-Slovenian border (e.g., Lapini et al. 1999). The findings of a few additional *V. aspis* on Mount Stol in Nadiza Valley, Slovenia, together with *V. ammodytes* and *V. berus*, confirmed this as the second valley where three viper species co-exist and partially share a habitat (Tomé 2002, Mebert et al. 2015).

The unusual triple contact zone of "similar" congeneric viper species provides the opportunity to raise the interesting questions, whether these closely related, potentially competing species will: 1) partition their habitat, 2) hybridize in natural condition, 3) show clearly distinguishable characters of colour pattern, and 4) exhibit similar body size, within and outside the syntopy area. While 1) and 2) have partially been answered by Mebert et al. (2015), our principal goals for this publication were to: (a) evaluate key dorsal colour pattern variation and integrity among syntopic *V. berus*, *V. ammodytes*, and *V. aspis* and define interspecific characters and/or intermediate forms (reflecting hybridization); (b) analyse body size differences among them; and c) discuss both body traits in regard to local and regional variation in diet, habitat, and climate.

Material and methods

Study area and field sampling

The core of the study area is situated on the slopes of Mount Stol, Nadiza Valley in Slovenia, which together with Valle Mea in adjacent Italy forms the first east-west oriented mountain valleys of the Julian Pre-Alps, stretching across ca. 30 km (Fig. 1). The altitudinal difference in Nadiza Valley, a lateral valley of the large Soča Valley, ranges from ca. 200 m a.s.l. near Kobarid to 1673 m a.s.l. on Mount Stol (46°16'42.54"N, 13°27'14.96"E). The southern slopes of the Julian Pre-Alps are covered mostly by dense forest at < 1000 m asl., and are replaced by montane grassland, interspersed with various types of rock/stone formations. The south-exposed slope below the peak Mount Stol is dissected by a rock-supported



Figure 1. North-eastern Italy and western Slovenia with the black arrow pointing to our study area in Nadiza Valley (modified from Free World Maps).

gravel road and various succession stages from scrub (bush land) to young deciduous forest, whereas its forest limit at 800 m a.s.l. is even lower than on average. For *V. berus*, eight specimens were included from nearby Mount Krn (46°15'10.24"N, 13°39'58.14"E), 14 km east of Mt. Stol. This proximate site exhibits a similar climate (latitude and elevation), equivalent habitat (south-exposed slope, mixture of open grassland rocky patches, few bushes and trees), and phenotype of *V. berus* (small, non-melanistic specimens) as on Mt. Stol (Mebert et al. 2015).

Usually, a group of 1–4 persons searched the field site for vipers during suitable weather on average 10 days per year in the period 2012–2015. Initial field searches included various sites along the entire 12 km stretch of the valley bottom, but due to low sampling success and lack of suitable habitat, field work was subsequently concentrated on the higher slopes (> 800 m a.s.l.) of Mount Stol, including open areas of the northern versant, which is covered mostly by dense forest up to or near the mountain ridge.

Vipers were searched by walking (visual encounter survey) of all suitable structures in the study area. Preferred sites exhibit a high degree of microstructures, potentially serving as shelter and hunting ground for vipers, including rocky outcrops, rock piles and slides, herbaceous plant cover, and low lying bushy vegetation with at least one side exposed to solar radiation. Exact locality data for each captured viper was recorded with a GPS device (UTM coordinates in European Datum 1950) to investigate interspecific differences in the use of habitat components and elevation (Mebert et al. 2015).

Morphological data

Captured individuals were sexed and their snout-vent length (SVL), tail length and body mass (BM) were measured. BCI (Body Condition Index) was evaluated by the residuals of the general regression between SVL and weight (BM) according to Castella et al. (2013), and as the ratio SVL/BM (Luiselli, 1993). Each viper was classified as *V. berus*, *V. aspis*, *V. ammodytes* or as intermediate according to their external phenotypes. Criteria for the species classification of specimens require a combination of mor-

phological traits (Tab. 1), as each trait by itself is not exclusive, except for the snout horn in *V. ammodytes*.

The combination of above criteria (Table 1) are sufficient to visually distinguish the three viper species. Each captured viper was marked by ventral scale clipping and/or photographed (dorsal and lateral of head and trunk, as well as venter) for future individual identification. For population genetics (presented in Mebert et al. 2015), DNA samples were taken with mouth-swabs and clipping of 3–4 ventral scales (only dead edges) without harming the animal.

Morphological variables (SVL and BM) were inspected for normality and homoscedasticity via Levene's test of homogeneity of variances. Intraspecific differences in morphological traits (SVL, BM) were tested by Student t-test. Interspecific differences in SVL and BM among the three viper species were examined by Welch's ANOVA F test for unequal variances, followed by Tukey's HSD posthoc test for assessing pairwise statistical differences. Juvenile vipers (SVL mm: *V. berus* < 30 cm, *V. ammodytes* and *V. aspis* < 35 cm) were excluded from this analysis. The two cut-off ranges reflect the situation at the study area, in which small vipers (SVL < 36 cm for at least mature males, but see Guiller 2012 and refs. therein for an elaboration) were more common in *V. berus* (ca. 25%) than equally small *V. ammodytes* (9%) or *V. aspis* (0%, no juveniles found). This is also reflected in an approximately 10 cm shorter adult size in *V. berus* (mean=45.3 cm) than in *V. ammodytes* (mean=55.9 cm) or *V. aspis* (mean=55.7 cm). All statistical tests were two tailed, with $\alpha = 5\%$, and analyses performed using the PASW Statistics software for Windows, Version 18.0 (SPSS Inc., Chicago, USA).

Results

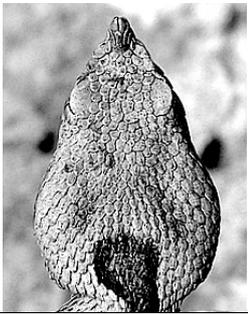
Distribution

A total of 104 vipers were sampled in the Mount Stol region up to 2015 at elevations > 800 m a.s.l., including eight *V. berus* from nearby Mount Krn: 58 *Vipera ammodytes* (56%), 21 *V. aspis* (20%), and 25 *V. berus* (24%), adding in particular more *V. aspis* than Mebert et al. (2015). We did not find vipers along the bottom of Nadiza Valley, not even on rock and wall structures with plenty of crevices occupied by other reptiles. Four viper records (confirmed from photographs or by reptilian experts) from below 600 m a.s.l. confirm a very low abundance of vipers on the valley bottom: one *V. ammodytes* from near Borjana in 2008, three *V. aspis* from Breginj in 2011 (Srečko Gašperut, pers. comm.), from Logje in 2001 (Torkar 2003), and from Podbela in 2014 (Daniel Jablonski, pers. comm.).

Colour pattern and body size

During the course of this study, all vipers were

Table 1. Morphological features used to distinguish among three sympatric vipers, *Vipera ammodytes*, *V. aspis*, and *V. berus* in western Slovenia. Apical scale classification according to Arnold & Ovenden (2002).

	Snout form and number of apical scales	Central head scales (sincipital = parietal and frontal)	Dorsal pattern
<i>Vipera ammodytes</i>	upturned snout like a horn, formed by 9–20 apical scales	only small scales, rarely 1–2 large scales 	broad to thin dorsal blotches, rounded-rhomboidal, often connected to form a wavy-rounded or zig-zag stripe with pointed tips, occasionally interrupted
<i>Vipera aspis</i>	snout slightly turned upwards to form a ridge with two to three apical scales	only small scales, rarely 1–2 large scales 	alternating widely spaced small bars (rarely triangle-shaped), extending laterally with an even width and end approx. right-angled, some connected by a thin vertebral line
<i>Vipera berus</i>	small, slightly downwards turned snout and two apical scales	3 large scales 	largely continuous longitudinal zig-zag band, or separated dorsal blotches that are large, numerous, and laterally taper off (rarely with an even width)

easily assigned to their respective species with our colour pattern key. A specimen of each species from that contact zone is depicted in Figure 2. Melanism or abundism (unusually dark specimens) remained a rare occurrence and was found once in *V. berus*, hence < 3% (Fig. 3). Only one viper with an intermediate phenotype (*Vipera aspis* × *V. ammodytes*) was collected but not preserved prior this study, whereas one juvenile *V. berus* showed a small affinity to *V. aspis* based on one microsatellite marker, but was morphologically indistinguishable from *V. berus* (see Mebert et al. 2015), implying that hybridization is a very rare event. On the other hand, the virtual lack of hy-



Figure 2. Sympatric vipers from Nadiza Valley, western Slovenia: upper left *Vipera ammodytes*; upper right *V. aspis*; lower right *V. berus*.



Figure 3. An abundistic (very dark) *Vipera berus* from 1136 m asl., Breginj, Nadiza Valley, Slovenia. It represents the only near-melanistic *V. berus* found in Nadiza Valley thus far.

bridization on Mount Stol permits a direct morphological comparison between all three viper species in sympatry and partial syntopy.

Morphometric data are summarized in Table 2. Gender were initially treated as separate groups to test for sexual dimorphism. Maximum total length for *V. ammodytes* were (f = 715 mm, m = 795 mm), for *V. aspis* (f = 739 mm, m = 680 mm), and for *V. berus* (f = 605 mm, m = 650 mm). There was no significant sexual dimorphism for any of the three viper species in both SVL (*ammodytes*: $t = -1.058$, $P = 0.296$; *aspis*: $t = 0.357$, $P = 0.716$; *berus*: $t = 1.383$, $P = 0.179$) and BM (*ammodytes*: $t = 0.796$, $P =$

0.430; *aspis*: $t = 1.319$, $P = 0.202$; *berus*: $t = 1.378$, $P = 0.182$). Hence, sexes were lumped for these analyses.

One-way ANOVA indicated significant differences between the species regarding SVL ($F_{2,92} = 26.1$, $P < 0.0001$) and BM ($F_{2,88} = 26.0$, $P < 0.0001$). Levene's test showed homogenous variances among SVL-means/medians ($p = 0.1209/0.1418$), but not so for BM-means/medians ($p = 0.003877/0.003845$). Hence, BM was subsequently tested with a Welch F test, yielding a significant difference ($F=47.84$, $df = 47.58$, $p < 0.0001$). Tukey's pairwise comparisons showed that *V. ammodytes* and *V. aspis* exhibited the same body size (SVL: $P = 0.9925$; BM: $P = 0.1464$). In contrast, Figure 4 reveals that *V. berus* was substantially smaller by approximately 30% compared to the other species in both body variables: in *berus* vs. *ammodytes* ($P < 0.001$ for either SVL or BM), and in *berus* vs. *aspis* ($P < 0.001$ for either SVL or BM). ANCOVA indicates that all three species yielded similar growth trajectories ($F_{2,87} = 2081$, $P = 0.13111$; and Fig. 5) for individuals SVL > 30 cm. However, comparing the residuals of the general regressions between SVL and BM as a BCI, there were significant differences among species (one-way ANOVA, $F_{2,91}=29.39$, $P < 0.001$), with Tukey's post-hoc test indicating that the BCI of *V. berus* was significantly lower compared to the other two species ($P < 0.0001$),

Table 2. Summary of body length (SVL: mm), body mass (BM: g) and body index (BCI) of three sympatric viper species, divided by sex. For statistical details, see the text.

	<i>V. berus</i>		<i>V. aspis</i>		<i>V. ammodytes</i>	
	females	males	females	males	females	males
Snout-Vent-Length (mm)						
N	11	14	15	6	22	27
Min	360	325	482	455	370	382
Max	535	575	660	580	650	695
Mean	461.5	427.9	554.0	546.0	542.0	564.1
Stand. dev	53.9	63.8	52.0	44.9	71.3	76.6
Median	472.5	437.5	545.0	560.0	550.0	560.0
Body Mass (g)						
N	10	14	15	6	21	24
Min	33	25	84	62	45	35
Max	101	116	259	168	217	219
Mean	71.9	58.7	161.0	133.5	141.1	129.1
Stand. dev	18.8	26.7	45.7	38.3	54.8	46.8
Median	70.0	54.5	162.0	142.5	135.0	126.5
BCI (SVL/BM)						
N	11	14	15	6	21	24
Min	5.0	5.0	2.5	3.5	2.6	2.9
Max	10.9	13.6	5.9	7.3	8.2	10.9
Mean	6.7	15.4	7.5	8.1	4.4	9.1
Stand. dev	1.6	2.9	1.0	1.5	1.6	1.8
Median	6.6	7.6	3.4	3.9	4.0	4.6

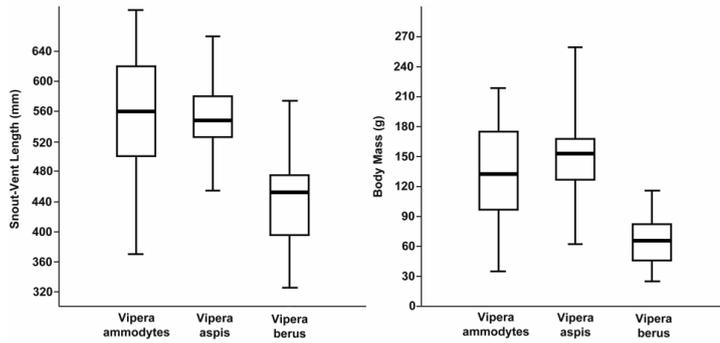


Figure 4. Snout-vent length (left) and body mass (right) among three sympatric vipers: *Vipera ammodytes*, *V. aspis*, and *V. berus* in western Slovenia. Sexes are combined, as sexual dimorphism was negligible (see statistical tests in the text). Only *V. berus* shows significant differences to each of the other two species (see text for values).

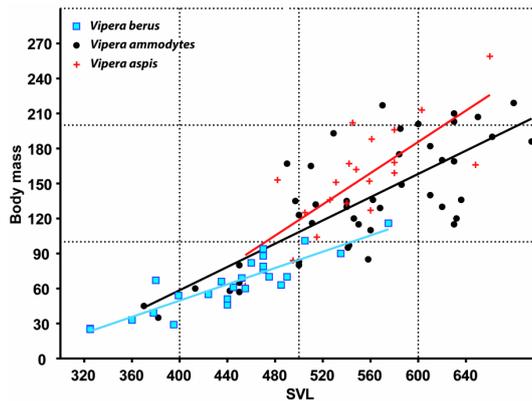


Figure 5. Relation between the body size (SVL: snout-vent length) and body mass among three sympatric vipers of the genus *Vipera* (*V. ammodytes*, *V. aspis*, *V. berus*). Sexes are combined, as sexual dimorphism was negligible for SVL and BM separately (see statistical tests). Blue squares: *Vipera berus*; black dots: *V. ammodytes*; red crosses: *V. aspis*.

whereas no differences emerged between the other two species ($P = 0.159$).

Discussion

Scarce information over the last 30 years indicated the exceptional presence of a contact zone of three congeneric, saxicolous (in montane areas), small mammal-feeding vipers (*Vipera berus*, *V. aspis*, *V. ammodytes*) in the two southernmost valleys of the Julian Pre-Alps (with Valle Mea, Italy, and Nadiza Valley, Slovenia) morphological evidence for occasional hybridization from both valleys (e.g., Lapini 1988, Schweiger 2009, T. Fiorenza, Udine, pers. comm. 2015). We previously investigated the gene flow, habitat segregation and/or separation between them on Mount Stol in Nadiza Valley (Mebert et al. 2015). Our principal goals now were to look first for morphological integrity of defined key dorsal colour pattern that distinguish among the syntopic viper species, as morphological characters and molecular markers do not need to be congruent (e.g., Mebert 2008). Second, we com-

pared body size differences among the three species and discuss the results in relation with potential hybridization, interspecific competition, and local to regional environmental properties of diet, habitat, and climate.

Body size, climate and diet

The similarity in body sizes between *V. ammodytes* and *V. aspis* does not offer any hint on different ecological niches. However, a habitat analysis did reveal a partial habitat segregation between these two species, reducing potential interspecific competition (Mebert et al. 2015). In addition, the large *V. aspis* in our sample, with six individuals (~30%) reaching a TotL (total length) between 65–74 cm, for a species that only occasionally reaches maximum TotL of 70 cm (e.g., Joger & Stümpel 2005, Meyer et al. 2009), does not imply a high negative pressure by sympatric *V. ammodytes*. Instead, *V. berus* were much smaller and lower in BCI than the other two species, thus paralleling a contact zone between *V. aspis* and *V. berus* in the Swiss Alps, where *V. berus* was also significantly smaller than *V. aspis* (Monney et al. 1996). In both studies,

the significantly smaller *V. berus* may indicate a reduced growth as a result of the particularly harsh (e.g., cooler, shorter season) climate the Julian Pre-Alps experience due to topographic, historic, and climatic reasons, resulting in heavier rainfalls and colder winds than in the more inner alpine areas (Morandini 1979). Furthermore, our personal observation regarding the rarity of otherwise common species, the Wall Lizard (*Podarcis muralis*) and Green Lizard (*Lacerta viridis/bilineata*) on the open grassy and rocky southern slopes of Mount Stol, seem to confirm a reduced survival rate due to the constraining local climate.

Interestingly, *Vipera berus* individuals from Sella Nevea, Italy, just 15 km north of our study site, were substantially larger and females were frequently melanistic between 1987 and 1992 (Capula & Luiselli 1994). Adult females from Sella Nevea reached on average a total length between 60–65 cm (occasionally specimens exceeding 70 cm, $n=105$, Luiselli 1992), whereas females from Mount Stol and the next eastern population at Mount Krn (our data) attain a mean total body length of 52 cm ($n=11$, Mount Krn has an equivalent environment and climate with Mt. Stol). Moreover, about 35% of female and 13% of male *V. berus* individuals from Sella Nevea were melanistic, whereas fully melanistic specimens have never been observed from the Slovenian sites in Valle Nadiza (Mount Stol) or on Mount Krn, albeit one abundant (significantly darkened) female was recently sampled near Breginj, Nadiza Valley (Fig. 3). The habitat is also quite different between the nearby Italian (Luiselli 1992) and our Slovenian sites. The slopes near Sella Nevea are covered with extensive pine forests, interspersed with open grassy-rocky patches. In contrast, the two Slovenian sites (high elevation on Mts. Stol and Krn), where melanism is lacking, consist of predominantly open grassland for decades (unpubl. photographs from 1950s–1960s) and likely even for centuries based on historic accounts (Stergulc 1987), with an extensive forest only along the northern slope of Mount Stol. Similarly, melanistic *V. berus* are commonly observed only in the forested environment of Valle Mea and Valle Ucceca, the next western valleys at 7–15 km distance from our population (Lapini 1988, T. Fiorenza and A. del'Asta, pers. comm.). Furthermore, comparisons among several Swiss and Italian populations of *V. aspis* and *V. berus* also suggest that melanism is particularly advantageous in viper habitat within the forested belt (Monney et al. 1995 and 1996,

Castella et al. 2013, Muri et al. 2015), and especially for females in the nearby Italian population (Luiselli 1992), albeit in other European populations males can be selected to become the more frequent melanistic sex (Strugariu and Zamfirescu 2011, and refs. therein). However, the lack or rarity of melanism even in one of our subpopulation of *V. berus*, that is surrounded by forests and on the northern slope of Mount Stol, may rather indicate recent gene flow from the nearby (~500 m) population on the open mountain ridge. Non-adaptive mechanisms, such as random genetic drift and founder effect, to maintain a melanism-free *V. berus* population on Mount Stol are unlikely scenarios, because the open landscape along the > 20 km mountain ridge is historic (centuries-old pastures, Stergulc 1987). The open terrain enabled a long-lasting and frequent presence of *V. berus* along the mountain ridge (no founder effect). Any random loss (drift) of a putative advantageous melanism would have been countered by gene flow from nearby populations with melanistic individuals. This leaves local selection pressure, such as highly efficient avian predation on vipers (e.g., Maumary 2013), as the principal force for or against the maintenance of melanism in our study population.

While melanism in *Vipera berus* from forested habitats renders an advantage for a more efficient thermoregulation and growth, which is crucial in a cool alpine habitat with constraining weather conditions, where clouds often reduce solar radiation (Luiselli et al. 1994, Monney et al. 1995). However, melanism may be counterbalanced in an open landscapes as on Mt. Stol by being less cryptic to predators (e.g. Castella et al. 2013, Broenimann et al. 2014), in particular avian predation likely is high with an abundance of birds of prey at our study site (pers. obs.). Distinct body sizes, on the other hand, can also reflect temporal fluctuations in the prey type, size or abundance (Arnold 1993, Luiselli et al. 2015, and refs. therein). No diet analysis has been conducted, but the small size of *V. berus* from Mts. Stol and Krn may indicate differences in food availability or prey types compared to those at Sella Nevea. Indeed, juvenile *V. berus* from Sella Nevea include largely salamanders in their diet (*Salamandra atra*) which are easy to catch and consume (Luiselli & Anibaldi 1991, Luiselli et al. 1995, our unpubl. data), whereas juveniles and possibly even adults on higher elevations and the northern slope of Mount Stol may include the Common Lizard (*Zootoca vi-*

vipera) in their diet, which occupies the same habitat as *V. berus* at least on the northern slope (E. Ostanek, unpubl. data). Lizards are more difficult to catch than salamanders and may limit the energy gain per gram mass and thus the growth, resp. size that vipers can attain. In contrast, *V. ammodytes* and *V. aspis* are more common at lower sites (~ 1000 m a.s.l.) along the southern slopes of Mount Stol, which is rich on hazelnut bushes (*Corylus avellana*) that is attracting micro-mammals and provides a particular energy-rich diet for these vipers to grow large. A positive correlation between a micro-mammal (and bird) diet and body size, including mammal versus lizard diet, has often been observed in snakes (e.g., Aubret 2012, Luiselli et al. 2015 and refs. therein).

Trophic competition has been suggested by Monney et al. (1995) to explain the small size of *V. berus* (similar in size to those from Mount Stol) in a contact zone with *V. aspis* in the Swiss Alps. In comparison, no such trend was found in a contact zone of these two viper species in the plains near the sea level of the Loire Atlantique region, western France (Saint Girons 1975), where both species attain similar body sizes (Guiller 2012). Similarly, in a contact zone of *V. aspis* and *V. latastei* on the Iberian Peninsula (latter species being an ecological equivalent to *V. ammodytes* at our study site), Martinez-Freiria et al. (2010) suggested that a high prey abundance, a slightly higher inclusion of reptilian diet in *V. latastei*, and some trend in temporal feeding separation throughout the annual cycle reduces competitive interactions among the sympatric vipers. Thus, it is more than likely that our systems of co-existing viper species may be prone to variations throughout time in terms of their body sizes due to temporal variations in prey type characteristics as well as because of intrinsically fluctuating intensity of interspecific competition, especially in years with low resource availability. In our study area, however, we did not analyse the diet habits of the three species, and thus we could not contribute to this issue at the present stage.

Competitive interaction between *Vipera aspis* and *V. berus* for available resources is not relevant in our study area, as the overlap of these two species on Mount Stol is small (few ha, Mebert et al. 2015). In contrast, a much larger overlap, and thus potential competition, exists between *V. berus* and *V. ammodytes* on the higher slopes and ridges of Mount Stol, for which the small size of *V. berus* may be indicative. However, *V. berus* is equally small on Mt. Krn, the next proximate population

east, where no 'competing' *V. ammodytes* was detected. This points to non-competitive mechanisms, such as climate and prey availability/preferences, regulating body sizes among the vipers of Mount Stol. Reflecting microhabitat differences among the three viper species on Mount Stol (Mebert et al. 2015) and findings for Iberian vipers by Martinez-Freiria et al. (2010), we anticipate that *V. aspis* (bush-grassland inhabitant) has a slightly higher proportion of Rodentia in its diet compared to *V. ammodytes* (rock inhabitant), although both species still consume mostly mammals. Certainly, we would suggest a diet analysis to be a next step in any future study on the three sympatric viper species. Finally, the comparison among the different viper studies and in particular the populations of *V. berus* from the Julian Alps and Pre-Alps suggest strong local selection pressures (e.g., diet, climate) forming external character expression, such as melanism and body size, that can change from region to region, and even from valley to valley, and possibly also through time.

Habitat and movement

The little morphological or genetic evidence of a reproductive exchange among the three medium-sized vipers from our research site does not necessarily indicate a lack of potential contact between the three viper species (Mebert et al. 2015). In contrast, all three viper species co-exist in an area of ca. 1000 × 500 m (horizontal length × slope length) from 1000–1350 m asl, and the overlap when considering only two species is even much larger (we have not detected a "larger" single species areas yet). In the triple contact zone, all three species inhabit the same type of rocky structures in grasslands along the south-exposed slope of Mount Stol, including rocky support structures and downward slope scree of the gravel road, all together providing suitable habitat for local vipers and likely promoting occasional direct contact among all three species. Below 1000 m asl, *V. ammodytes* and *V. aspis* share also extensive scrub and lightly wooded areas (Mebert et al. 2015). Even though we have not found two viper species basking side by side, seasonal migration to even daily activities should bring individuals of any two viper species into contact. This is feasible, considering our largest recorded seasonal movement of 493 m by a recaptured female *V. ammodytes*, and movements of *V. berus* from comparable alpine habitats, with monthly movements ranging from

max. 505 m (Neumeyer 1987) to 1200 m (Moser 1988). Distances moved in the latter study increased to an annual 1876 m (male) and 3331 m (female), suggesting that our triple contact zone of a ca. < 1 km² is sufficiently small for frequent direct contacts among all three species. Despite this potential contact, gene flow or at least F1-hybridization between the three viper species was virtually non-existent in our study area, with only one apparent F1-hybrid based on an intermediate phenotype (Mebert et al. 2015).

Nonetheless, there was one *Vipera berus* with a 10% genetic allocation to *V. aspis*, which may be caused by a single adjunction in a frequent *V. berus*-microsatellite allele (Mebert et al. 2015). Alternatively, this *V. berus* individual may represent a backcross from a past hybridization between parental *V. berus* and *V. aspis*, although such hybrids have only rarely been documented (but see Saint Girons 1975 and Geniez 2015 for accounts on such natural hybridization; see also Guiller et al. 2017). The *V. berus* juvenile was found on the northern slope of Mount Stol at a surface distance of only 1 km from the nearest locality for a *V. aspis*, a species known here only from the southern slope. Hence, *V. berus* and *V. aspis* are separated by the Stol mountain ridge of ~1400 m asl and higher, where *V. berus* and *V. ammodytes* are present today, but no *V. aspis* has been detected. The cool and windy climate on the mountain ridge possibly precludes the migration of *V. aspis* from the southern to the northern slope of Mount Stol today, disabling a potential contact between *V. berus* and *V. aspis* on the northern slope. However, it is also plausible that an initial hybridization event may have taken place on the southern slope, followed by an extended migration of a juvenile hybrid/backcross from the southern slopes across the ridge onto the northern side during warmer days in the summer. The only viper species other than *V. berus* found on the northern slopes were two juvenile *V. ammodytes*, rendering some credit that dispersal across the ridge is executed mostly by juveniles. Juvenile dispersal of 90 m per day have been reported by Saint Girons (1981). Accounts on juvenile migration are still scarce, but are increasing (e.g., Secor 1994, Bonnet et al. 1999, Dubey et al. 2008 and 2011, Alfermann & Böhme 2009, Vacher 2010, Howze et al. 2012, Rugiero et al. 2012, Zappalorti 2012, Alfermann et al. 2013, Wang et al. 2015), whereby short-distance dispersal prevents inbreeding or kin competition, and long-distance dispersal facilitates colonization of

new territories, and serves the species' expansion (Clobert et al. 2001).

In summary, the results from this study on a triple contact zone of congeneric vipers reported herein and previously by Mebert et al. 2015 demonstrate that similar species can co-exist as a result of inherent differences in habitat preferences/tolerances and, correspondingly, in a contact zone rich on required micro-niches. Morphological and genetic evidences show that hybridization is rare, likely due to sufficient availability of mating partners for each species. Environmental constraints and some degree of interspecific competition, for example for the same diet, in the contact zone is likely responsible for differences in body size and local density among all three viper species. A future analysis on the trophic interactions and differences among the viper species would be required to better understand that aspect. However, strong regional geographic variation in colour pattern and size within *V. berus* appears to be essentially the result of environmental pressures. These results infer that extra- or interpolations of results from a single population study should be interpreted cautiously and primarily viewed in a local context, as diet, climate, predation, and competitive species can have profound effects in forming external character expression and population traits that change from region to region, and even from valley to valley.

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