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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 recognized 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.

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,b; 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; 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, 2007; Dzieweczynski and Hebert, 2013; Sih et al., 2004a, 2012). 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

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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 coloration 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; Václav 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 (López 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 follows: (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.

2. Materials and methods

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 0.1 g; their snout-vent length (SVL), head length (HL), head width (HW), head height (HH), and tail length (TL) were measured to the nearest 0.1 mm 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 0.1 g. 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 0.1 mm. 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.

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 fibre-optic probe (Ocean Optics, Inc., Dunedin, FL). 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 3 mm distance and 90° angle with the surface. To get a representative sample of the uneven throat colouration, 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, FL, 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., 2010, 2011, 2012; Molnár et al., 2012, 2013): (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 ($R_{400–490}/R_{320–700}$).

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 (5 cm × 5 cm) on white paper under the bottom of the arena.

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