European green lizard (*Lacerta viridis*) personalities: linking behavioural types to ecologically relevant traits at different ontogenetic stages

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Abstract

Consistent individual differences within (animal personality) and across (behavioural syndrome) behaviours became well recognised during the past decade. Nevertheless, our knowledge about the evolutionary and developmental mechanisms behind the phenomena is still incomplete. Here, we explored if risk-taking and exploration were consistent and linked to different ecologically relevant traits in wild-caught adult male European green lizards (*Lacerta viridis*) and in their 2-3 weeks old laboratory-reared offspring. Both adults and juveniles displayed animal personality, consistency being higher in juveniles. We found correlation between risk-taking and exploration (suggestive of a behavioural syndrome) only in adults. Juveniles were more explorative than adults. Large or ectoparasite-free adult males were more explorative than small or parasitized males. Juvenile females tended to be more risk-taking than males. Behaviour of fathers and their offspring did not correlate. We conclude that European green lizards show high behavioural consistency and age is an important determinant of its strength and links to traits likely affecting fitness.

Keywords: animal personality; behavioural syndrome; temperament

1.1 **Introduction**

Behaviour is one of the most plastic quantitative traits in animals (West-Eberhard, 2003). However, between-individual behavioural variation in the same context and situation became accepted as a valid and biologically important phenomenon lately (Gosling, 2001; Sih et al. 2004a, 2004b; Smith and Blumstein, 2008; Stamps, 2007; Wilson, 1998). Individual consistency within (repeatability in statistical terms) and across (correlation in statistical terms) different behaviours is called animal personality and behavioural syndrome, respectively (Garamszegi and Herczeg 2012; Herczeg and Garamszegi 2012; Jandt et al. 2014). Behavioural consistency could be seen as a disadvantageous trait, since it constraints plasticity and thus limits the individual behavioural repertoire, which might be maladaptive in variable environments and certain contexts (Bell, 2005, 2007; Dzieweczynski and Hebert, 2013; Sih et al. 2012, 2004a). Thus, for instance, an individual aggressive towards conspecific competitors remains aggressive in other contexts (e.g. towards predators / during mating) when this behaviour is likely to decrease fitness (e.g. Berning et al. 2012). Hence, one of the most important aims of current evolutionary behavioural ecology is to understand the ultimate and proximate mechanisms that resulted in the emergence of behavioural consistency.

Estimating individual quality or ‘true’ fitness is notoriously hard, and thus linking animal personality to individual quality is not straightforward in most possible models. Further, individual quality could mean different things to different researchers, and even proxies of quality might depend on the conceptual framework of the study (Wilson and Nussey, 2010; Bergeron et al. 2011). One possible solution for non-model species is to focus on ecologically relevant traits with proven, or at least highly probable, link to fitness. Establishing the relationships between them and personality would be relevant for understanding how behavioural consistency emerges in nature.

European green lizard (*Lacerta viridis*) is an excellent candidate for such a study. Males have ultraviolet-blue nuptial throat colouration that is a multiple honest signal and has important roles in both intra- and intersexual selection (Bajer et al. 2010, 2011, 2012; Molnár et al. 2012, 2013; Vaclav et al. 2007). Other morphological traits have also been shown to be important determinants of lizards' fitness, like the number and symmetry of femoral pores (Lopez et al 2002) or the size of head (Gvozdik and Van Damme, 2003; Roughgarden, 1974; Vitt, 2000). One can also include traits that are known to be strongly connected to fitness in almost any species, like body size or body condition (Peters 1983; Roff 1992; Stearns 1992). Hence, it is easy to measure a number of ecologically relevant traits that are highly probable to be linked to fitness in *L. viridis*. Reptiles are neglected in the study of behavioural consistency when compared to birds, mammals or fish (Garamszegi et al. 2012; Smith and Blumstein, 2008). Hence, by using a lizard as a model, not only general questions about animal personality can be tested, but important data on behavioural consistency on terrestrial vertebrate taxa can be gathered.

In the present paper, we studied the behavioural consistency of *L. viridis*. Our main questions were as following. (i) Are animal personality / behavioural syndrome present in the species? (ii) Are there correlations between fitness-linked traits and behavioural type? (iii) Are personality / syndrome structures age-dependent? (iv) Are behavioural traits heritable? To this end, we performed behavioural experiments to quantify exploration and risk-taking of adult males and their F1-generation offspring repeatedly and under standardized laboratory settings.

We predicted males of higher-quality (having more intensive sexual signals, being larger, in better body condition, etc. during the reproductive season) being faster explorers and taking more risk than low quality males. Our predictions were similar in juveniles. In addition, we assumed that behavioural type has a heritable component.

1.2 **Material and methods**

1.2.1 *Study animals*

70 adult males and 35 adult females were captured by noosing, at the beginning of the mating season, late April in 2011. The population from which the animals are originating can be found near Tápiószentmárton, Hungary (47°20’25”N, 19°47’11”E). The study site is a forest-scrubland mosaic segmented with dry grasslands. After capturing, males were weighed with a digital scale to the nearest 0.1g; their snout-vent length (SVL), head length (HL), head width (HW), head height (HH), and tail length (TL) were measured to the nearest 0.1mm with a digital calliper. The number of femoral pores of the left and right hind leg and the number of ectoparasites (*Ixodes* spp.) on the body surface were also counted. The colour of the males’ nuptial throat patch was also measured (see below). The male and female lizards were housed individually in plastic boxes (60 cm × 40 cm × 30 cm, length, width, height, respectively) at a temperature-controlled facility of the Eötvös Loránd University. Before the onset of the experiment, the animals were acclimated for 3-5 days. During the captivity, lizards were fed *ad libitum* with crickets (*Gryllus domesticus*) and mealworms (*Tenebrio molitor*) dusted with vitamin powder (ReptoCal, TETRA, Germany). Water was provided *ad libitum*.

After the male and female lizards were acclimated, mate-choice tests were performed following Bajer et al. (2010) for other scientific purposes. After these tests, every female was allowed to mate with one of the males she has chosen from. After the copulation, males were removed and females were kept in their home boxes till they laid their eggs into moist soil provided in their home boxes. The eggs were incubated during ca. 60 days in 28-30 C° using air incubators (Hova Bator 1602n, Interhatch, UK). Thirty-five females laid 172 eggs from which 98 juveniles hatched.

Juveniles were measured at the age of one day. Body weight (BW) was measured using a digital scale to the nearest 0.1g. Snout-vent length (SVL), head length (HL), head width (HW), head height (HH), tail length (TL), front leg length (FLL) and hind leg length (HLL) were measured with digital calliper to the nearest 0.1mm. The sex of the hatchlings was determined by gently pressing out their genitals by hand. Before testing, juveniles were kept in plastic boxes (15 cm × 20 cm × 15 cm, respectively). They were fed with small crickets dusted with vitamin powder and water was provided *ad libitum.*

The animals did not show any signs of health problems or injuries during the experimental period and were released at their own or at their mothers' initial capturing location in the field at the end of experiment.

1.2.2 *Spectrometry of colouration*

Reflectance of the lizards' throat was measured with a spectrometer type Ocean Optics 2000, complete with a Mini-D2 deuterium-halogen lamp and a R700-4 bifurcated fiber-optic probe (Ocean Optics, Inc., Dunedin, Florida). We used an RPH-1 probe holder to avoid all possible light from the environment to influence our measurement. The illuminated area was 6 mm in diameter and it was constant 3mm distance and 90° angle with the surface. To get a representative sample of the uneven throat coloration, three scans were taken on random spots of the ventral side of the throat patch. The probe was removed between each scan. We used the mean of the three measurements for the analyses. Reflectance was calculated relative to a WS-1 Diffuse Reflectance Standard as a white standard (reflectivity: >98% at 250-1500 nm wavelengths) using the SpectraSuite software (Ocean Optics, Inc., Dunedin, Florida, USA). Measurements were taken across 320-700 nm wavelengths. As we are not aware of the visual system of *L. viridis*, we used this as the broadest range of wavelengths known to be visible to lizards. White reference was standardized between each individual and dark reference (= no incoming light to the sensor) was also re-measured periodically to avoid problems with spectrophotometer 'drift' (Endler and Mielke, 2005). We calculated three variables describing throat colour (following Bajer et al. 2012, 2011, 2010; Molnár et al. 2013, 2012): (1) brightness: the total reflectance from 320 and 700 nm; (2) UV chroma (relative UV intensity): the percent of reflectance measured in the UV range compared to total reflectance ($R_{320-400}/R_{320-700}$); and (3) blue chroma (relative blue intensity): the percent of reflectance in the blue range compared to total reflectance ($R_{400-490}/R_{320-700}$).

1.2.3 *Behavioural experiment*

We measured two behavioural traits, risk-taking and novel area exploration, which were found to generally to represent functionally different personality domains (Garamszegi et al. 2013). The behavioural tests were performed with 70 adult male and 97 juvenile lizards (at the age of 14-21 days). During the experiment, observations were made from a blind and the movement of the animals was scored. Each behavioural test was performed twice. Four days elapsed between the subsequent tests.

The experiments were performed in arenas made of fibreboard (100 cm × 100 cm × 25 cm [in the case of adult males] and 60 cm × 60 cm × 25 cm [in the case of juveniles]; length, width, height, respectively) with a transparent plastic bottom. We placed a grid (5cm × 5cm) on white paper under the bottom of the arena. A smaller opaque box (starter-box; 12 cm × 6 cm × 5 cm, (length, width, height, respectively) with string-operated sliding door was placed in the middle of the test arena. First, we placed the test individual into the closed starter box and let it acclimatize. After three minutes, we opened the sliding door and measured the time (i) till the lizard's head (TTH) and (ii) full body (from head to the cloaca region; TTB) emerged from the shelter. Willingness to leave a refuge in a potentially dangerous environment is often used as a risk-taking proxy (e.g. Brown et al., 2007; Brydges et al., 2008; Hedrick and Kortet 2012), thus we used TTH and TTB to describe risk-taking. If a lizard's head did not emerge for five minutes or its full body did not leave the refuge in the subsequent five minutes, the trial was stopped. According to our personal observations, animals that do not emerge during this period will almost always stay in the refuge for a long time. Because individuals that do not leave the refuge are actually expressing one extreme of the studied behaviour, we did not exclude them from estimating risk-taking. However, simply giving them the maximum score would be misleading for calculating consistency. Therefore, we rank transformed the data and gave these individuals a random rank at the end of the distribution (instead of all having the same rank), variation being based on the number of these individuals. Then, we normalized the data using the Rankit procedure (Solomon and Sawilowsky 2009). After a test individual left the starting box, we followed its movements using the grid to estimate exploration. We counted how many times an individual moved between the grids (GRID) during a five minutes interval. Starter box was not removed from the arena during the exploration test. We washed the arena and the starter box thoroughly with detergent after every test to remove chemical stimuli that may have left by the last individual.

1.2.4 *Statistical analysis*

Because we had two repeated estimates for every individual, we used the Spearman correlation coefficients to test for repeatability (i.e. animal personality). This was done for the three behavioural variables separately in adults and juveniles. To compare the correlation coefficients, we applied Fisher's r-to-z transformation, which gives satisfying results on Spearman correlation coefficients (Myers and Sirois, 2006). To test for correlations between repeatable behaviours (i.e. behavioural syndromes) we ran Spearman rank correlations between behavioural types represented by the individual mean values. Besides significance testing, we also bootstrapped (1000 runs) the correlation coefficients in both cases to get a 95% confidence interval around them. Whenever behavioural types correlated across individuals, we ran a Principal Component Analysis (PCA) on the correlated variables to gather new variables describing behavioural type. This procedure was used both within (TTH and TTB, both representing risk-taking) and between (TTH, TTB and GRID; representing risk-taking and exploration, respectively) the functionally different behaviours (see Results).

To test the link between individual behavioural type and sexual signal intensity or other fitness-related traits in adults, we ran separate General Linear Models (GLMs) for every behaviour. Behavioural types (exploration, risk-taking and the composite boldness; see Results) were the response variable and SVL, body condition (relative BW; 'relative' traits were estimated as regression residuals from the given variable – SVL regressions), relative head size, ectoparasite infection, number of femoral pores, asymmetry of femoral pores, throat brightness, UV chroma and blue chroma the predictors. Behavioural type was represented by individual means, using only repeatable behaviours (i.e. behaviours where lizards showed personality). To estimate exploration behavioural type, only data of those individuals could be used that actually emerged from the refuge in both rounds (N = 36). To characterise head size, we ran a PCA on HL, HW and HH. We got a single PC with strong positive loadings (proportion of variation explained = 94%; factor loadings > 0.97). Because previous results supported left-biased directional asymmetry in femoral pore numbers (Molnár et al. 2012) we used the signed difference (right side – left side) to describe asymmetry. The distribution of ectoparasite counts was heavily zero-inflated, hence, we transformed the data into binary, i.e. infected or not.

To test the link between individual behavioural types and other individual traits in juveniles, we ran separate General Linear Mixed Models (GLMMs) with behavioural types as response variables, SVL, body condition, relative head size, relative front leg length, relative hind leg length and relative tail length as continuous predictors and family as a random effect to account for the non-independence of individuals within a single family. To characterise head size we ran a PCA on HL, HW and HH. We got a single PC with strong positive loadings (proportion of variation explained = 59%; factor loadings > 0.73).

Both the GLMs and GLMMs were initially built with all predictor variables without interactions. Then we applied a backward stepwise model selection based on the $P < 0.05$ criterion, removing the nonsignificant effects in a decreasing order. We are aware of the numerous model selection approaches, but the one based on the P-value is considered as a conservative one (Murtaugh, 2009). We chose to use residuals corrected for SVL in the models (i.e. the ‘relative’ traits) instead of raw variables to avoid multicollinearity.

We also tested for the potential effect of habituation and if it differed between adults and juveniles. To this end, we ran three separate repeated measures GLMs with the subsequent measures of each behavioural variable as repeated measures and age (adult *vs*. juveniles) as fixed factor, including the interaction.

To estimate the heritability of the behavioural type, we ran father-offspring regressions (Lynch and Walsh, 1998). We estimated the heritability only for male offspring and for all offspring (including males and females) as well. In the heritability analyses we could only consider families with at least 2 offspring. This left us with 23 families out of the original 26 in the ‘all sexes’ method and 16 families in the ‘only males’ method.

We note that in the analyses of juveniles we could correct for the non-independence of families in the GLMMs, but not in the habituation-testing GLMs. However, as the number of families was fairly high, we are confident that it is not a significant problem. All analyses were performed with SPSS 18 (PASW Statistics 18) for Windows (SPSS Inc., Chicago, IL, USA).

1.3 **Results**

1.3.1 *Behavioural consistency*

In adults, only TTH and GRID was repeatable, while in juveniles all three behaviours showed high repeatability (Table 1). However, adult TTB was also marginally significant ($P = 0.052$; Table 1), and thus considering the arbitrary nature of the $P = 0.05$ criterion (e.g. Nuzzo 2014) we treated it as a valid behavioural trait describing personality. Our pair-wise comparisons of correlation coefficients between adult and juvenile lizards showed a trend: juvenile behaviour was more repeatable than adult behaviour (Table 1). Our repeated measures GLMs revealed that habituation patterns differed between adults *vs*. juveniles (age) and between first *vs*. second measurement (time) and also between behaviours. We found that time had a significant effect on TTH (age: $F_{1,165} = 0.003$, $P = 0.96$; time: $F_{1,65} = 10.7$, $P = 0.001$; age × time: $F_{1,165} = 2.59$, $P = 0.11$): lizards became more risk-taking in the second round (Fig. 1a). None of the variables affected TTB significantly (age: $F_{1,165} = 0.006$, $P = 0.94$; time: $F_{1,165} = 2.63$, $P = 0.11$; age × time: $F_{1,165} = 3.57$, $P = 0.06$) (Fig. 1b). Note however, that the interaction of age and time was marginally significant, suggesting that adult males become more risk-taking in the second round (data not shown). In GRID, only age was significant (age: $F_{1,112} = 26.85$, $P < 0.001$; time: $F_{1,112} = 0.29$, $P = 0.59$; age × time: $F_{1,112} = 1.16$, $P = 0.28$), showing that juveniles were more explorative than adults (Fig. 1c).

In adults, there was a positive correlation between risk-taking (TTH and TTB) and exploration (GRID), indicative of a behavioural syndrome (Table 2). In juveniles, only the two measures of risk-taking (TTH and TTB) were positively correlated, while they were clearly separated from exploration (GRID) (Table 2). Correlation coefficients from TTB-GRID correlations differed significantly between adults and juveniles, adults having higher coefficient (Table 2).

The PCA ran on TTH and TTB resulted in one PC in both adults (proportion of variation explained = 87%; factor loadings = 0.93) and juveniles (proportion of variation explained = 79%; factor loadings = 0.89) representing a gradient from risk-averse to risk-taking individuals. These PCs were used to describe the risk-taking behavioural types in both ontogenetic groups. Individual mean GRID was used as the variable describing the exploration behavioural types in both ontogenetic groups. The PCA ran on TTH, TTB and GRID in adults resulted in one PC (proportion of variation explained = 62%; factor loadings > 0.76) describing a gradient from risk-averse and slow explorer individuals to risk-taking and fast explorer individuals. We treat this PC as one placing our study individuals along the general shyness-boldness continuum, providing a complex boldness behavioural type.

1.3.2 *Behaviour and fitness-linked traits*

In the GLMs on adult behavioural type, we found that exploration increased with increasing SVL ($F_{1,35} = 6.69$; $P = 0.014$) and decreasing parasite infection ($F_{1,35} = 6.63$; $P = 0.015$). Large males and males without ectoparasites were faster explorers than small or parasitized males (Fig. 2 and Fig. 3). None of the other explanatory variables affected adult behaviour (Supplementary Table 1). In juveniles, the GLMMs revealed a marginally significant effect of sex on risk-taking ($F_{1,89.5} = 3.84$; $P = 0.053$), females taking more risk than males (Least Squares means ± Standard Error; males: 0.19 ± 0.14; females: -0.2 ± 0.15). The family effect was significant in the explorative behaviour of the juveniles ($Z = 2.05$; $P = 0.04$). None of the other explanatory variables affected juvenile behaviour. (Supplementary Table 2).

1.3.3 *Heritability*

None of the behavioural traits showed significant heritability neither when only the male offspring (TTH: $R^2 = 0.016$, $F_{1,15}= 0.23$, $P= 0.64$; TTB: $R^2 = 0.08$, $F_{1,15}= 1.19$, $P= 0.29$; risk-taking PC: $R^2 < 0.001$, $F_{1,15}= 0.007$, $P= 0.94$; exploration: $R^2 = 0.019$, $F_{1,5}= 0.08$, $P= 0.8$), nor when all offspring were considered (TTH: $R^2 = 0.002$, $F_{1,22}= 0.05$, $P= 0.82$; TTB: $R^2 = 0.04$, $F_{1,22}= 0.89$, $P= 0.36$; risk-taking PC: $R^2 = 0.037$, $F_{1,22}= 0.8$, $P= 0.38$; exploration: $R^2 = 0.25$, $F_{1,8}= 2.28$, $P= 0.18$)

1.4 **Discussion**

The most salient finding of the present study is that the behavioural consistency of *L. viridis* has age-dependent strength. Regarding within-behaviour consistency, i.e. animal personality, both adult males and juveniles were consistent in risk-taking and exploration, juveniles showing significantly higher consistency than adults in both personality traits. On the other hand, across-behaviour consistency, i.e. behavioural syndrome, showed the opposite trend: risk-taking and exploration correlated only in adults. Lab-born naive juveniles were more explorative than wild-caught adults. We could not detect any correlation between the intensity of the male sexual signal and behavioural type. However, larger males and males without ectoparasites were faster explorers than smaller or infected males. In juveniles, females tended to take more risk than males. We could not detect significant heritability of behavioural type based on father-offspring regressions.

We found that risk-taking and exploration are repeatable both in adult males and juveniles. The repeatability of behaviour is generally low, approximately around 0.3-0.4 (Bell et al. 2009). Hence, behavioural consistency of *L. viridis* ($r_s = 0.37 – 0.84$) is particularly high. Given that naive juveniles were also consistent, it seems that *L. viridis* in our study population has an ‘inbuilt’ personality. As we had only F1 laboratory generation, maternal or cross-generational environmental effects cannot be ruled out (Lynch and Walsh, 1998), but the genetic contribution to behavioural type is probable, especially in exploration where families differed significantly. In contrary, we could not detect any sign of heritability. However, this result can only be used to reject the hypothesis of a strong, age-independent genetic effect, because we could not measure the offspring at the same ontogenetic stage as we tested their fathers. Further, juvenile lizards were more consistent than adults. Such comparisons are rare in the literature. For instance, adults showed higher consistency than juveniles in Siamese fighting fish (*Betta splendens*) (Dzieweczynski and Hebert, 2013). This is the exact opposite to our results, however, the two studies are hard to compare directly given that Dzieweczynski and Hebert (2013) exposed their experimental animals to some chemicals (17α -ethinylestradiol), while we were interested in patterns observed in unmanipulated animals. Our results suggest that animal personality does not emerge as a result of personal experience, lizards are rather born with it, and the strength of consistency is negatively dependent on age. The detected phenotypic behavioural correlation (suggestive of a risk-taking – exploration behavioural syndrome) showed the opposite pattern: it was absent in naive juveniles, but present in adults, with considerable strength (TTH–GRID: $r_S = 0.34$; TTB–GRID: $r_S = 0.49$; the average correlation being around 0.2, see Garamszegi et al. 2012). This pattern strongly suggests that behavioural correlations are developing through ontogeny, potentially through a series of individual experiences affecting different behaviours in concert. This mechanism might be common in nature as similar patterns were recently found in spiders too (Sweeney et al. 2013), while examples for behavioural syndromes in predator- and conspecific-naive lab-reared animals are scarce at best. However, we note that based on our approach, we could not differentiate between-individual and within-individual correlations (see Dingemanse et al. 2012) and thus we can only discuss phenotypic behavioural correlations but not behavioural syndromes *sensu stricto*. At least two mechanisms can account for the reported age-dependence in behavioural consistency: (i) individual behaviour changes during ontogeny or (ii) certain individuals are filtered out from the population via phenotype-dependent mortality. However, separating between the above two would require targeted investigations (see Bell and Sih 2007 for an example where both mechanisms are in action).

We note that one might question whether the behavioural consistency we detected represents ‘true’ animal personality or not. As we performed the behavioural tests with 4 days between the repeats, behavioural consistency might be a result of short-term environmental effects rather than stable individual differences. We admit that we cannot fully reject this possibility (as we did not manipulate the environment), but we think that stable individual differences detected in a 4 days period can be interpreted as personality, but the presence of these differences cannot be extrapolated for longer periods, like the whole year or whole lifetime. Further, we note that all experiments were ran under standardised laboratory settings after proper time of acclimation, thus direct environmental effects were controlled for. Hence, the differences seen in adult males might be representative for the short and synchronized mating season (Vaclav et al 2007), while the juveniles were born in lab and kept under standardised conditions from the beginning.

Previous work showed that the nuptial throat colour patch (reflects mainly in ultraviolet) of male *L. viridis* is an important predictor of male success both in female mate choice (Bajer et al. 2010) and male-male combats (Bajer et al. 2011), and is a multiple honest signal (Bajer et al. 2012; Molnár et al. 2013, 2012). However, we could not detect any sign of a colour signal – behavioural type relationship. We note that the information content of sexual signals can vary between years and populations; hence, this result is not necessary general for the species.

More studies with other personality traits like sociability or aggression (Réale et al. 2007) are needed to test this hypothesis further. However, we could detect links between personality and fitness linked traits in adult lizards: larger males and males without ectoparasites were faster explorers than small males or infected males. Faster explorer individuals tend to have higher locomotor activity and they explore their surroundings more rapidly, which means that these individuals have a proactive behavioural type (Kolhaas et al. 1999; Sih et al. 2004a). In another view, these ‘more explorative’ individuals have a superficial exploration strategy as they spend less time in a unit area to gather information of their environments (Careau et al. 2009). If the environment is highly productive or more predictable, selection might favour superficial exploration (Careau et al. 2009). Of course, exploration comes with costs, for instance predation (Lima and Dill, 1990; Biro et al. 2004) and parasite infection (Barber and Dingemanse, 2010; Kortet et al. 2010). In our case, males of better quality (larger = older [reptiles have indeterminate growth, see Shine and Charnov (1992) and Kozlowski (1996)] and parasite-free) were more explorative. Given that our study is correlative, we cannot build a clear causation. Regarding size, it is equally plausible that individuals with fast/superficial exploration gained more benefits than costs and thus survived better and grew faster, or larger individuals explore their surroundings faster. It is the same with the parasites: either individuals with better immune response explore faster, or individuals already parasitized explore less. The fact that fitness related traits were only linked to personality in adults suggests that the link is established during ontogeny or as a result of phenotype-dependent survival, and perhaps temporally variable selective forces maintain the behavioural variation observed within our population. We found a weak trend showing that juvenile females tend to take more risk than males. We cannot interpret this pattern yet, but sexual dimorphism in risk-taking soon after birth is an interesting pattern deserving further investigations.

Although families differed significantly in exploration, the behavioural type of *L. viridis* was not heritable according to our father-son regression. Historically it was believed that – because they have a major influence on fitness while being extremely plastic – behavioural traits has no or just little additive genetic variance and therefore they have low heritability (Ariyomo et al. 2013; Jones, 1987; Smith and Blumstein, 2008). Moreover, heritability estimates were believed to being insignificant because of the large effect of environmental factors, particularly in wild animals (Dingemanse at el. 2002). However, heritability of behaviours was established lately in a variety of taxa (Ariyomo et al. 2013; Dingemanse et al. 2002, 2009; Kralj-Fišer and Schneider, 2012; Sinn et al. 2006; van Oers et al. 2005). Our result cannot be safely treated as one actually proving lack of heritability, because one of the main assumptions of father-son regressions, namely the similar age and state of the parental and offspring generation (e.g. Lynch and Walsh, 1998), was violated. The picture becomes even more confusing if we consider that we had full-sib families, and thus the fathers' and mothers' contribution could not be separated. Hence, whether personality of European green lizards is heritable or not requires more focussed quantitative genetic experiments, but the fact that full-sib families differed significantly in their behavioural type makes such experiments promising.

Finally, we found signs of habituation in risk-taking, lizards taking more risk in the second round of measurement, and an ontogenetic difference in exploration, juveniles being faster explorers than adults. We note that adult and juvenile behaviour was assessed on a similar scale (i.e. 5cm × 5cm grid for exploration and similarly sized refuge for risk-taking), but since juveniles were faster explorers than adults, this only makes the difference in this behaviour more robust. Such ontogenetic shift along the shyness-boldness continuum is documented in various other species as well, for instance, in Mangrove killifish (*Kryptolebias marmoratus*;

Edenbrow and Croft, 2011) or in field crickets (*Gryllus assimilis*; Hedrick and Kortet, 2012). This is easy to interpret from a life-history perspective (Roff, 1992; Stearns, 1992): in systems where predation-caused mortality is a relevant factor, quick growth at juvenile stage is a good strategy both in order to mature as early as possible (Civantos and Forsman, 2000; Civantos et al. 2010) and to reach a size refuge from gape-limited predators (Civantos and Forsman, 2000), while after maturity is reached, survival till the next reproductive event becomes a key aspect of increasing fitness. As high feeding/foraging rate is needed for maximising energy uptake for growth (Biro and Stamps, 2008) and is generally linked to increased activity/boldness (Biro and Stamps, 2008; Brodin and Johansson, 2004), juveniles must be bolder to increase their growth, while adults can be shyer to increase their survival. Again, the mechanism behind the shift can be either individual change or phenotype-dependent mortality, but based on the data in hand, we cannot separate the two.

Taken together, *L. viridis* has personality that is revealed in both exploration and risk-taking. Personality weakens with age, while correlations between personality and fitness related traits emerge and individuals become shier along ontogeny. Interestingly, a phenotypic behavioural correlation (suggestive of a risk-taking–exploration behavioural syndrome) emerged only in adult males. This suggest that while within-behaviour consistency (personality) is ‘inbuilt’ in *L. viridis* from hatching, either as a result of genetic or maternal effects, across-behaviour consistency (behavioural syndrome) emerges only during ontogeny, probably as a result of phenotypic plasticity. However, whether the ontogenetic changes in the presence/absence or strength of behavioural consistency are results of ontogenetic shift, phenotype-dependent survival or a combination of both cannot be established based on the current study. We recommend that ontogenetic stage should be always considered, or better, targeted in personality studies.

1.5 Acknowledgements

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Figure Legends

Figure1. Effects of age (adults *vs*. juveniles) and time (1st and 2nd rounds) of measurement on the behaviours a) TTH (time till the lizard's head emerge from shelter), b) TTB (time till the lizard's full body emerge from shelter) and c) GRID (represented by the number of change between grids in the exploration trial) in *L. viridis*. Risk-taking (TTH and TTB) is a latency variable, i.e. lower values represent higher risk-taking. Means + 95% confidence intervals are shown.

Figure 2. Correlation between exploration (model residuals) and snout-to-vent length (SVL, mm) in adult male *Lacerta viridis*.

Figure 3. Relationship between parasite infection and exploration (model residuals). Means + 95% Confidence Intervals are shown.

Figure 1.

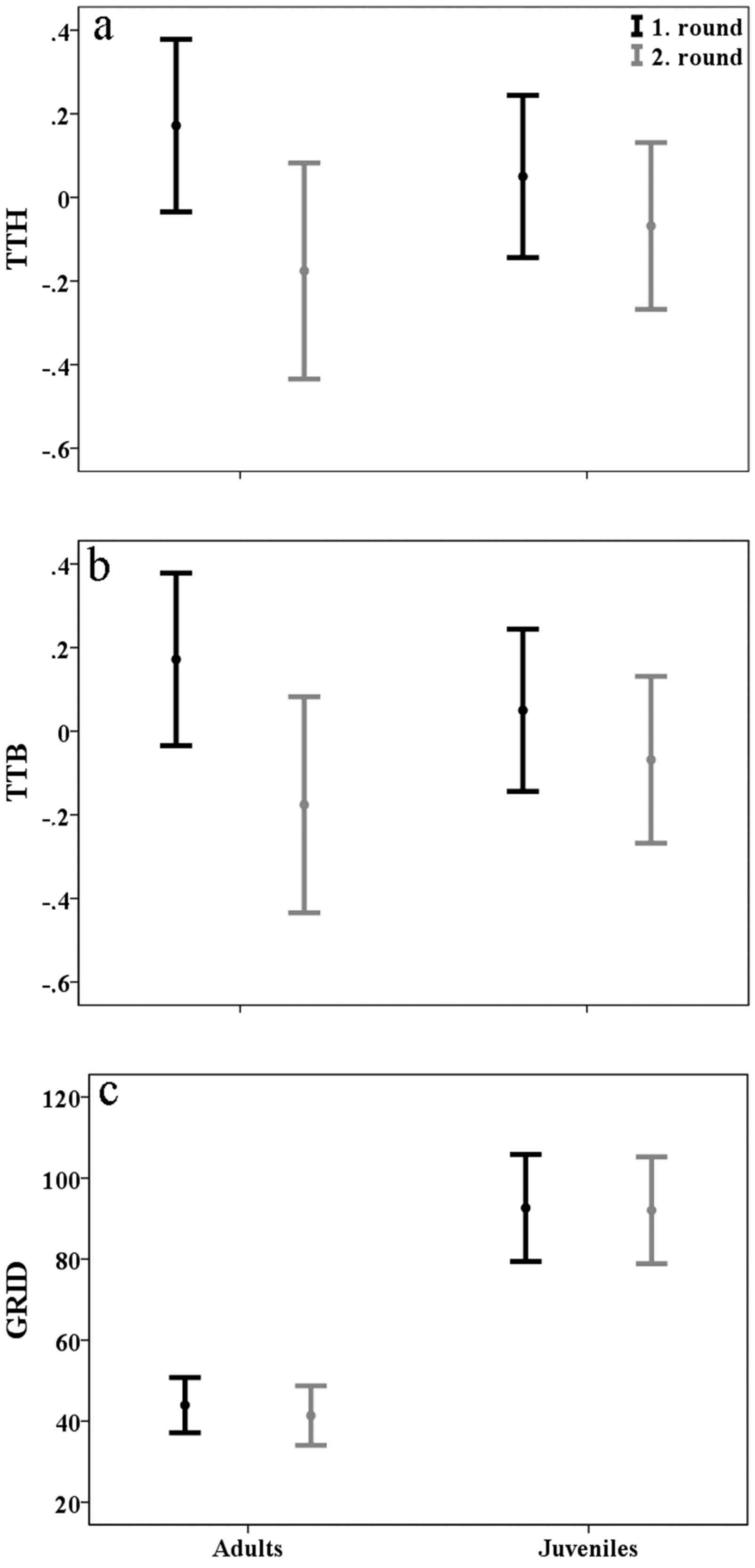
a
1. round
2. round
TTH
.4
.2
0
-.2
-.4
-.6
b
TTB
.4
.2
0
-.2
-.4
-.6
c
GRID
120
100
80
60
40
20
Adults
Juveniles

Figure 2.

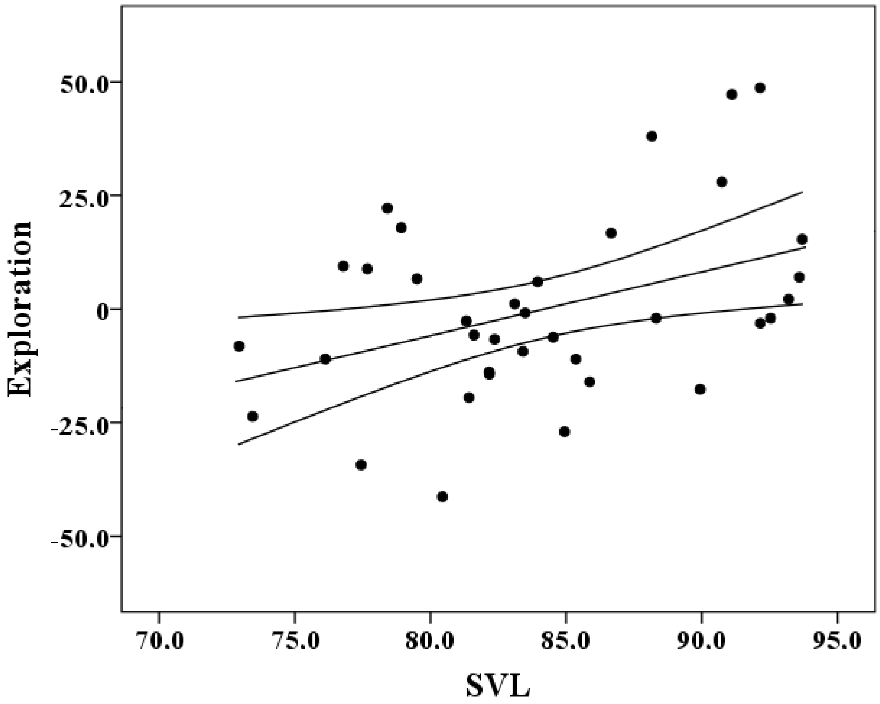

Figure 3.

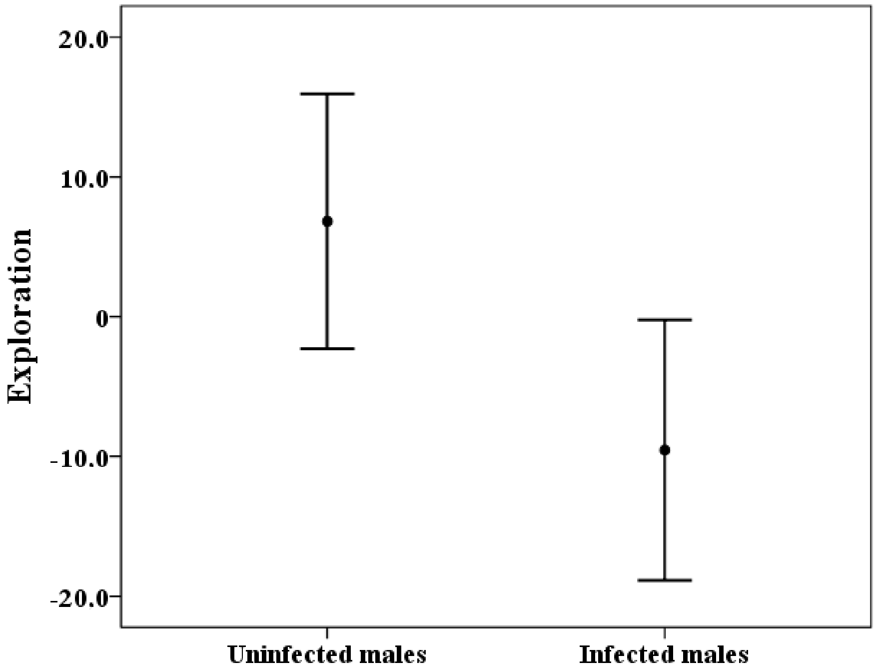

Table 1. Spearman rank correlations between subsequent measures of the same behavioural variables in adult and juvenile *Lacerta viridis*. TTH = time till the head emerged from refuge; TTB = time till the full body emerged from refuge; GRID = number of grid changes during the observation. Spearman correlation coefficients (r_S), their significance and 95% confidence intervals (CI) are shown. Formal comparisons of the correlation coefficients between adult and juvenile lizards are also given in the form of Fisher's r-to-z transformation; difference (Z) and significance are shown.

	Adults (N = 70)	Juveniles (N = 97)	Adults *vs.* juveniles
TTH	$r_S = 0.37$, $P = 0.002$; CI = 0.12 – 0.56	$r_S = 0.71$, $P < 0.001$; CI = 0.54 – 0.83	$Z = -3.12$; $P = 0.002$
TTB	$r_S = 0.23$, $P = 0.052$; CI = 0.02 – 0.46	$r_S = 0.6$, $P < 0.001$; CI = 0.43 – 0.73	$Z = -2.87$; $P = 0.004$
GRID	$r_S = 0.63$, $P < 0.001$; CI = 0.36 – 0.8	$r_S = 0.84$, $P < 0.001$; CI = 0.71 – 0.94	$Z = -2.3$; $P = 0.02$

Table 2. Spearman rank correlations between individual mean behaviours of adult and juvenile *Lacerta viridis*. TTH = time till the head emerged from refuge; TTB = time till the full body emerged from refuge; GRID = number of grid changes during the observation. Spearman correlation coefficients (r_S), their significance and 95% confidence intervals (CI) are shown. Formal comparisons of the correlation coefficients between adult and juvenile lizards are also given in the form of Fisher's r-to-z transformation; difference (Z) and significance are shown.

	Adults (N = 36)	Juveniles (N = 78)	Adults *vs*. juveniles
TTH – TTB	rs = 0.45, P = 0.006	r_S = 0.42, P < 0.001	Z = 0.18; P = 0.86
	CI= 0.13 – 0.69	CI = 0.2 – 0.6	
TTH – GRID	r_S = 0.34, P = 0.045	r_S = -0.05, P = 0.67	Z = 1.93; P = 0.054
	CI = -0.01 –0.63	CI = -0.28 – 0.19	
TTB – GRID	rs = 0.49, P= 0.002	r_S = 0.09, P = 0.4	Z = 2.13; P = 0.03
	CI = 0.18––0.74	CI = -0.12 – 0.35	

Supplementary Table 1. Results of the General Linear Models on adult *Lacerta viridis* behavioural types and behavioural syndrome. Nonsignificant results are shown as seen at the one-by-one back-substitution to the final model. Significant effects are in bold font.

Behaviour	Effect	$F(\mathrm{df}_1, \mathrm{df}_2)$	*P*
risk-taking	SVL	0.17 (1; 69)	0.68
	condition	0.03 (1; 69)	0.86
	relative head size	0.015 (1; 69)	0.9
	parasite infection	0.33 (1; 69)	0.57
	number of femoral pores	0.54 (1; 69)	0.47
	asymmetry	0.17 (1; 69)	0.69
	brightness	1.97 (1; 69)	0.17
	UV chroma	0.63 (1; 69)	0.43
	blue chroma	1.66 (1; 69)	0.2
exploration	**SVL**	**6.69 (1, 35)**	**0.014**
	condition	2.75 (1, 35)	0.11
	relative head size	0.33 (1; 35)	0.57
	parasite infection	**6.63 (1; 35)**	**0.015**
	number of femoral pores	0.41 (0; 35)	0.53
	asymmetry	3.63 (1; 35)	0.07
	brightness	<0.001 (1; 35)	0.99
	UV chroma	1.29 (1; 35)	0.27
	blue chroma	1.14 (1; 35)	0.29
risk-taking – exploration syndrome	SVL	1.54 (1; 35)	0.22
	condition	1.14 (1; 35)	0.29
	relative head size	0.2 (1; 35)	0.66
	parasite infection	2.29 (1; 35)	0.14
	number of femoral pores	0.01 (1; 35)	0.92
	asymmetry	<0.001 (1; 35)	0.99
	brightness	0.06 (1; 35)	0.81
	UV chroma	0.37 (1; 35)	0.55
	blue chroma	1.35 (1; 35)	0.25

Supplementary Table 2. Results of the General Linear Mixed Models on juvenile *Lacerta viridis* behavioural types. Nonsignificant results are shown as seen at the one-by-one back-substitution to the final model. The family effects (of the final models) are: $Z = 0.34$; $P = 0.73$ for risk-taking and $Z = 2.05$; $P = 0.04$ for exploration.

Behaviour	Effect	$F(\mathrm{df}_1, \mathrm{df}_2)$	*P*
risk-taking	SVL	0.03 (1; 45.7)	0.86
	condition	0.216 (1; 61.6)	0.644
	relative head size	0.223(1; 86.2)	0.638
	relative front leg length	0.29 (1; 89.5)	0.59
	relative hind leg length	0.7 (1; 78.2)	0.41
	relative tail length	0.19 (1; 67.04)	0.67
	sex	3.84 (1; 89.5)	0.053
exploration	SVL	0.48 (1; 50.2)	0.49
	condition	1.38 (1; 71.6)	0.24
	relative head size	2.94 (1; 75.9)	0.09
	relative front leg length	1.92 (1; 72.3)	0.17
	relative hind leg length	1.46 (1; 75.9)	0.23
	relative tail length	0.07 (1; 72.6)	0.8
	sex	2.28 (1; 63.7)	0.14