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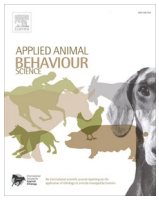

Negligible behavioural variation in Hungarian meadow vipers (*Vipera ursinii rakosiensis*) captive-reared intensively and the effects of simple environmental enrichment

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ABSTRACT

Captive breeding and reintroduction are typically seen as a last resort to save a certain taxon or population from going extinct. However, it is hard to decide between intensive (maximum growth, high number of individuals, lack of environmental experience) or quasi-natural extensive rearing (decreased growth, less individuals, more environmental experience) strategies. As behaviour is the first mean to cope with the unpredictable challenges (predation risk, finding food, optimal microhabitat or refuge) met upon release, standing behavioural variation between individuals before release is a key to success. Here, we studied between-individual behavioural variation (animal personality) in captive-bred Hungarian meadow vipers (*Vipera ursinii rakosiensis*; Europe's most endangered venomous snake) under the most intensive rearing method (individual housing in small terraria, food *ad libitum*, no wintering) together with the effects of a simple abiotic (adding a clump of dried grass) environmental enrichment. We assessed their feeding (two prey types: banana cricket, *Gryllus assimilis*, house cricket, *Acheta domesticus*) and risk-taking behaviours 12–12 times over 46 days. *G. assimilis* and *A. domesticus* differed in their antipredator behaviour: *G. assimilis* stops more and for longer durations in a new potentially risky environment and hops less and freezes for longer durations after a simulated predatory attack than *A. domesticus*. Regarding the vipers, we found low to negligible between-individual behavioural variation. Enrichment canalised risk-taking and diversified swallowing time. Risk-taking increased with size. Feeding success was affected by an enrichment × size interaction: body size had a positive effect, but only in the absence of enrichment. Female vipers struck on *A. domesticus* faster than on *G. assimilis*, while males did not differentiate. Males struck more times and swallowed longer than females. We conclude that the low behavioural variation observed under the studied intensive rearing protocol may limit the range of behavioural responses available to vipers when encountering novel conditions after release, although the consequences for field performance remain to be tested. However, we also found that already minor environmental enrichment or prey type can affect the snakes' behaviour. Future studies are needed to establish the critical environmental factors and the enrichment strategy (e.g. during whole development or for some period before release), which would increase behavioural variation sufficiently with minimised logistical costs for optimising the captive breeding and reintroduction strategy.

1. Introduction

The declining trends in biodiversity over the past century have been reported generally (Butchart et al., 2005) or with a focus on specific taxa (Houlahan et al., 2000). Among vertebrates, amphibians have been in the spotlight in the past decades as the rate of amphibian species (and population) extinction observed both regionally and globally is comparable to historical mass extinction events (Global Amphibian Decline; Alford and Richards, 1999, O'Hanlon et al., 2018, Houlahan et al., 2000, Leung et al., 2020). However, amphibians are not alone in facing a crisis, as studies have revealed that reptiles, and especially snakes are showing similar trends (Reading et al., 2010, Falaschi et al., 2019). The primary

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drivers are largely human-induced habitat destruction or alteration, overexploitation, the introduction of invasive species, diseases, pollution and climate change (e.g. Alford and Richards, 1999, Falaschi et al., 2019, Gibbons et al., 2000).

Conservationists respond to extinction risk by focusing on endangered species or habitats (Griffith et al., 1989, Sainsbury et al., 2021). Species-based conservation encompasses various approaches, but it often involves the idea of 'ex-situ' breeding with the intention of future reintroduction of captive-bred individuals (Dodd and Seigel, 1991, Griffiths and Pavajeau, 2008, Converse et al., 2013, Soorae, 2008, 2010, 2011, 2013, 2016, 2018, 2021). 'Ex-situ' breeding is generally based on the target species' life history adaptability to simple captive environments or the creation of quasi-natural conditions in ex-situ facilities (Seddon et al., 2005, Scott et al., 2010, Ewen et al., 2014, Sainsbury et al., 2021). Due to obvious logistical constraints, species with simpler life-history and high adaptability to artificial environments are better candidates for mass breeding. On the other hand, such adaptations may become problematic later if post-release survival depends on complex behavioural strategies that may not develop properly in simplified captive environments (Seddon, 1999, Germano and Bishop, 2009).

Environmental enrichment is one potential means of mitigating the behavioural consequences of simplified captive environments. Although reptiles remain comparatively understudied (Burghardt, 2013), captive snakes have been shown to use and prefer structurally enriched enclosures and to alter their behavioural profiles under enriched conditions (Almli and Burghardt, 2006; Hoehfurtner et al., 2021; Nagabaskaran et al., 2022). Enrichment can also affect specific cognitive responses, including odour discrimination (Nagabaskaran et al., 2021), while developmental exposure to enriched housing has recently been associated with differences in brain morphology (Nagabaskaran et al., 2025). However, previous studies have focused primarily on welfare, enclosure preference or mean behavioural responses, whereas the effects of enrichment on consistent among-individual behavioural variation remain poorly understood.

In addition to its potential effects on behavioural repertoires and cognitive performance, intensive captive rearing may also influence the amount of behavioural variation among individuals. Following an abrupt environmental change – such as release from a simple, stable, and low-challenge artificial environment into the natural environment with its unpredictable biotic (e.g. predation pressure, food availability) and abiotic (e.g. variation in temperature and humidity) stressors – high between-individual behavioural variation is required within the released group. This is because such variation may increase the likelihood that a proportion of individuals, by chance, express behaviours that match the novel environmental challenges during the initial phase. Subsequently, the surviving subset of individuals may fine-tune their behaviour through behavioural plasticity, including learning. Studying different levels of behavioural variation is central to animal personality research and is also relevant to conservation biology (Smith and Blumstein, 2013). Animal personality research focuses on consistent between-individual behavioural variation (Gosling, 2001; Sih et al., 2004; Dingemanse and Réale, 2005; Wolf and Weissing, 2012; David and Dall, 2016; Kaiser and Müller, 2021). Therefore, the advanced methodologies developed in this field can be adapted to assess the behavioural adaptability of captive-bred individuals prior to release.

The Hungarian meadow viper (*Vipera ursinii rakosiensis*) is Europe's most endangered venomous snake. It was declared protected in Hungary in 1974 and has been strictly protected since 1988. The subspecies is included in Appendix II of the Bern Convention (Council of Europe, 1979 [revised 2002]), is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES, 2014), and is classified as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Halpern and Bowles, 2024). It is also listed in Annex II of the Habitats Directive (Council Directive 92/43/EEC, 1992), meaning that its occurrences must be included in the Natura 2000 network of protected areas (Edgar and Bird, 2005). Following the severe decline of the subspecies observed by the late 1990s, a cooperative conservation effort was initiated in Hungary to prevent its extinction. The Species Conservation Plan targeted the restoration of populations and habitats through various measures, including captive breeding and reintroduction into restored habitats (Dankovics et al., 2004; Halpern, 2007).

The ex-situ population was established in 2004 at a remote farm in the Kiskunság region, with the construction of the Hungarian Meadow Viper Conservation Centre (Péchy et al., 2015). Founder individuals were collected from all known wild populations in Hungary (the Hanság and Kiskunság regions) and housed in outdoor terraria under semi-natural conditions. Newborn vipers were kept individually in indoor terraria and were not subjected to hibernation during their first winter, resulting in faster growth rates in the first year compared to natural populations. Releases have been conducted annually since 2010, with a total of 1434 captive-bred vipers released into the wild to date. However, due to the difficulty of field monitoring – stemming from low population density, secretive behaviour, and cryptic coloration – post-release survival is challenging to estimate.

A recent population viability analysis based on studbook data collected between 2004 and 2023 indicated that the ex situ population is demographically robust and can sustain the planned production of individuals for release over the coming decades (Halpern et al., 2024). The simulations also supported reintroduction as an important means of reducing the extinction risk of small wild populations. However, the limited demographic information available from the wild currently prevents robust estimates of population trends and post-release survival, and the corresponding model predictions therefore require further field validation. The analysis identified mortality during the subadult life stage as a particularly influential demographic parameter. Consequently, as the breeding programme has developed from establishing a viable captive population towards maintaining a long-term source of animals for release, it is timely to examine not only the number of individuals produced but also whether intensive rearing conditions affect behavioural variation among release candidates.

Meadow vipers are unusual among viperids in feeding extensively on invertebrates, with orthopterans forming an important component of the diet in several *Vipera ursinii* populations; large orthopterans are also ecologically relevant prey for V. u. rakosiensis (Baron, 1992; Újvári et al., 2000). Consequently, differences among orthopteran prey in movement and defensive behaviour may influence their detection and capture by vipers. We therefore compared the behaviour of the two cricket species, routinely supplied in the breeding programme, to determine whether prey-specific behavioural differences could help explain variation in prey detection, strike latency and handling. This captive comparison was not intended to reproduce the diversity or relative abundance of prey encountered in the wild.

The aim of the present study was to assess behavioural variation among captive-bred vipers reared under an intensive protocol (individual housing in small terraria, no hibernation, *ad libitum* feeding) using the animal personality framework. Additionally, we tested the effects of 'minimalist' environmental enrichment and the provision of different prey types. Specifically, we investigated whether (i) six months of development in highly simplified and standardised environments would lead to behavioural homogenisation, and whether (ii) the application of simple environmental enrichment (adding a dry grass clump), (iii) the provision of different prey types, or (iv) individual state (sex, size) influenced behavioural variation. To this end, we conducted a common garden experiment in the Hungarian Meadow Viper Conservation Centre, using 32 individuals from 10 families. We assessed feeding and risk-taking behaviours 12 times per individual over a 46-day period. Feeding behaviour was tested using two prey types: the banana cricket (*Gryllus assimilis*) and the domestic cricket (*Acheta domesticus*). We also tested for differences in the antipredator behaviour between the prey cricket species.

2. Methods

2.1. Experimental setup

Adult Hungarian meadow vipers were housed in pairs in outdoor terraria (3 m × 1.5 m × 1 m; length × width × height, respectively). Breeding pairs were selected based on kinship to minimise inbreeding, prioritising combinations of unrelated individuals and allowing maximum kinship coefficient of 5% when no other option was available. Gravid females were separated prior to parturition in July 2021, placing them individually in smaller outdoor terraria (1.5 m × 1.5 m; length × width, respectively). From each family, right after birth, one or two healthy males and one or two healthy females were chosen randomly, and housed individually in terraria (30 cm × 20 cm × 25 cm). Each terrarium contained one plastic cup (3 cm in diameter) for water, a hide (5 cm × 5 cm × 2 cm) made from terracotta, with locally available sandy soil used as substrate. Above each terrarium, a commercially available 25 W halogen spot lamp provided light and radiant heat for 8 h daily. Additionally, a 22 W Lucky Reptiles Thermo-Mat Strip was placed beneath one end of each terrarium to provide heating. The substrate temperature was regulated between 22°C and 28°C according to the following schedule: 25°C from 08:00–10:00, 28°C from 10:00–17:00, 25°C from 17:00–21:00, and 22°C from 21:00–08:00. As a form of minimalist environmental enrichment, one handful of dry grass was placed at the end of the terrarium directly beneath the lamp in half of the terraria. In all terraria, the hide and water dish were positioned next to each other at the opposite end, away from the lamp. Within each family, individuals were randomly assigned to either the enriched treatment (dry grass present) or the unenriched treatment (no dry grass), with equal numbers assigned to each treatment. The amount of grass was standardised operationally as one handful by the same person and was not weighed.

Newborn vipers were fed twice weekly with *A. domesticus*. Two months prior to behavioural testing, prey provision was modified to alternate weekly between *A. domesticus* and *G. assimilis*; that is, each species was offered for two consecutive feeding events. During the study period, vipers were fed every four days, with two live crickets provided per feeding. Any unconsumed crickets were left in the terraria until the temperature measurement and risk-taking assessment two days later, allowing the vipers an additional opportunity to feed under routine husbandry conditions. At that time, we recorded whether any uneaten crickets remained and removed them. Consequently, no crickets remained in the terraria during the two days preceding the next feeding event.

2.2. Cricket behavioural assays

The behaviour of *A. domesticus* and *G. assimilis* (N = 40 per species, with adults and nymphs equally represented) was assayed in terraria identical to those in which vipers were kept. Upon introduction to the terrarium, cricket movement was monitored for five minutes, during which the number and duration of stops were recorded. Subsequently, a startle response was induced by gently touching the cricket with a fine paintbrush. Crickets responded to this stimulus by hopping away and then freezing. The number of hops and the duration of freezing (s) were recorded for an additional five minutes. This way, we assessed cricket behaviour in a new, potentially dangerous environment and after a simulated predatory attack. Cricket behaviour was scored live rather than from video recordings. Each trial was scored once by one of two observers and was not independently scored by both observers.

2.3. Viper behavioural assays

Feeding behaviour was recorded during standard feeding events conducted every four days, for a total of 12 trials over a 44-day period, starting when vipers were five months old (mean age 152.2 ± 4.5 days, range 149–161 days). All viper trials were observed live by the first author, who identified and verbally indicated each behavioural event. An assistant recorded the observations and operated the smartphone used as a stopwatch, registering lap times only when instructed by the first author. The assistant did not independently identify or classify behavioural events. Trials were not video-recorded or subsequently video-coded. The snake's surface body temperature was measured immediately before the cricket was introduced into the terrarium. A timer was started when the cricket landed in the centre of the terrarium. We recorded the following time data: first reaction of the focal viper to the prey (T_1), time of first and subsequent strikes ($TS_{1\text{-}X}$), time of start of swallow (T_{SW}) and time of end of swallow, marked by yawning (T_F). The observation lasted for 10 min. This standardised observation window was selected because, based on our husbandry experience, vipers responding immediately to prey generally did so within the first few minutes following prey introduction. If the focal viper did not successfully capture prey during this period, the observation was terminated and the feeding attempt was recorded as unsuccessful for the behavioural assay. Although prey could subsequently be consumed during the routine feeding period, the exact timing of consumption after the 10-min observation window was not recorded. The following variables were analysed: *feeding success* (yes/no), *number of strikes*, *latency to first strike* ($TS_1 - T_1$), *holding time*, i.e. time between last strike and start of swallowing ($T_{SW} - TS_X$), *time of food manipulation*, i.e. time between first strike and end of swallowing ($T_F - TS_1$), and *swallowing time*, i.e. the time between the start of a successful swallowing effect and the end of swallow ($T_F - T_{SW}$).

Immediately before each feeding trial, the surface body temperature of the focal viper was measured from approximately 20 cm at the dorsal mid-body region using a handheld, non-contact infrared thermometer with a laser pointer (Craft; measurement range: −50–500 °C; exact model unavailable). Two days after feeding, the measurement was repeated as part of the risk-taking assessment. During this assessment, the same observer introduced the same thermometer vertically from above, approximately perpendicular to the substrate surface, with the laser directed towards the dorsal mid-body region, and moved it to approximately 10 cm from the snake to provide a standardised, salient approaching stimulus. Both distances were estimated visually rather than measured during each trial. Snakes were assessed at their current position within the home terrarium and were not handled or repositioned. Their response to the approaching thermometer was recorded as a binary variable (0 – neutral or escaping; 1 – defensive posture, hissing or striking).We note that this behaviour is equal to defensive aggression (e.g. Horváth et al., 2020), which is part of the risk-taking strategy, but for simplicity, we call it risk-taking.

During the experiment, 15 vipers shed their skin or showed clear signs of imminent shedding (pale skin coloration, bluish eyes, reduced movement, and lack of appetite). As shedding has a substantial effect on snake behaviour (Turmo 1996; Carnes-Mason 2023), we excluded data from the two weeks preceding the detection of these signs, as well as data from the subsequent week, from the analyses. The final dataset comprised 295 behavioural observations.

2.4. Statistical analyses

To analyse cricket behaviour, we fitted separate generalized linear models (GLMs) with negative binomial error distribution for each behavioural response. Species, age (nymph or adult) and sex were included as fixed factors, and body size was included as a covariate. The models included all possible two-way interactions among species, age and sex, as well as the species × age × sex interaction. To interpret the significant species × age interaction identified for the number of stops, we fitted follow-up GLMs separately for the two cricket species. These models used the same negative-binomial error distribution as the global model and included age, sex and body size together with the age × sex interaction. For the analysis of the number of stops, one observation was

Table 1
Repeatability estimates for the binary behavioural traits risk-taking and feeding success in juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*). Generalized linear mixed models (GLMMs) with binomial error distributions and logit links were fitted, and repeatability was estimated on the underlying latent (logit-link) scale. Agreement repeatability (R), enhanced agreement repeatability (eaR), and their 95% confidence intervals (CIs) are shown.

		All (N = 32)		Female (N = 16)		Male (N = 16)		Enrichment (N = 16)		No enrichment (N = 16)	
		R	eaR	R	eaR	R	eaR	R	eaR	R	eaR
Risk-taking	Random effect	**R = 0.19 P < 0.001 CI = 0–0.28**	**R = 0.16 P < 0.001 CI = 0–0.21**	**R = 0.23 P = 0.03 CI = 0–0.38**	**R = 0.23 P = 0.03 CI = 0–0.38**	**R = 0.23 P = 0.03 CI = 0–0.4**	**R = 0.12 P = 0.02 CI = 0–0.23**	R = 0.06 P = 0.15 CI = 0–0.21	R = 0.06 P = 0.15 CI = 0–0.19	**R = 0.18 P = 0.04 CI = 0–0.35**	**R = 0.18 P = 0.04 CI = 0–0.31**
	Fixed effects		**R = 0.14 P = NA CI = 0.08–0.45**		R = 0.04 P = NA CI = 0.03–0.69		R = 0.3 P = NA CI = 0.12–1.5		R = 0.13 P = NA CI = 0.04–1.62		R = 0.14 P = NA CI = 0.06–0.75
Feeding success	Random effect	**R = 0.1 P = 0.02 CI = 0–0.19**	**R = 0.09 P = 0.02 CI = 0–0.17**	R = 0.14 P = 0.14 CI = 0–0.41	R = 0.14 P = 0.14 CI = 0–0.41	R < 0.001 P > 0.99 CI = 0–0.04	R < 0.001 P > 0.99 CI = 0–0.04	R = <0.01 P = 0.45 CI = 0–0.11	R < 0.01 P = 0.45 CI = 0–0.1	R < 0.001 P > 0.99 CI = 0–0.16	R < 0.001 P > 0.99 CI = 0–0.16
	Fixed effects		R = 0.13 P = NA CI = 0.09–0.37		R = 0.24 P = NA CI = 0.13–1.82		R = 0.09 P = NA CI = 0.05–0.42		R = 0.1 P = NA CI = 0.06–0.43		R = 0.25 P = NA CI = 0.09–1.86

excluded before model fitting because it was an extreme value considered likely to reflect a transcription error. No observations were excluded as outliers from the analyses of the other cricket responses.

Regarding viper behaviour, binary behavioural variables (risk-taking and feeding success) were analysed with generalized mixed models (GLMMs) with binomial distribution and logit link. GLMM with Poisson distribution and log link was fitted for the variable number of strikes. The latency variables were log-transformed to achieve normal distribution, after which we applied linear mixed models (LMMs) for modelling. Importantly, when testing non-binary variables describing feeding behaviour, we excluded those observations where feeding was unsuccessful. Further, for testing swallowing time, we excluded observations with zero values. Error distribution and link function applied in the GLMMs were chosen after inspection of Q-Q plots of the model residuals. GLMMs and LMMs were all fitted similarly: behavioural variable in question was included as the response variable, while sex, cricket species (*A. domesticus vs. G. assimilis*; excluding the GLMM on risk-taking), environmental enrichment' (presence/ absence of a clump of grass in the enclosures) and size of the focal individual (snout-to-vent length measured before the start of the experiment; hereafter: SVL), were added as fixed effects. All two-way interactions between these variables were included in all models. We also included three-way interaction of sex × cricket × enrichment. Potential habituation effects were tested by including the order of trials (hereafter: time) in our models as fixed effects. Body temperature was added as a covariate to the models. The continuous fixed effects were standardized (mean = 0, standard deviation = 1) to aid the model fit. Random intercepts (random effect: individual identity; family identity) were added to the models. We simplified our models by inspecting parameter estimates of continuous-discrete interactions and removing the least significant interaction term until we got the minimal adequate model (Murtaugh, 2009). When a retained interaction involved a continuous predictor and a categorical factor, we fitted follow-up models separately within each level of the categorical factor to quantify the corresponding within-group relationships. These models retained the same response distribution, link function and random-effect structure as the global model, while terms involving the grouping factor were necessarily omitted. The interaction itself was evaluated in the global model; the treatment-specific models were used only to estimate, test and visualise the within-treatment relationships. We extracted the model's estimated marginal means using the *emmeans* package (Lenth, 2023). Fixed effects were tested by Wald's chi-squared tests and random effects by likelihood ratio tests. *P* values for the likelihood ratio tests were calculated following Zuur et al. (2009). All models were built using the R package *lme4* (Bates et al., 2015).

The *rptR* add-on package (Stoffel et al., 2017) was used to calculate repeatability (a statistical test for the presence and 'strength' of animal personality), i.e., consistent among-individual differences over time or across ecological contexts (see Réale et al., 2007; Niemelä and Dingemanse, 2018). Enhanced agreement repeatability (hereafter: eaR) estimates were calculated for every behavioural trait in the pooled sample, in females and males separately, and by environmental enrichment treatments separately. This method allowed us to fit improved models, in which the variance explained by fixed effects is calculated by the variance in the linear predictor, including the fixed effects' variance in the denominator (see Stoffel et al., 2017). Models were parameterised as described above, we built GLMMs for feeding success and risk-taking (binomial distribution, logit-link) and number of strikes (Poisson distribution, log-link), following the methods of Nakagawa and Schielzeth (2010), which utilise multiplicative overdispersion GLMM and using penalised quasi-likelihood (PQL) estimation for repeatability on the original scale. The significance of eaR estimates (i.e., for random terms) was provided by randomisation tests, giving robust measures of statistical significance in the case of non-Gaussian data (Nakagawa and Schielzeth, 2010). However, we report repeatabilities estimated on the underlying latent (link) scale as most original-scale repeatabilities are conditional for non-Gaussian data (Nakagawa and Schielzeth, 2010). Quantification of uncertainty for the variance explained by fixed effects (as for other variance components) was provided by parametric bootstrapping. LMMs were run to estimate repeatability for latency traits. Confidence Intervals (CIs) were calculated by nonparametric bootstrapping, while significance for eaR estimates is provided by likelihood ratio test, both sampled at each 1000th iteration. We report 95% CIs for better inference (Payton et al., 2003). All analyses were performed using R 4.3.1 (R Developmental Core Team, 2023).

3. Results

3.1. Cricket behaviour

In the novel-environment assay, our first GLM of the number of stops revealed a significant species × age interaction ($\chi^2 = 4.33$, df = 1, P = 0.04; Fig. S1a). Species-specific follow-up analyses indicated no difference between adults and nymphs in A. domesticus, whereas adult G. assimilis stopped less frequently than nymphs. In addition, larger crickets made fewer stops than smaller individuals, independently of age

Table 2
Repeatability estimates for feeding-related count and latency traits in juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*). A generalized linear mixed model (GLMM) with a Poisson error distribution and log link was fitted for the number of strikes, and repeatability was estimated on the underlying latent (log-link) scale. Linear mixed models (LMMs) were fitted to the log-transformed values of the remaining traits. Agreement repeatability (R), enhanced agreement repeatability (eaR), and their 95% confidence intervals (CIs) are shown.

Behaviour		All (N = 30)		Female (N = 15)		Male (N = 15)		Enrichment (N = 15)		No enrichment (N = 15)	
		R	eaR	R	eaR	R	eaR	R	eaR	R	eaR
Latency to first strike	Random effect	R = 0.07 P = 0.09 CI = 0–0.16	R = 0.06 P = 0.09 CI = 0–0.15	R = 0.06 P = 0.36 CI = 0–0.2	R = 0.06 P = 0.36 CI = 0–0.19	R = 0.06 P = 0.16 CI = 0–0.19	R = 0.06 P = 0.16 CI = 0–0.19	R = 0.06 P = 0.24 CI = 0–0.21	R = 0.06 P = 0.24 CI = 0–0.23	R < 0.001 P > 0.99 CI = 0–0.16	R < 0.001 P > 0.99 CI = 0–0.16
	Fixed effects		R = 0.08 P = NA CI = 0.07–0.22		R = 0.15 P = NA CI = 0.08–0.48		R = 0.02 P = NA CI = 0.02–0.21		R = 0.04 P = NA CI = 0.03–0.26		R = 0.19 P = NA CI = 0.09–0.55
Number of strikes	Random effect	R < 0.001 P > 0.99 CI = 0–0.04	R < 0.001 P > 0.99 CI = 0–0.03	R < 0.001 P > 0.99 CI = 0–0.1	R < 0.001 P > 0.99 CI = 0–0.10	R < 0.001 P > 0.99 CI = 0–0.04	R < 0.001 P > 0.99 CI = 0–0.06	R < 0.001 P > 0.99 CI = 0–0.05	R < 0.001 P > 0.99 CI = 0–0.04	R < 0.001 P > 0.99 CI = 0–0.12	R < 0.001 P > 0.99 CI = 0–0.11
	Fixed effects		R = 0.10 P = NA CI = 0.08–0.27		R = 0.1 P = NA CI = 0.05–0.5		R = 0.07 P = NA CI = 0.04–0.29		R = 0.15 P = NA CI = 0.07–0.44		R = 0.07 P = NA CI = 0.04–0.4
Time of food manipulation	Random effect	R < 0.001 P > 0.99 CI = 0–0.13	R < 0.001 P > 0.99 CI = 0–0.13	R = 0.04 P = 0.36 CI = 0–0.25	R = 0.04 P = 0.36 CI = 0–0.26	R = 0.02 P = 0.45 CI = 0–0.21	R = 0.02 P = 0.45 CI = 0–0.22	R < 0.001 P > 0.99 CI = 0–0.2	R < 0.001 P > 0.99 CI = 0–0.19	R < 0.001 P > 0.99 CI = 0–0.2	R < 0.001 P > 0.99 CI = 0–0.21
	Fixed effects		R = 0.09 P = NA CI = 0.07–0.27		R = 0.11 P = NA CI = 0.06–0.49		R = 0.1 P = NA CI = 0.05–0.42		R = 0.09 P = NA CI = 0.05–0.39		R = 0.12 P = NA CI = 0.07–0.53
Holding time	Random effect	**R = 0.16** **P < 0.01** **CI = 0–0.33**	**R = 0.15** **P < 0.01** **CI = 0–0.28**	R = 0.2 P = 0.17 CI = 0–0.49	R = 0.2 P = 0.17 CI = 0–0.48	R = 0.08 P = 0.29 CI = 0–0.26	R = 0.08 P = 0.29 CI = 0–0.27	**R = 0.24** **P < 0.01** **CI = 0–0.46**	**R = 0.24** **P < 0.01** **CI = 0–0.44**	R = 0.09 P = 0.25 CI = 0–0.31	R = 0.09 P = 0.25 CI = 0–0.34
	Fixed effects		R = 0.06 P = NA CI = 0.07–0.25		R = 0.05 P = NA CI = 0.05–0.52		R = 0.08 P = NA CI = 0.06–0.40		R = 0.11 P = NA CI = 0.07–0.49		R = 0.06 P = NA CI = 0.05–0.47
Swallowing time	Random effect	R < 0.01 P = 0.45 CI = 0–0.14	R < 0.01 P = 0.44 CI = 0–0.11	R = 0.2 P = 0.17 CI = 0–0.47	R = 0.2 P = 0.17 CI = 0–0.5	R = 0.05 P = 0.41 CI = 0–0.23	R = 0.08 P = 0.3 CI = 0–0.26	**R = 0.22** **P = 0.01** **CI = 0–0.44**	**R = 0.22** **P = 0.01** **CI = 0–0.42**	R = 0.09 P = 0.24 CI = 0–0.34	R = 0.09 P = 0.24 CI = 0–0.32
	Fixed effects		R = 0.10 P = NA CI = 0.08–0.26		R = 0.05 P = NA CI = 0.03–0.45		R = 0.08 P = NA CI = 0.04–0.38		R = 0.12 P = NA CI = 0.08–0.51		R = 0.06 P = NA CI = 0.05–0.46

Table 3
Results of GLMMs on risk-taking behavioural types of juvenile *Vipera ursinii rakosiensis*. Non-significant effects were gathered by back-substitution after the minimum model was reached.

	Risk-taking	
	χ^2 (df)	*P*
Fixed effect		
SVL	**4.63 (1)**	**0.03**
Sex	0.78 (1)	0.38
Enrichment	1.64 (1)	0.2
Time	**4.54 (1)**	**0.03**
Body temperature	0.38 (1)	0.54
SVL × sex	2.26 (1)	0.13
SVL × enrichment	0.23 (1)	0.63
Sex × enrichment	0.75 (1)	0.39
Random effect		
Individual	**16.87 (1)**	**< 0.001**
Family	**5.94 (1)**	**< 0.01**

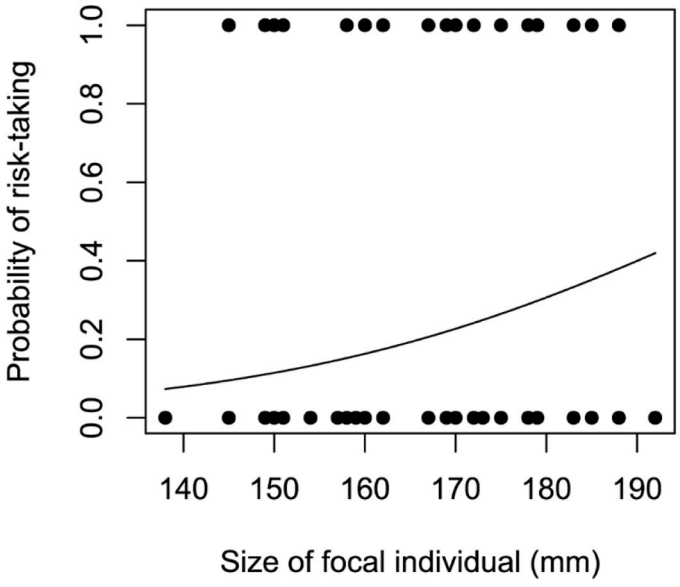

Fig. 1. The effect of size (snout-vent length, in mm) on risk-taking behaviour of juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*).

($\chi2 = 7.22$, df = 1, P = 0.008, Fig. S1b). Our second GLM on the total duration of stops revealed a significant effect of species ($\chi2 = 79.83$, df = 1, P < 0.001; Fig. S2): stop duration was significantly shorter in *A. domesticus* than in *G. assimilis*.

Regarding behaviour after a simulated attack, our third GLM on number of hops revealed a significant effect of species ($\chi2 = 7.71$, df = 1, P < 0.01, Fig. S3a): *A. domesticus* hopped significantly more than *G. assimilis*. We also found a significant effect of age ($\chi2 = 7.29$, df = 1, P < 0.01, Fig. S3b): nymphs hopped significantly more than adult crickets (irrespective of species). Our fourth GLM on duration of freezing behaviour revealed a significant effect of species ($\chi2 = 5.03$, df = 1, P = 0.03, Fig. S4): *G. assimilis* stays immobile after a simulated predator attack significantly longer than *A. domesticus*. Remaining nonsignificant results are shown in Supplementary Table S1.

3.2. Viper behaviour

Repeatability estimates for the tested behavioural traits are given in Tables 1 and 2. We found significant, but rather low repeatability (based on Bell et al., 2009) in risk-taking in the pooled sample (eaR = 0.1) and in all subgroups defined by sex and enrichment, except for the enriched group. In the enriched group, repeatability was not significant (see Table 2). Feeding success showed low, but significant repeatability in the pooled sample (eaR = 0.1), but not in the subgroups (see Table 2). Holding time showed low, but significant repeatability in the pooled sample (eaR = 0.16), and in the environmentally enriched group (eaR = 0.24), but not in the other groups (see Table 3). Swallowing time showed no significant repeatability in the pooled sample, while found to be significant in the environmentally enriched group (eaR = 0.22), but not in the other groups. In the rest of the variables (i.e., number of strikes, latency to first strike, time of food manipulation), repeatability was nonsignificant. Fixed effects generally explained only a fragment of phenotypic variation (Tables 1 and 2).

Our GLMM on risk-taking revealed a significant effect of SVL ($\chi^2 = 4.63$, df = 1, P = 0.03; Fig. 1): larger juveniles were more risk-prone. We found a significant time effect as well ($\chi2 = 4.54$, df = 1, P = 0.03; see Table 3): vipers became more risk-prone over time (data not shown). The global GLMM for feeding success revealed a significant interaction between SVL and enrichment treatement ($\chi^2 = 7.39$, df = 1, P < 0.01). Treatment-specific follow-up GLMMs showed that feeding success was not associated with SVL in enriched terraria ($\chi^2 = 0.4$, df = 1, P = 0.53; Fig. 2a), whereas feeding success increased with SVL in unenriched terraria ($\chi^2 = 4.15$, df = 1, P = 0.04; Fig. 2b). We also found a significant time effect ($\chi^2 = 8.16$, df = 1, P < 0.01): feeding success increased over time (data not shown). Our LMM on the latency to first strike revealed a significant effect of food type ($\chi^2 = 7.49$, df = 1, P < 0.01): vipers take significantly longer time to strike when they encounter *G. assimilis* compared to *A. domesticus* (Fig. 3a). Also, we found a significant effect of sex × food type interaction ($\chi^2 = 3.95$, df = 1, P = 0.046): female vipers take significantly longer time to strike to *G. assimilis* than *A. domesticus*, while no such difference existed between males (Fig. 3b). Our GLMM on number of strikes and our LMM on swallowing time revealed a significant effect of sex (number of strikes: $\chi^2 = 5.57$, df = 1, P = 0.02; swallowing time: $\chi^2 = 4.00$, df = 1, P = 0.04): males strikes more times and swallow for a longer duration than females (Fig. 4a,b). Our LMM on food manipulation time revealed a significant effect of trial order ($\chi^2 = 4.42$, df = 1, P = 0.04): vipers took progressively longer to manipulate their food over the course of the experiment (data not shown). Holding time was not affected by any of the explanatory variables. We found significant individual effects only for risk-taking, feeding success and holding time, and significant family effects for risk-taking and feeding success and number of strikes. For remaining non-significant effects, see Tables 3 and 4.

4. Discussion

Short-term survival upon release in a completely new environment is a crucial part of a reintroduction/translocation project's success (e.g. DeGregorio et al., 2017, Nguyen et al., 2023). The aim of our study was to quantify the between-individual behavioural variation using the modern animal personality approach in a captive-bred population of the highly endangered Hungarian meadow viper (*Vipera ursinii rakosiensis*) reared with the intensive method (headstarting strategy: individual housing in small terraria, food *ad libitum*, no wintering; targeting the largest amount of vipers with the largest body size achievable during a given time period). The rationale behind our aim was that high between-individual behavioural variation pre-release is necessary for short term survival when facing the unpredictable ecological challenges in nature, because such variation would allow the survival of the subset that matches the actual environmental situation. Later, the initial survivors could fine-tune their behaviour *via* behavioural plasticity and learning (e.g. Carstairs et al., 2019). Trade-offs between growth / survival and performance in natural situations have been recognised in captive breeding programs (e.g. Alberts, 2007; Tetzlaff et al., 2019a, Chandler et al., 2023), but our knowledge on behavioural variation of captive bred animals reared with a headstarting focus without complex enrichment or behavioural training is lacking. Because our assays were conducted under captive conditions before release, however, the observed patterns should be interpreted as characteristics of the

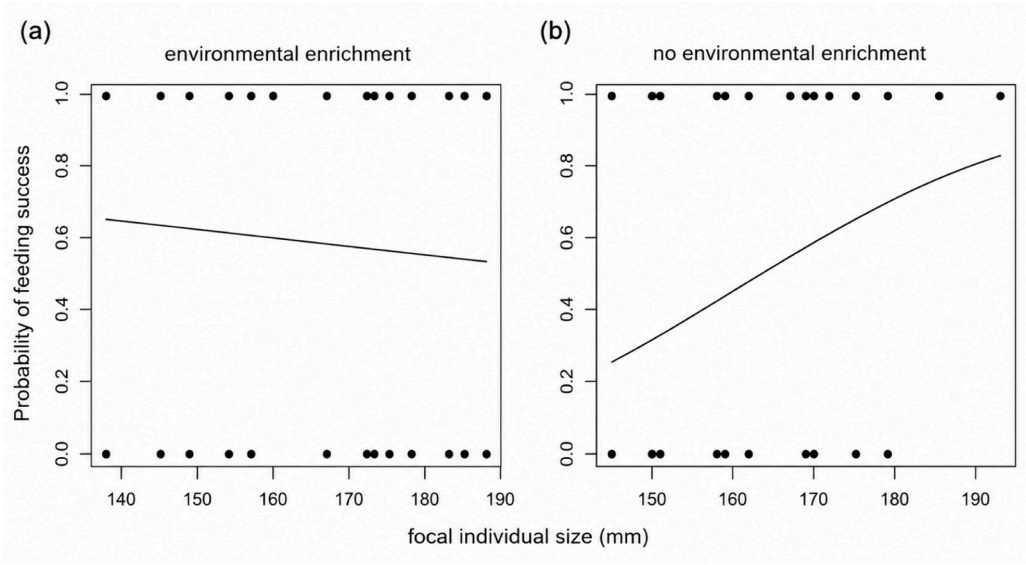

Fig. 2. Model-predicted probability of feeding success in relation to body size (snout–vent length, mm) in juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*) housed (a) with and (b) without environmental enrichment. Predictions were generated from the corresponding treatment-specific follow-up GLMMs. Points represent the observed binary outcomes.

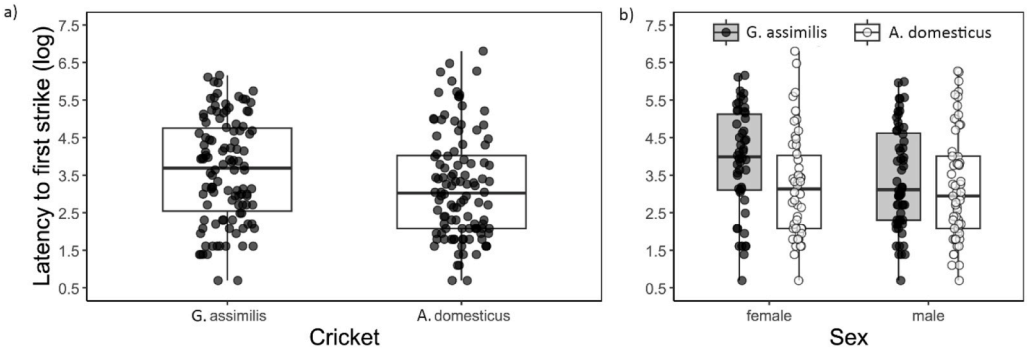

Fig. 3. The effect of food type (i.e., species of crickets) on latency to first strike of juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*) a) in general and b) between sexes. Box-plots representing the median (line inside box), 25th and 75th percentiles (lower and upper box boundaries, respectively), 10th and 90th percentiles (lower and upper error lines, respectively), circles representing raw data points.

captive-rearing environment rather than as direct evidence of post-release performance.

Studies in snakes likewise show that the expression and structure of personality can change during ontogeny and with social experience (Šimková et al., 2017; Skinner et al., 2022). According to the literature, it is possible that behavioural individuality is born with the studied individuals and later strengthens further during development, even in the lack of genetic and environmental variation (Bierbach et al., 2017; Laskowski et al., 2022). However, there is also evidence for behavioural individuality not developing without ecologically relevant environmental triggers (Urszán et al., 2015; 2018) and thus uniform and simple environments might have a strong canalising effect, resulting in uniform behaviour. Animal personality (i.e. consistent between-individual behavioural variation over time and ecological contexts or situations; Gosling, 2001; Sih et al., 2004; Sih and Bell, 2008; David and Dall, 2016; Kaiser and Müller, 2021) is typically tested by repeatability, which is the proportion of between-individual variation within total variation, making this framework suitable to assess between-individual variation. In our seven behavioural traits tested, we found three behaviours with significant repeatability in the total sample, and even in these cases, repeatability values were low (eaR: 0.1 – 0.19) when compared to the average repeatability of 0.37 reported for animals in general by the seminal meta-analysis from Bell et al. (2009). Previous studies on reptiles, conducted under conditions and timescales similar to ours, focused mainly on 'classic' behavioural traits, such as activity, exploration and boldness (e.g. Gibert et al., 2022). Here, we are able to make a comparison regarding reports on risk-taking, which indicates that although most estimates on this behavioural trait are rather high in reptiles (e.g., *Lampropholis delicata*, R = 0.24–0.37 [Polverino et al., 2023]; *Terrapene ornata*, R = 0.0–0.75 [Reed et al., 2023]; *Zootoca vivipara*, R = 0.43–0.58 [Mell et al., 2016]; *Tiliqua rugosa*, R = 0.27–0.51 [Payne et al., 2021]), reports of some studies are comparable to our findings (e.g., *L. delicata*, R = 0.09–0.15 [Littlewood et al., 2021]; *Iberolacerta cyreni*, R = 0.22 [Horváth et al., 2016]). Importantly, our estimates indicate low behavioural variation between our study vipers even when sexes and treatments were pooled. When male *vs.* female and enriched *vs.* unenriched groups were assessed separately, risk-taking had significant, but still low–modest (eaR: 0.12–0.23) repeatabilities in all, but the enriched treatment. This is an unexpected finding, because it shows that our enrichment treatment had a canalising effect. Previous enrichment studies in snakes have mainly examined mean behavioural responses, enclosure preference or cognitive performance. Enriched ratsnakes developed distinct behavioural profiles and showed greater behavioural adaptability than snakes housed under standard conditions (Almli and Burghardt, 2006), while environmental enrichment affected odour-discrimination performance in corn snakes (Nagabaskaran et al.,

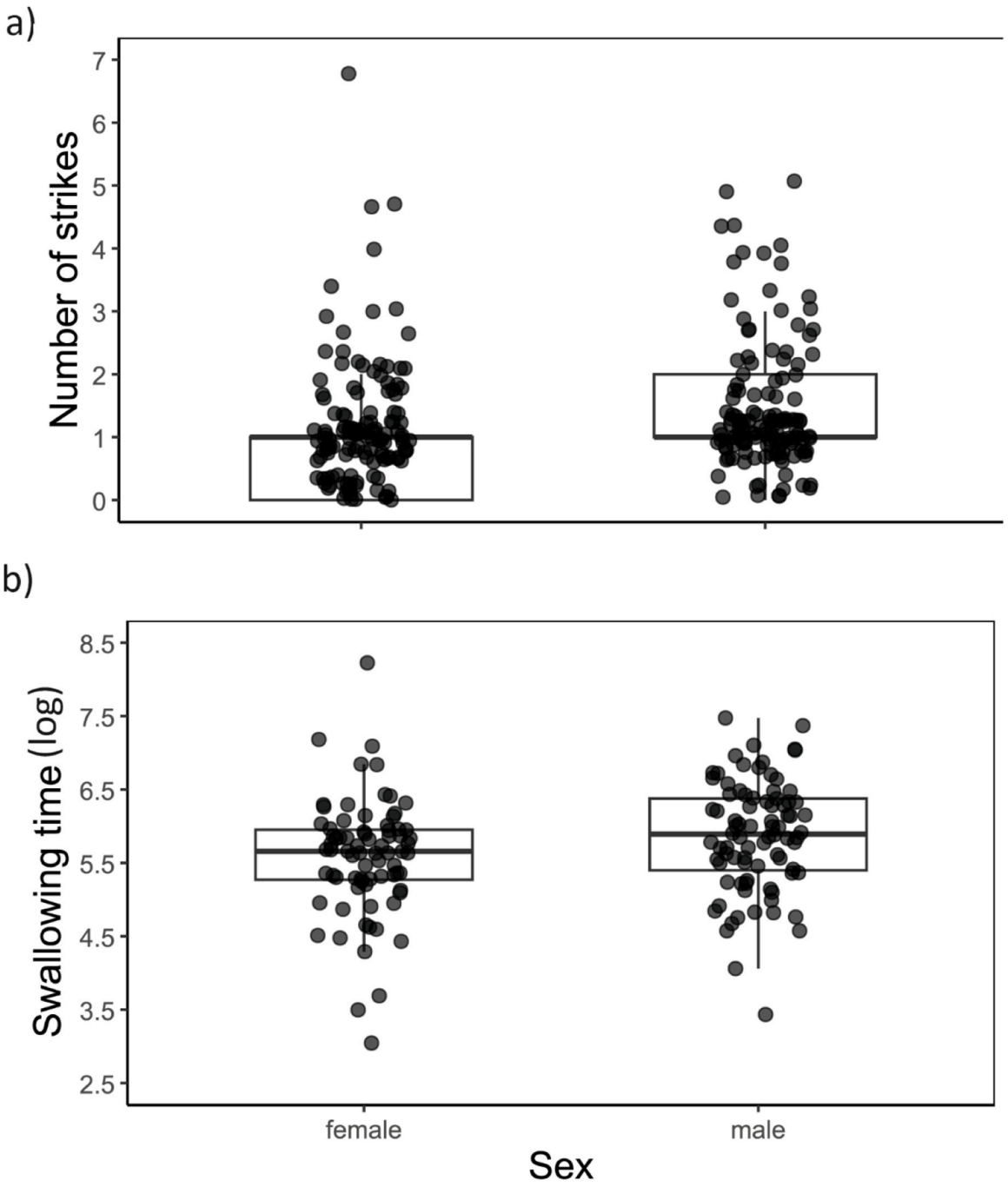

Fig. 4. Sex differences in a) number of strikes and b) swallowing time of juvenile Hungarian meadow vipers (*Vipera ursinii rakosiensis*). Box-plots representing the median (line inside box), 25th and 75th percentiles (lower and upper box boundaries, respectively), 10th and 90th percentiles (lower and upper error lines, respectively), circles representing raw data points.

2021). Western hognose snakes also preferred enriched conditions, although individual differences in enrichment preference were unrelated to boldness (Nagabaskaran et al., 2022). Our results extend this literature by showing that even minimalist enrichment may alter the magnitude of consistent among-individual behavioural variation and that the direction of this effect can differ among behavioural traits. It is possible that adding a clump of dry grass to the minimalist environment induced a plastic response with a single optimal risk-taking strategy, masking the genetically determined differences. In contrary to this, only the enriched group showed significant repeatability in holding time and swallowing time, producing higher values, translating to a modest repeatability (eaR: 0.22 *vs.* 0.24, respectively). In these cases, enrichment had a diversifying effect on highly relevant components of feeding behaviour. The lacking or weak between-individual behavioural variation suggests that prolonged intensive headstarting may have an overall canalising effect.

Despite patterns reported in clonal poecilid fish (Bierbach et al., 2017; Laskowski et al., 2022), population bottlenecks and inbreeding are generally expected to reduce phenotypic variation (Fowler and Whitlock, 1999; Bouzat, 2010), providing an alternative explanation to the patterns we report, assuming low genetic diversity in our captive population. However, genetic diversity in our population ($H_{obs} = 0.54$; unpublished data by Szabó 2026) is comparable to what is seen in wild populations of Hungarian meadow vipers and closely related other (sub)

Table 4
Results of models on behavioural types of traits describing feeding behaviour in juvenile *Vipera ursinii rakosiensis*. Significant effects are bolded. Non-significant effects were gathered by back-substitution after the minimum model was reached.

	Feeding success		Latency to first strike		Number of strikes		Time of food manipulation		Holding time		Swallowing time	
	χ^2 (df)	*P*	χ^2 (df)	*P*	χ^2 (df)	*P*	χ^2 (df)	*P*	χ^2 (df)	*P*	χ^2 (df)	*P*
Fixed effect												
SVL	1.94 (1)	0.16	1.47 (1)	0.23	2.18 (1)	0.14	2.1 (1)	0.15	0.19 (1)	0.66	1.09 (1)	0.29
Sex	2.37 (1)	0.12	2.39 (1)	0.12	**5.57 (1)**	**0.02**	2.51 (1)	0.11	1.87 (1)	0.17	**4.00 (1)**	**0.04**
Cricket	1.45 (1)	0.23	**7.49 (1)**	**< 0.01**	1.02 (1)	0.32	1.00 (1)	0.32	2.55 (1)	0.11	1.49 (1)	0.22
Enrichment	0.46 (1)	0.49	0.71 (1)	0.4	0.04 (1)	0.86	0.003 (1)	0.96	< 0.001 (1)	0.98	0.10 (1)	0.75
Time	**8.16 (1)**	**< 0.01**	0.01 (1)	0.91	3.09 (1)	0.08	**4.42 (1)**	**0.04**	0.01 (1)	0.92	0.21 (1)	0.64
Body temperature	0.09 (1)	0.77	1.86 (1)	0.17	< 0.01 (1)	0.96	1.57 (1)	0.21	1.49 (1)	0.22	0.16 (1)	0.69
SVL × sex	0.02 (1)	0.88	1.21 (1)	0.27	3.09 (1)	0.08	0.71 (1)	0.39	0.09 (1)	0.75	3.52 (1)	0.06
SVL × cricket	0.003 (1)	0.96	2.81 (1)	0.09	1.93 (1)	0.17	0.55 (1)	0.46	0.52 (1)	0.47	0.72 (1)	0.39
SVL × enrichment	**7.39 (1)**	**< 0.01**	0.79 (1)	0.38	2.05 (1)	0.15	1.33 (1)	0.25	0.06 (1)	0.81	0.03 (1)	0.85
Sex × cricket	0.17 (1)	0.68	**3.95 (1)**	**0.046**	1.68 (1)	0.19	1.75 (1)	0.19	2.56 (1)	0.11	1.91 (1)	0.17
Sex × enrichment	0.79 (1)	0.37	0.73 (1)	0.39	0.07 (1)	0.79	0.89 (1)	0.34	0.09 (1)	0.76	3.15 (1)	0.08
Cricket × enrichment	1.27 (1)	0.26	2.22 (1)	0.14	0.77 (1)	0.38	0.35 (1)	0.55	0.85 (1)	0.36	0.02 (1)	0.88
Sex × cricket × enrichment	0.32 (1)	0.57	1.21 (1)	0.27	< 0.01 (1)	0.93	0.06 (1)	0.81	1.24 (1)	0.27	0.77 (1)	0.38
Random effect												
Individual	**12.91 (1)**	**< 0.001**	0.3 (1)	0.29	0.66 (1)	0.21	< 0.001 (1)	> 0.99	**3.06 (1)**	**0.04**	< 0.001 (1)	> 0.99
Family	**10.39 (1)**	**< 0.001**	< 0.001 (1)	> 0.99	**5.59 (1)**	**< 0.01**	0.86 (1)	0.18	< 0.001 (1)	> 0.99	< 0.001 (1)	> 0.99

species with natural populations (H_{obs} (CI) = 0.44 [0.16–0.83]; Vörös et al., 2022), making this explanation unlikely. In our models, the individual effect was significant only for risk-taking, feeding success and swallowing time, also pointing towards the minimal between-individual variation. Likewise, family effect was significant only for risk-taking and feeding success, suggesting that genetic and/or maternal influences on behavioural variation were generally weak.

Body size had a positive effect on risk-taking, consistent with previous findings in hatchling snakes (Mayer et al., 2016). Our risk-taking variable combined the tendency to escape and the tendency to engage in antipredator defensive aggression, together describing a tendency of vipers holding their ground, where larger body size can be an advantage in a fight (Horváth et al., 2020). Body size also positively affected feeding success, but only in the absence of enrichment. The fact that size has a positive effect on feeding success in a predatory species that relies on successfully biting its prey and later swallowing it in one piece is not surprising (Madsen and Shine, 2002). But how did our simple enrichment treatment eliminate this common pattern? We can only speculate about that. The added clump of dry grass helped either successfully carrying out an ambush predatory attack and envenoming the prey or by providing more grip in manipulating and swallowing the dead prey for smaller vipers. The latter seems unlikely; hence, we suggest that dry grass helped successful strikes by somehow affecting the behaviour of the predator, ie. giving more confidence for the ambush predation or simply slowing down the movement of the prey. At any rate, it draws attention to how such a simple environmental modification can aid successful feeding. Although our dry-grass manipulation was considerably simpler than the enrichment treatments used in previous studies, structural or naturalistic enrichment has similarly been associated with changes in activity, behavioural diversity and other welfare-related behaviours in captive snakes (Spain et al., 2020; Hoehfurtner et al., 2021). Responses may nevertheless depend on the species, behavioural trait and type of enrichment (Rosier and Langkilde, 2011); Krishnan et al. (2022) reported short-term behavioural responses to several enrichment items across multiple snake species, but most changes were not statistically significant. Cross-taxonomic evidence from captive-reared fishes further shows that enrichment can influence cerebellar development (Kihslinger and Nevitt, 2006), reduce maladaptive risk-taking in conservation-reared salmon (Roberts et al., 2011), and enhance locomotor performance (Bergendahl et al., 2017). Recent snake-specific evidence also indicates that enrichment during development can affect brain morphology, as enriched western hognose snakes had larger brain volumes than snakes reared under standard conditions (Nagabaskaran et al., 2025), although the functional behavioural consequences of this anatomical difference remain unknown. We found no direct enrichment effects in any of the studied behaviours, despite its effects on between-individual variation on risk-taking and swallowing time. This pattern draws attention to the fact that an environmental factor can have an ecologically/evolutionarily relevant effect on variance besides or even without inducing shifts in means (Kralj-Fišer et al., 2025; Biró et al. 2026).

Latency to first strike depended on prey species, vipers struck faster on *A. domesticus* than on *G. assimilis*. This effect showed sex-specificity: females were more hesitant to strike on *G. assimilis*, meanwhile males were striking independently of prey type. The prey type effect is in line with what we found in the comparison of the prey species' behaviour: *A. domesticus* stops less and for shorter time than *G. assimilis* in a new environment, aiding vipers in detecting their moving prey. Further, *G. assimilis* has stronger mandibles and perhaps young vipers are more cautious with them, therefore they spend more time finding the perfect ambush moment. Since success in foraging in the natural environment is a key difference between captive-bred and wild snakes (Roe et al., 2015) and we found that intuitively similar prey species ("small crickets") might have significant differences in their antipredator tactics affecting our vipers feeding behaviour, we recommend rearing snakes with as variable prey as possible for increasing their survival upon release.

Finally, we found two cases of sexual dimorphism: males' swallowing time was longer than that of females, and males struck more times than females. Meanwhile, there was no evidence of a marked difference in body size or growth from birth until the start of the experiment or during the observation period (SVL: $F = 2.43$, $df = 1, 29$; $P = 0.13$; body mass: $F = 0.32$, $df = 1, 17.26$, $P = 0.58$). Hence, we cannot interpret this pattern based on the available data; for instance, it could be explained by sex differences in venom efficacy or prey-handling efficiency. The time of assessment affected three behaviours: risk-taking, feeding success, and food manipulation time all increased over the course of the experiment, probably representing habituation in the former two and sensitization in the latter (Blumstein, 2016).

5. Conclusion

Taken together, we found low to negligible between individual behavioural variation in captive-bred Hungarian meadow vipers reared with pure headstarting focus. Directly introducing them to the wild (hard release) might therefore be a suboptimal strategy, since no prior experience with natural challenges coupled with minimal pre-existing behavioural variation could make them more vulnerable under certain post-release conditions. We note that in the Hungarian Meadow Viper Conservation Program, we employ at least one full season long acclimation period in large seminatural outdoor enclosures before release, and in all release sites some level of temporary or permanent protection measures (predator exclusion fencing or netting) are helping the realisation of 'soft' release (Tetzlaff et al., 2019b). Our findings suggest that the suitability of pure headstarting rearing strategy combined with hard release (Tetzlaff et al., 2019b) warrants further evaluation before this approach can be recommended for Hungarian meadow vipers, which is in line with observations of other snake translocations (Choquette et al., 2023). Establishing the optimal strategy where the tradeoffs between vipers' survival, number and size maximised by headstarting *vs.* providing ecologically relevant environmental challenges (both biotic and abiotic) and antipredator training in the expense of less and smaller vipers is considered and finding the optimal combination requires further studies that are currently ongoing. Another significant finding of our study is that even minor enrichments of the minimalist rearing environment (adding a clump of dry grass, providing two, intuitively similar prey types instead of one) could affect the between-individual behavioural variation and also the mean behaviours. This draws attention to the often-neglected potential of minor changes in rearing environment (being simple, cost-free additions or logistic, intuitively irrelevant alterations) having significant and unpredictable biological effects. We recommend that even for pure headstarting protocols, adding any simple form of physical enrichment or introducing variation in food should be considered.

CRediT authorship contribution statement

Bálint Halpern: Writing – original draft, Investigation, Funding acquisition. **Gergely Horváth:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Gergely Szövényi:** Writing – review & editing, Validation. **Gábor Herczeg:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2026.107162.

Data availability

Data and detailed code for the analyses can be found at the Open Science Framework (OSF): https://osf.io/hdwn7/overview?view_only=54647333dc2a40d2991740c7d7197255

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