The Herpetological Bulletin 171, 2025: 20–24
RESEARCH ARTICLE

https://doi.org/10.33256/hb171.2024

Comparison of scale anomalies in populations of northern viper *Vipera berus* from habitats differing in size and degree of fragmentation

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ABSTRACT – Northern vipers *Vipera berus* are declining and increasingly confined to fragmented and isolated populations in England. Scale anomalies that occur during development can potentially be related to environmental stressors. Using photographs of the dorsal view of viper heads, we compared levels of head scale fragmentation and asymmetry between four populations to identify the extent of anomalies. Although all populations had vipers that displayed scale fragmentation and asymmetry, the incidence of such anomalies was lowest at Fackenden Down which supports the largest population and is probably the least isolated. Two populations that displayed particularly high levels of scale anomalies – Talbot Heath and Turbary Common – are isolated and surrounded by urban and suburban development. Supraocular and intercanthal scales showed a higher incidence of fragmentation and asymmetry than did apical scales, and there was a general tendency for the vipers with scale fragmentation to also display asymmetry. We speculate that the relatively high incidence of scale anomalies in small, isolated populations may be a result of environmental or genetic pressures and that head scale fragmentation and asymmetry may provide an early indication of such stressors.

INTRODUCTION

How and why living organisms deviate from bilateral symmetry has long fascinated biologists. Such deviations may frequently be a result of injury, such as the loss of digits or limbs. However, there has been a longstanding debate over whether genetic and environmental stressors can lead to asymmetry (e.g. Parsons, 1992; Lens et al., 2002; Beasley et al., 2013). Within a population, deviations from symmetry may be non-directional and occur randomly on traits on both sides of the body (fluctuating asymmetry) or may occur more on one side than the other (directional asymmetry). Either way, reptiles are good models for such studies as their scale patterns are easily quantified and compared between both sides of the body. Moreover, several studies have indicated links between genetic and environmental stressors and asymmetry (see review by Laia et al., 2015). Equally, it has been shown that suboptimal incubation conditions can cause developmental instability and increase the incidence of scale anomalies in hatchling reptiles (e.g. Brown et al., 2017). Consequently, measuring scale anomalies in reptiles can potentially be used as an index of stressors that might be impinging on a population (Shamiminoori & Bull, 2015).

In Britain, concerns over declines of *Vipera berus* have led to its classification as Vulnerable in England and Near Threatened in Scotland, Wales and Great Britain as a whole (Foster et al., 2021). Small populations are particularly vulnerable to anthropogenic threats including habitat loss and fragmentation as well as seasonal temperature fluctuations due to climate change (Gardner et al., 2019). Moreover, nearly 40% of viper habitat had been lost by 2011, and the species now only occurs in fragments of its historic range in Great Britain (Gardner et al., 2019). However, both the drivers of these declines and the interventions needed to mitigate them may be complex (Julian & Hodges, 2019). Such recent trends have precipitated a number of long-term studies across the country with the aim of determining drivers of population dynamics and potential threats (e.g. Hills, 2018; Hodges et al., 2023; Struthers, 2023). As individual northern vipers are relatively easy to identify through their distinctive head scalation and colour patterns, these studies are providing valuable datasets from which head scale anomalies can be analysed.

In this study, *V. berus* individuals from four populations differing in size, geographic location and proximity to human encroachment in southern England were analysed after being photographed; and head scalation was examined with specific emphasis on degrees of fragmentation and asymmetry. Scale fragmentation and asymmetry were visually scored with the specific aims of 1) identifying and comparing the extent of scale fragmentation and asymmetry in the four populations of vipers; and 2) discussing the potential drivers of scale anomalies in relation to population histories and environmental factors.

MATERIALS & METHODS

Study sites

Observations of *V. berus* were compiled from four sites in southern England studied from 2005 to 2021; two sites in Dorset: Talbot Heath and Turbary Common, and two sites in Kent: Fackenden Down and Kings Wood. Talbot Heath and Turbary Common are approximately 37 ha and 40 ha in area respectively, each site supporting a population of less than 100 vipers which may also be in decline (Dobbs, pers. obs). Both sites are isolated and surrounded by urban and suburban development. The Kings Wood study sites comprise three small clearings that total 3 ha, separated by distances of between 0.5 km and 3 km within a wider mixed woodland of 588 ha. The population of vipers in these clearings has declined over the past 20 years and currently comprises less than 50 individuals (Hills, 2018). Fackenden Down is a 28 ha chalk downland site that has supported a largely stable population of over 500 vipers between 2007 and 2019, with about 50 individuals recognised per year (Myall, 2021; Struthers, 2023).

A total of 1,287 images were processed from the four populations, ultimately identifying 391 individuals using visual identification of scale patterns and natural markings. Photographs were taken of each individual with a clear view of the head; individuals in Dorset and Fackenden were photographed in-situ, while those in Kings Wood were captured and photographed on a piece of light-coloured foam (ethical approval for the procedure was provided by the University of Kent). Images were organised into six datasets by location, with Kings Wood divided into three smaller sites, designated main site, earthworks and Soakham Down, with associated dates of sighting and the individual snake identification code or name. Images were visually compared to examine scale patterns between populations. The analysis omitted vipers whose images were too out of focus to accurately delineate scales, and the small number of juvenile individuals that were photographed.

Criteria for assessing asymmetry and fragmentation

The methodologies used to assess scale fragmentation and asymmetry were adapted from those used in previous studies of snakes (Brown et al., 2017; Bauwens et al., 2018). Three groups of scales were used to score fragmentation and asymmetry in each individual; the apical scales, the intercanthals and the supraoculars (Fig. 1).

The symmetric configuration that occurred most often (Fig. 1) consisted of two apical scales, a group of five intercanthals and six small supraoculars stacked in groups of three on either side of the centre frontal scale. Fragmentation and asymmetry in these three types of scales were defined as follows:

1. Fragmentation: Clear fracture lines splitting one of the scales. Such fragmentation did not always result in asymmetry. An individual may have had additional scales due to fragmentation, but if those scales occurred equally on the left and right sides of the head, they did not contribute to the asymmetry score (Brown et al., 2017). Any scales that had suffered trauma (e.g. through a predator attack) usually showed evidence of scarring and healing and were excluded from the analysis. Individual snakes were then scored as 1 = any fragmentation present, 0 = fragmentation absent.

2. Asymmetry: A difference in the number of scales of the same type on either side of the head. Thus, if the total count of scales of the same type was an even number those scales were scored as symmetric, while if the total count was an uneven number the scales were scored as asymmetric. Individual snakes were then scored as 1 = any asymmetry present, 0 = asymmetry absent.

Figure 1. Dorsal view of the head of a male northern viper showing the most common symmetric scale pattern, (in descending order from the apex) two unfused apical scales (red), five intercanthals (blue) and six (three on each side) supraoculars (yellow)

Statistical analysis

Preliminary analyses showed no difference in fragmentation or asymmetry between vipers at the three sites in Kings Wood and were therefore pooled for further analysis. Binomial Generalised Linear Models (GLMs) were then used to compare fragmentation and asymmetry between the four sites using R version 4.1.0 (Field et al., 2012). As Fackenden Down historically supported the largest population of vipers, this was used as a baseline against which other populations were compared.

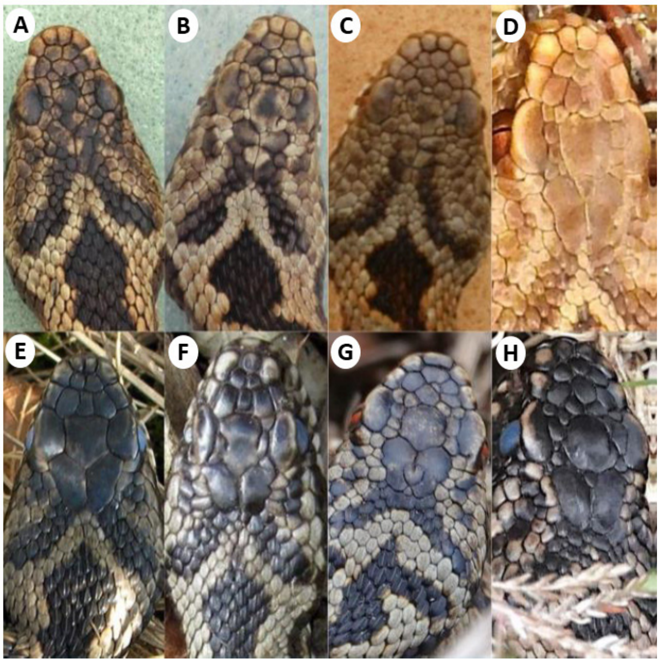

Figure 2. Examples of variation in scalation between individuals, top row are females, bottom row are males. From left to right, top row images **A.**–**C.** Kings Wood, **D.** Turbary Common, **E.** & **F.** Fackenden Down, **G.** & **H.** Talbot Heath

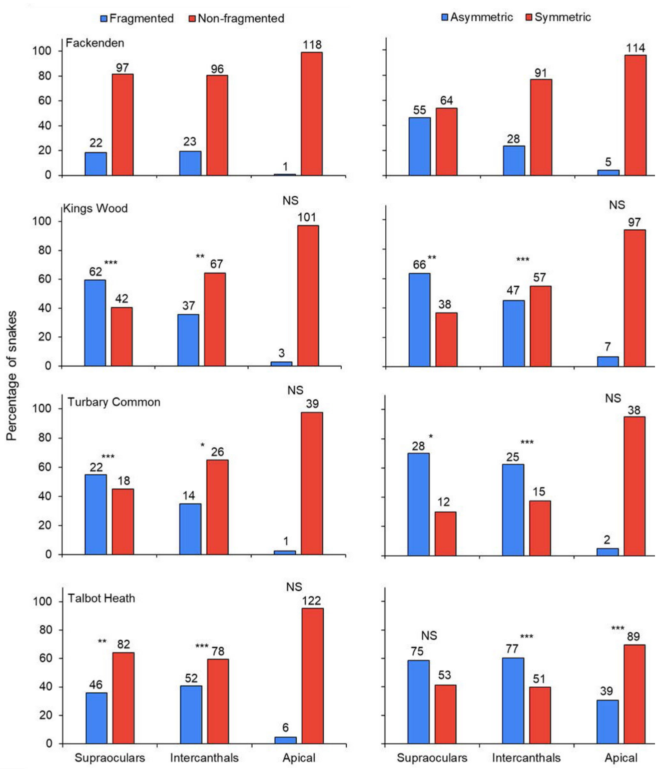

Figure 3. Comparison of (left) degree of scale fragmentation and (right) asymmetry in northern vipers at four sites in southern England. Numbers of vipers showing that character are given above the bars. A binomial GLM compared Kings Wood, Turbary Common and Talbot Heath to Fackenden Down; NS P > 0.05, *P < 0.05, **P < 0.01, ***P < 0.001. Further details of the GLM are provided as Supplementary Material.

RESULTS

Over half of the vipers displayed some degree of scale fragmentation or asymmetry. Asymmetry comprised either additional intercanthals or supraoculars on one side, or fragmented scales split into extremely small fragments tucked between scales within the scale pattern. Additionally, larger scales such as the frontal were often apparently fused with supraoculars (seen in Fig. 2 B, C & F) and intercanthals were frequently fused to form large kidney shaped scales.

There were clear differences between the sites in degree of scale fragmentation and asymmetry. While only 33% of vipers at Fackenden displayed some fragmentation, over 63% of vipers at the other three sites had fragmented scales (Fig. 3 and Supplementary Material). Likewise, whereas 57% of vipers at Fackenden had some form of scale asymmetry, the incidence of asymmetry at the other three sites was at least 79%. With the exception of the supraoculars of vipers at Talbot Heath, the vipers at Kings Wood, Turbary Common and Talbot Heath all had more fragmentation and asymmetry of supraoculars and intercanthals than those at Fackenden. Between the sites, patterns of fragmentation and symmetry in the apical scales were less clear with the only difference being that vipers at Talbot Heath had more asymmetry than Fackenden (Fig. 3 and Supplementary Material).

When data were pooled across all the sites, over half of the snakes displayed both scale fragmentation and scale asymmetry, and there was a significant association between the two conditions ($\chi 2 = 57.3$, df = 1, $P < 0.001$).

DISCUSSION

Although more snakes displayed scale asymmetry than scale fragmentation, those snakes showing fragmentation also tended to show asymmetry. Additionally, the intercanthals and supraoculars showed more fragmentation and asymmetry than the apicals. These findings are consistent with previous studies of single populations of vipers that also found variation between individual vipers in the incidence of scale fragmentation and asymmetry (Hodges & Seabrook, 2014; Bauwens et al., 2018). As observed by Bauwens et al. (2018), recaptures of individuals indicated that head scalation was stable over time in the majority of snakes.

The degree of scale fragmentation and asymmetry in vipers varied between the populations. Indeed, the viper population at Fackenden Down displayed a lower degree of fragmentation and asymmetry than the other three populations, particularly with respect to the intercanthals and supraoculars. The vipers at Kings Wood, Talbot Heath and Turbary Common occupy sites that are either small or isolated by surrounding urban or suburban development. Equally, surveys at these sites have indicated that the populations are either historically small or have declined in recent years. In contrast, although the population at Fackenden Down may also have declined, it is a historically large population occupying a site that is interconnected to different habitat types including woodland, scrub and rough grassland which promote a variety of habitat corridors, facilitating ecological edge effects. Although a road runs along the edge of Fackenden Down and may be a potential barrier, vipers also occur on the field margins across the road from the main population (Hodges et al., 2023).

A previous study by Hodges & Seabrook (2014) commented on the apparent instability of the head scales of some individuals at Fackenden and provided evidence that a scale anomaly on the frontal scale may be heritable. In slatey-grey snakes in Australia, Brown et al. (2017) showed that although scale asymmetry was associated with reduced heterozygosity, this trait was not heritable. In contrast, in the same species scale fragmentation appeared to be heritable. Forsman et al. (1994) found that vipers with anomalies in the midbody ventral scales probably had reduced survival, but there was no evidence that the scale anomalies were heritable. Löwenborg & Hagman (2016) showed a link between ventral scale asymmetry and rib deformity in *Natrix natrix*, and that scale asymmetry impacted terrestrial locomotion of hatchings. Clearly, more research is needed to establish the relationships between loss of genetic diversity, the heritability of scale anomalies and their impact on survival and fitness in snakes.

Although the reasons for the differences between the populations are unclear, it is well-known that asymmetry and fragmentation may reflect potential stressors on populations. Such stressors may be environmental or genetic, or a combination of both. For example, in addition to a link between asymmetry and lower heterozygosity in slatey-grey snakes, both asymmetry and fragmentation was higher in snakes that developed faster (Brown et al., 2017). Herczeg et al. (2005) showed that two populations of dice snakes *Natrix tessellata* varied in the degree of fluctuating asymmetry and suggested that these differences may be due to genetic or environmental stressors. Likewise, wall lizards *Podarcis muralis* display more fluctuating asymmetry in disturbed urban populations than in rural populations (Lazić et al., 2013). There may also be links between head scale symmetry and some measures of fitness in pygmy bluetongue lizards (Shamiminoori & Bull, 2015). We speculate that the levels of asymmetry and fragmentation shown in our populations could be related to historically small populations occupying habitats that have been increasingly subjected to fragmentation, isolation, disturbance and habitat change in recent years. Indeed, those populations showing the highest levels of asymmetry and fragmentation may be suffering higher levels of such impacts than those at Fackenden Down. Although the genetic diversity of vipers may be maintained despite historic population bottlenecks (Madsen et al., 2023), further genetic analyses may help clarify the relationship between scale anomalies and population stressors in vipers. If such a relationship is established, measuring scale asymmetry and fragmentation could prove to be a useful early warning of viper populations at risk from wider landscape change that may be driving declines.

ACKNOWLEDGEMENTS

We are grateful to Rick Hodges and Clifford Seabrook for providing access to viper images from the Kent Wildlife Trust reserve of Fackenden Down and for helpful discussions. Brittany Nagora provided support and a valuable review of early drafts of the manuscript and we thank Rick Hodges and Thomas Madsen for further helpful comments. RG is grateful to the many students and volunteers that have assisted with fieldwork and Forestry England for permissions to work at Kings Wood.

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Accepted: 16 September 2024

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