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On elevation-related shifts of spring activity in male vipers of the genera *Montivipera* and *Macrovipera* in Turkey and Cyprus
(Squamata: Serpentes: Viperidae)

Zur höhenabhängigen Frühjahrsaktivität männlicher Vipern der Gattungen *Montivipera* und *Macrovipera* in der Türkei und Zypern
(Squamata: Serpentes: Viperidae)

NIKOLAUS STÜMPEL & OLEKSANDR ZINENKO & KONRAD MEBERT

KURZFASSUNG

Der zeitliche Ablauf von Lebenszyklen wechselwarmer Wirbeltiere wird in hohem Maße vom Temperaturregime des Lebensraumes bestimmt. In Gebirgen sinkt die Umgebungstemperatur mit zunehmender Höhenlage. Deshalb liegt es nahe, anzunehmen, daß die Höhenlage den Zeitpunkt des Beginns der Frühjahresaktivität von Vipern beeinflußt. Um diesen Zusammenhang zu untersuchen, haben die Autoren im Zeitraum von 2004 bis 2015 in der Türkei und auf Zypern den Beginn der Frühjahrshäutung bei männlichen Vipern der Gattungen *Montivipera* und *Macrovipera* zwischen Meereshöhe und 2300 m ü. M. untersucht.

Sexuell aktive Männchen durchlaufen nach der Winterruhe und vor der Paarung eine obligatorische Frühjahrshäutung. Im Häutungsprozeß werden äußerlich klar differenzierbare Stadien durchschritten, von denen die Eintrübung des Auges besonders auffällig und kurzzeitig ist. Dieses Stadium ist daher prädestiniert, um den nachwinterlichen Aktivitätsbeginn zwischen Populationen unterschiedlicher Höhenlagen miteinander zu vergleichen. Während der Freilandstudien wurden insgesamt 15 adulte männliche Vipern mit milchig-opaken Augen angetroffen, welche ihren Häutungsstatus anzeigten.

Die vorliegenden Ergebnisse zeigen einen signifikanten positiven Zusammenhang zwischen dem Beginn der Frühjahreshäutung der untersuchten Vipern und der Höhenlage ihres Fundortes. Je höher der Lebensraum lag, desto später im Jahr setzte die Frühjahrshäutung der Männchen ein. Diese Ergebnisse können helfen, für die untersuchten Arten die Dauer der Überwinterungsperiode in Abhängigkeit von der Höhenlage ihres Vorkommens abzuschätzen. Nach bestem Wissen der Autoren ist die vorliegende Studie die erste Untersuchung, die einen Zusammenhang zwischen der Phänologie und der Höhenverbreitung bei eurasischen Vipern aufzeigt.

ABSTRACT

At a local scale, the timing of periodic life-history events of ectothermic vertebrates is strongly influenced by the ambient temperature. In the mountains, temperature decreases with increasing elevation. This is why the onset of spring activity of vipers can be expected to vary regionally between warm lowland and cold montane climates. To analyze the relationship between elevation and onset of spring activity, the authors surveyed habitats for emerging male vipers of the genera *Montivipera* and *Macrovipera* between April and May in Turkey and Cyprus.

Sexually active male vipers shed soon after leaving their hibernacula and before mating. The male spring shedding is obligatory and therefore represents a chronometer for the onset of the vipers' surface activity. During field trips between 2004 and 2015, fifteen male vipers were found in habitats between sea level and 2,300 m a.s.l. elevation with milky-opaque eyes reflecting their state of pre-ecdysis.

The observed significant positive correlation between onset of the vipers' spring activity and the elevation of the record site represents an ecological cline. The information can help to forecast duration of hibernation and activity of the vipers in the field. To the best knowledge of the authors, this is the first study about spring phenology of vipers from the eastern Mediterranean.

KEY WORDS

Reptilia: Squamata: Serpentes: Viperidae; *Macrovipera lebetina*, *Montivipera bulgardaghica*, *Montivipera wagneri*, *Montivipera xanthina*, physiology, behavior, phenology, ecdysis, molting, spring shedding, activity, Turkey, Cyprus

INTRODUCTION

The ecosystems of the Near and Middle East harbor the highest diversity of true vipers within Eurasia. Currently, 13 viper species out of three genera (*Vipera*, *Montivipera* and *Macrovipera*) are recorded from the Turkish territory (e.g., NILSON

et al. 1988; Stümpel & Joger 2009). With a few exceptions, the species within the genera are allopatrically distributed (Joger 1984). Mountain Vipers, *Montivipera* spp., and Blunt-nosed Vipers, *Macrovipera* spp., were subjects to studies on zoogeography (Joger 1984; Mebert et al. 2016), taxonomy (Nilson & Andrén 1986) and phylogeny (Stümpel & Joger 2009; Stümpel et al. 2016). However, comparatively little is known on their ecology (e.g., Nilson et al. 1999; Ettling et al. 2013, 2016), while phenological data are completely lacking or hidden in grey literature. *Macrovipera* is generally associated with steppe-like to semi-arid habitats situated between sea level and 1,700 m a.s.l. and reaches its western range limit in the Eastern Mediterranean. Species of the genus *Montivipera* are found in a broader ecological and elevational spectrum. For example, in western and south-western Anatolia, these mountain vipers inhabit Mediterranean and Oromediterranean biomes, whereas in eastern Anatolia these vipers are associated with boreal and subalpine Irano-Turanian floras.

In ectothermic animals, climatic factors influence life history traits. Many of them, such as seasonal and diurnal activity, reproductive performance, growth rate and metabolic rate depend on the thermal profiles of the habitats (e.g., Duvall et al. 1985; Van Wyk 1995). Therefore, temperature is a relevant environmental factor to a reptile, defining part of its living space and shaping its abiotic components (Walker et al. 1994; Körner 1998; Greenland & Losleben 2001). Along with the increase of elevation, also climatic, spatial, biotic and evolutionary factors change (McCain & Grytnes 2010). The most obvious is the generally linear decrease in temperature by an average of approximately 0.68 °C per 100 m increase in elevation (Barry 2008). Consequently, the seasonal and temporal activity of vipers inhabiting different elevations can be expected to be affected by extrinsic abiotic factors.

One such temporal activity is the shedding process in snakes (ecdysis). In general, ecdysis happens continuously throughout the lifetime and is associated with growth, whereby a higher frequency correlates with increased feeding, metabolic rate and temperature (Semlitsch 1979; Appleby 1980; Gibson et al. 1989). It also varies by reproductive state and cycle, respectively, hormonal status, gender and ontogenetic stage (e.g., Kubie et al. 1978; Nilson 1980; Jacobson 2007; Lillywhite 2014). Other influential factors may include exposure to dry air and the resulting risk of increasing cutaneous evaporative water loss (Lillywhite & Maderson 1982; Maderson 1984; Lillywhite 2006), wear and damage of the skin, as well as detachment of ectoparasites (Loomis 1951; Heatwole 1999).

During ecdysis, histological processes, which occur in the epidermis, affect the external appearance of the snake gradually. However, several stages of the process are very prominent and identifiable. The ecdysis process lasts a minimum of 14 days in captivity (the authors' personal observations) and is visually marked by a dull appearance of the snake. Eight days prior to the actual skin shedding, the eyes turn visibly opaque (milky). This prominent external change lasts for at least two days under controlled lab conditions (the authors' personal observations). Ecdysis culminates in the shedding of the old outer keratinized epithelial layer about six days after the eyes have become clear again (see Maderson 1965). The entire process of skin renewal is influenced by environmental factors (temperature, solar radiation) and, e.g., can last about 40 days in *Vipera berus* (Linnaeus, 1798) at cool northern latitudes (see Olsson et al. 1997), and likely is shorter in warmer regions or climate zones. Furthermore, recent evidence from the laboratory and field show that ecdysis can be a synchronous process within snake populations, likely in correlation with environmental factors and/or pheromones, which influence physiology including reproductive cycles (Lilliwhite & Sheehy III 2016 and references therein). Intrapopulation synchrony of the first ecdysis following emergence from hibernacula was observed in different snake groups in North America (e.g., Kubie et al. 1978; Ford 1996; Parker & Anderson 2007) and places this synchronization into a seasonal context. The pheromones released into the

environment during ecdysis inform other snakes in the area about the reproductive status of the newly shed snake (KUBIE et al. 1978; PARKER & MASON 2011). Such a first annual (spring) ecdysis synchronization that triggers mating activities has also been observed in the palearctic *V. berus* (SAINT GIRONS 1980; and reviewed in NILSON et al. 2005). Female Aspic Vipers, *Vipera aspis* (LINNAEUS, 1758), shed their skin prior to ovulation, and ecdysis provides a reliable reference date for the onset of gestation (LORIOUX et al. 2013). Hence, the release of cutaneous pheromones plays an essential role in the reproductive behavior of temperate zone snakes, and thus, it is plausible that ecdysis coincides with the mating periods (KUBIE et al. 1978; MASON 1992; LILLIWHITE & SHEEHY III 2016).

Species of the genera *Macrovipera* and *Montivipera* belong to the "*berus*" type (NILSON & ANDRÉN 1997) with the spring shedding of male vipers being the initiation of the reproductive activity (e.g., NILSON 1980; SAINT GIRONS 1980). Consequently, the synchronized spring shedding can be used as a chronometer for phenology and allows comparison of activity patterns of populations from different elevations across a broad region, if the same stage of ecdysis is compared. Hence, milky eyes are an appropriate marker, as this stage is the shortest and visually simplest to identify during ecdysis.

The authors hypothesize that the spring activity of vipers (including their reproductive behavior) is seasonally delayed at high elevations in comparison to lowland populations. The high amplitude of the topographic relief of the eastern Mediterranean and its exceptionally rich viper diversity provides a suitable opportunity to analyze across taxa the association between the beginning of male spring activity as indicated by the onset of ecdysis, and the elevation of occurrence. Despite the increasing amount of literature dealing with many aspects of seasonal and reproductive behavior in snakes (SHINE 2003; ALDRIDGE & SEVER 2011; LILLYWHITE 2014), such a correlation has not been subject to an observational study yet.

The aim of the present study was to test the hypothesis that in adult male vipers of the genera *Montivipera* and *Macrovipera* the date of first ecdysis after hibernation is positively correlated with the elevation of their occurrence in their natural habitat.

MATERIALS AND METHODS

Data were gathered during eight fieldtrips to Turkey and Cyprus between 2004 and 2015. From March to May, potential habitats of four species of *Montivipera* and one of *Macrovipera* were surveyed to detect vipers after emergence from their hibernacula. Snakes were observed between 07:00 am and 07:00 pm. Shedding adult males were identified visually by their thickened tailbase and the presence of milky eyes and opaque skin. Basic temporal (date, time of day) and geographical (latitude, longitude and elevation) information were recorded from each sampling site. The visited habitats were situated at elevations between 5 m and 2,300 m a.s.l. *Montivipera* species were studied at the Turkish Aegean coast, and in the western and central Taurus Massif [*M. xanthina* (GRAY, 1849)], Bolkar Mts. [*M. b. bulgardaghica* (NILSON & ANDRÉN, 1985)], Dibek Mts. [*M. bulgardaghica albizona* (NILSON, ANDREN & FLÄRDH, 1990)], and Aras Valley in northeastern Turkey [*M. wagneri* (NILSON & ANDRÉN, 1984)], *Macrovipera lebetina* (LINNAEUS, 1758) at Birecik and Şanlıurfa in southeastern Turkey, Aras Valley and Pafos on the Island of Cyprus. In total, 54 specimens were seen, 15 of which (eight specimens of *Macrovipera* and seven of *Montivipera*) were identified as males in spring shedding and characterized by opaque (milky) eyes (Table 1).

The study area had a maximum latitudinal extension of 600 km in a north-south direction between records of *Montivipera wagneri* (40°10' N) and *Macrovipera lebetina* (34°51' N) and covered a longitudinal distance of 1,350 km from records of

Table 1: Records of adult male vipers of the genera *Macrovipera* and *Montivipera*, including date and location of observation during their first spring ecdysis at the stage when the eyes turn visibly milky (opaque). Elevation in m a.s.l.

Tab. 1: Fundortangaben zu den untersuchten adulten männlichen Vipern der Gattungen *Macrovipera* und *Montivipera* sowie Zeitpunkt während der ersten Frühjahrshäutung im Stadium milchig-trüber Augen. Seehöhe in m.ü.M.

Species Art	Number Anzahl	Date Datum	Elevation Seehöhe	Locality Fundort	Coordinates Koordinaten
Montivipera b. albizona	1	2011.V.17	1,850	Göksun	37°56'27.06"N / 36°31'49.00"E
Montivipera b. bulgardaghica	1	2011.V.24	2,300	Arslanköy	37°02'45.82"N / 34°17'13.86"E
Montivipera wagneri	1	2004.V.08	1,550	Karakurt	34°17'13.86"N / 42°38'16.66"E
Macrovipera l. lebetina	3	2013.III.29	300	Cyprus	34°51'28.10"N / 32°25'40.17"E
Macrovipera l. lebetina	1	2013.III.29	20	Cyprus	34°49'19.98"N / 32°23'32.01"E
Macrovipera l. euphratica	2	2015.IV.06	750	Şanlıurfa	37°13'20.92"N / 38°55'06.67"E
Montivipera xanthina	2	2011.V.25	1,450	Gündoğmuş	36°51'29.87"N / 32°04'07.82"E
Montivipera xanthina	2	2006.IV.15	280	Selçuk	37°57'11.08"N / 27°29'07.67"E
Macrovipera l. obtusa	2	2015.V.27	1,730	Günindi	40°13'20.36"N / 43°16'44.27"E

Montivipera xanthina in the west (27°28' E) to *Montivipera wagneri* in the east (42°38' E). Data of all species, populations and times were pooled due to the small sample size and because the phenomenon of spring shedding is known to be consistently present in all viper species in this study (BRODMANN 1987 and the authors' personal observations).

Statistical evaluation of the data included a check for normality using the Shapiro-Wilk test. Statistics rejected the null hypothesis (H_0 = data tested are from a normally distributed population) for the date values but not for the elevation values. Therefore, the authors used the nonparametric Spearman's rho to test the correlation (r_s) between the variables date (in the form of number of days following the first sighting) and elevation.

Statistical analyses were conducted online using the software packages Social Science Statistics (STANGROOM 2018) and SciStatCalc (AHMED 2013). The graph was visualized using the software STATISTICA 6.0.

RESULTS AND DISCUSSION

The data reveals the strong positive correlation ($r_s = 0.72$, $p < 0.01$) between the onset of spring shedding of male vipers and the elevation of their record localities (Fig. 1). The significant ($p < 0.01$) linear regression ($y = 29.6x + 196.4$; $r^2 = 0.85$) indicates that the onset of spring shedding is temporally delayed with increasing elevation (m a.s.l.). For example, ecdysis of male *Macrovipera lebetina* was observed at sea-level on Cyprus at the end of March and at 1,730 m a.s.l. in northeastern Turkey in the second half of May (ca. 40-50 days later). Similarly, males of *Montivipera xanthina* were found in molting stage near the Aegean Sea at 280 m a.s.l. during mid-April, whereas a population monitored at 1,450 m a.s.l. was still in hibernation at the beginning of April and courtship was observed at the end of May, 52 days later. At the elevation of 2,300 m a.s.l., males of *Montivipera b. bulgardaghica* reached the shedding state even later, at end of May.

It is widely known that geographical location on a broad scale (latitude, longitude) are major determinants of temperature conditions. In general it can be expected that these drivers put restrictions on life history and phenology of ectotherm reptiles, as they have strong effects on seasonality, such

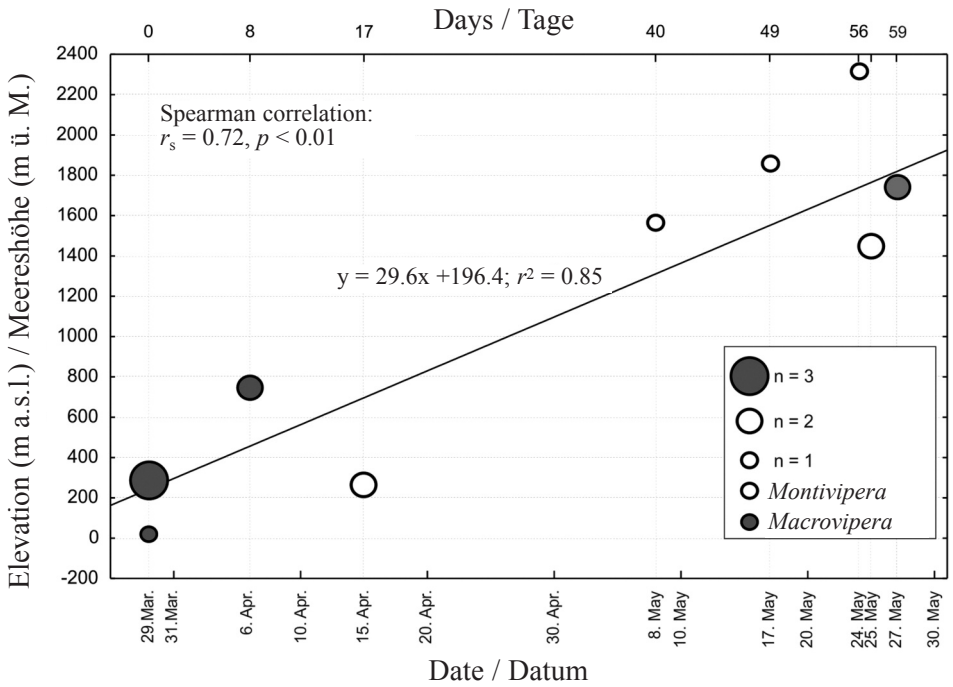

Fig. 1: Scatter plot showing temporal dependence between elevation of the record locality (m a.s.l.) and date of occurrence of milky-opaque eyes (developing 4-8 days prior to spring shedding) in mature male *Montivipera* (empty dots) and *Macrovipera* (filled dots) in Turkey and Cyprus. The statistical dependence is significant for the Spearman rank correlation at the $p < 0.01$ level.

Abb.1: Zeitliche Abhängigkeit des Auftretens der Augentrübung (4-8 Tage vor der Frühjahreshäutung) bei türkischen und zyprischen adulten männlichen Vipern der Gattungen *Montivipera* (leere Kreise) und *Macrovipera* (gefüllte Kreise) von der Höhenlage (m ü. M.) ihres Fundortes. Der Zusammenhang ist für die Spearman-Rangkorrelation auf dem Niveau $p < 0{,}01$ signifikant.

as timing of spring and duration of winter. SPERRY et al. (2010) analyzed the seasonal activity of the snake *Pantherophis obsoletus* (SAY, 1823) across a latitudinal distance of more than 1,500 km and associated temperature data in North America. Even though the authors did not notice any variation in activity throughout the study area, they mentioned that ratsnakes in Texas did not hibernate, whereas ratsnakes in both, Illinois and Ontario hibernated.

Enhanced seasonality also affects reproductive functions such a mating, gametogenesis or steroidogenesis, due to its correlation with cyclic fluctuations in climate conditions, e.g., temperatures and other environmental parameters. For the Common Garter Snake, *Thamnophis sirtalis* (LINNAEUS, 1758), a temporal dissociation between mating behavior (in spring), and gametogenesis and maximal sex steroid hormone concentrations (in late summer) was reported (CREWS 1984; CREWS et al. 1984).

In *Macrovipera* and *Montivipera* species, males produce mature sperm solely in spring, which initiates their mating activity after the first post hibernation shedding, a process that is highly synchronized within a population as in *V. berus* (NILSON 1980). Male spring-shedding is hormonally in-

duced (Saint Girons & Kramer 1963) and, unlike the metabolically induced shedding, not connected to feeding rate and growth. Hence, spring-shedding can act as a benchmark within the reproductive cycle of these male vipers.

However, topographic differences between lowland and alpine habitats in the eastern Mediterranean have strong effects on the temperature profiles comparative to those of latitudinal distances. The present study indicates that seasonal activity patterns are not static within species and depend on the elevation of its habitat. Annual surface activity is shorter in subalpine *Montivipera* populations than at coastal low elevation *Macrovipera lebetina* or *Montivipera xanthina* in which the mating season begins up to two months earlier and snakes enter hibernation later. The thermal regime in the mountains condenses vital life history traits (reproduction, feeding) to a six month time frame at most.

In summary, the present study compares for the first time the onset of male spring shedding among different localities and species of eastern Mediterranean vipers and shows a delayed beginning of male activity by a later emergence from hibernation with increase of elevation. Climate change will affect life history of reptiles and populations may shift their active seasons to earlier in the year. Further research is needed to generate a solid phenological data base and to record how the activity of oriental vipers will be affected by climate change.

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AUTHORS: Nikolaus Stümpel (Corresponding author < nikolaus.stuempel@gmx.de >) [1], Oleksandr Zinenko [2] & Konrad Mebert [3]

[1] Staatliches Naturhistorisches Museum Braunschweig, Gausstrasse 22, Braunschweig, D-38106, Germany;
[2] V.N. Karazin Kharkiv National University, Svobody sq. 4, Kharkiv 61058, Ukraine;
[3] Institute of Development, Ecology, Conservation and Cooperation, Via G. Tomasi di Lampedusa 33, 00144 Rome, Italy.