Behav Ecol Sociobiol (2017) 71:27
DOI 10.1007/s00265-016-2257-1

ORIGINAL ARTICLE

Food and vitamin D_3 availability affects lizard personalities: an experiment

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Received: 17 August 2016 / Revised: 9 December 2016 / Accepted: 12 December 2016

Abstract
It has been proposed recently that labile state variables (e.g. energy reserves) can have a key role in the development and maintenance of consistent between-individual behavioural variation (i.e. animal personality) within population. In male Carpetan rock lizards (*Iberolacerta cyreni*), the provitamin D_3 component of femoral gland secretion acts as an honest signal in sexual communication. Further, vitamin D_3 has many important metabolic functions in reptiles. Therefore, by employing a factorial experiment with food (high vs. low) and vitamin D_3 (supplemented vs. control) treatments in wild-caught reproductive male *I. cyreni*, we tested whether changing labile components of individual state affected (i) behavioural consistency (the degree of between-individual difference) and (ii) behavioural type (mean behaviour). Animal personality in activity was present in all treatments; however, personality was present only in the high food × vitamin D_3 supplementation treatment in shelter use and it was present in all but the low food × placebo treatment in risk taking. Lizards (i) decreased activity in the high food treatment, (ii) increased shelter use in the vitamin D_3 supplementation treatment and (iii) increased risk taking in the low food × vitamin D_3 supplementation treatment. We conclude that short-term changes in individual state affect both behavioural consistency and behavioural type of reproductive male *I. cyreni*. Unfavourable conditions resulted in decreased behavioural consistency, while high-state individuals became less active in general. Individuals with high specific (vitamin D_3) but low general (energy reserves) state took higher risk. We discuss several evolutionary explanations for the reported patterns.

Significance statement
The evolutionary and developmental mechanisms resulting in consistent between-individual behavioural differences across time and situations (i.e. animal personality) are of high scientific interest. It has been recently proposed that links between individual state (e.g. how well-fed the individual is) and behaviour can maintain such between-individual differences even on an evolutionarily timescale. However, whether short-term state changes are able to affect animal personality in adults is an open question. In a manipulative experiment, we found that the amount of food and vitamin D_3 (known to increase physiological quality and attractiveness of male Carpetan rock lizards, *I.* cyreni) affected the expression of animal personality and the actual behavioural types of reproductive male Carpetan rock lizards. Therefore, we provide evidence that short-term environmental variation does induce or suppress animal personality, and it also affects individual behaviour.

Keywords Animal personality · Individual state · Energy reserves · Reproductive value · Asset protection · Terminal investment

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Communicated by S. J. Downes

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Introduction

The concept of behavioural consistency states that between-individual behavioural differences are consistent and represent individual behavioural strategies rather than random noise or measurement error (Komers 1997; West-Eberhard 2003; Sih et al., 2004a, b; Carere and Masterpieri 2013). Animal personality (consistent individual differences in one behaviour) and behavioural syndromes (consistent individual differences across two or more functionally different behaviours) turned to be both statistically and biologically significant in several invertebrate and vertebrate taxa (Réale et al. 2007; Smith and Blumstein 2008; Garamszegi et al. 2012a; Mather and Logue 2013). Moreover, behavioural consistency can be present during long periods across different ecological contexts and situations and thus potentially play an important role in adaptive evolution (Sih et al. 2004a, 2012; Dochtermann and Dingemanse 2013). However, explaining the existence of consistent behavioural differences is challenging, due to its seemingly negative effects on fitness by constraining behavioural plasticity (Sih et al. 2004a, b). Classic theories emphasize the role of less plastic or fixed underlying variables constraining behaviour (e.g. genetic or neuroendocrine; see van Oers et al. 2005; Øverli et al. 2007) or the adaptive benefits of consistent individual behavioural variation (Wilson 1998; Dall et al. 2004; Luttbeg and Sih 2010; Wolf and Weissing 2010; Mathot et al. 2012).

New conceptual approaches have also been introduced in the last decade to explain the emergence of between-individual behavioural differences in a holistic, ecological and evolutionary context. A growing body of theory-based studies suggests that links between behaviour and state variables can be responsible for the observed behavioural consistency (Dall et al. 2004, 2012; Biro and Stamps 2008; Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Wolf and Weissing 2010; Mathot et al. 2012; Sih et al. 2012, 2015). Recent empirical data support this notion; however, results reveal no general pattern, behavioural consistency is sometimes increased, sometimes decreased by state-dependent changes (David et al. 2012; Dosmann et al. 2014; Kekäläinen et al. 2014; DiRienzo et al. 2015, 2016; DiRienzo and Montiglio 2016). Classically, internal state reflects various inherently stable (e.g. size, sex differences, brain structure) and labile features (e.g. energy reserves, health state, reproductive value) of an individual affecting the costs and benefits of its behavioural actions (Houston and McNamara 1999). Behavioural differences depending on labile intrinsic state variables are expected to change fast, as the underlying mechanisms are highly variable in time. In addition, these labile differences may include not only internal characteristics but the social and ecological environment as well (Sih et al. 2015). Environmental differences experienced during early stages of ontogeny seem to have high importance in the emergence of behavioural consistency (Dingemanse et al. 2007; DiRienzo et al. 2015; Urszán et al. 2015a, b; DiRienzo and Montiglio 2016). However, environmental factors, indirectly or in interaction with body condition, could affect the strength of behavioural consistency in opposite ways, either promoting or reducing between-individual variation (DiRienzo et al. 2015; DiRienzo and Montiglio 2016). It is still an unresolved question if state-based variation influences the strength of behavioural consistency during adulthood and whether the strength of behavioural consistency can change during relatively short periods (see Sih et al. 2015).

Energy reserves, body condition, dominance and various other traits are all important state variables contributing to expected future reproductive success, which is considered as one of the most important assets, and thus are among the most widely recognized characteristics with connection to behavioural strategies (Wolf et al. 2007; Sih et al. 2015). For instance, everything else being equal, individuals with low energy reserves need to take extra risk by increasing their foraging time to increase their future reproductive success, while individuals with high energy reserves should risk less during foraging because of their already high future reproductive success (asset protection principle, Clark 1994; Dall et al. 2004; Wolf et al. 2007; Harcourt et al. 2009; Luttbeg and Sih 2010; Dosmann et al. 2014; Engqvist et al. 2015). An alternative possibility comes from the state-dependent safety principle (Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Dosmann et al. 2014; Sih et al. 2015); taking the extra risk of high behavioural activity is beneficial for high-state individuals (e.g. with higher reserves, condition, etc.), as their higher state (= higher performance) reduces the risk of predation, while they can further increase their state. Finally, as future reproductive success is getting lower (e.g. by ageing, decreasing condition, illness) it may also be beneficial to take every risk to maximise current reproductive efforts and giving up unlikely future chances (terminal investment principle, Clutton-Brock 1984; Candolin 2000; Nielsen and Holman 2012; Lee et al. 2014; Engqvist et al. 2015). Empirical testing of these mechanisms is not easy. However, using species with well-studied biology and traits known to play a role in sexual selection or being linked to fitness could reveal more details on the relationship between state and behaviour.

Chemical signalling is one of the most important modes of intraspecific communication in many reptiles (Martín and López 2010; Mason and Parker 2010). Moreover, there is empirical evidence that femoral gland secretion of male lizards plays a particularly important role in sexual selection (Aragón et al. 2001; López and Martín 2002; López et al. 2003; Martín and López 2010). The Carpetan rock-lizard (*Iberolacerta cyreni*) is a small diurnal lacertid lizard endemic to the central mountain regions of the Iberian Peninsula, and during the last decades, it became one of the best studied reptiles regarding the role of chemical communication in sexual selection (e.g. López and Martín 2005, 2011; Martín and López 2006a, b, 2010, 2013). Femoral glands of *I. cyreni* males, among many other compounds, secrete provitamin D_3 (= cholesta-5,7-dien-3-ol), which is the precursor of vitamin D_3, a chemical essential for calcium metabolism and a potent immune system modulator (Allen et al. 1994; Laing and Fraser 1999; Griffin et al. 2003; Hayes et al. 2003). Therefore, the amount of provitamin D_3 that could be invested into the femoral secretion might give information about the individual's quality. Females prefer males with high levels of provitamin D_3 in their femoral secretion, making this chemical an honest signal (López et al. 2006; Martín and López 2006a, b, 2008, 2010, Martín and López, 2012), and thus a male lizard's vitamin D_3 level is a highly relevant state-variable within the given reproductive season.

In the present paper, we studied how different attributes of diet (quantity and quality) affected the behaviour of male *I. cyreni* during the reproductive season. We were interested in behaviour at two levels: first, we asked whether diet influenced the strength of behavioural consistency (i.e. the degree of between-individual differentiation in one or across two behaviours), and second, whether diet influenced behavioural type (individual mean behaviour). To this end, we applied a full factorial experimental design with two treatments: high vs. low food and vitamin D_3 supplementation vs. placebo. It is known that dietary intake of vitamin D_3 allows male *I. cyreni* to allocate more provitamin D_3 to femoral secretion (Martín and López 2006b). We had two hypotheses regarding treatment effects on behavioural consistency. First, as conditions were controlled in our semi-natural setup, environmental variation, and as consequence, individual states were expected to be less variable within than across treatments. We hypothesised that environmental and state variations are important in maintaining behavioural consistency in adulthood and predicted that behavioural consistency will be lower (i.e. animal personality or behavioural syndrome will be weaker) within, than across the treatment groups. Second, we hypothesised that behavioural consistency is adaptive in some, but not in other environments (see, e.g. Bell and Sih 2007) and predicted that strength of behavioural consistency will vary among the treatment groups. Further, as it has been shown that animals under favourable conditions are more likely to express extreme behaviours (Lichtenstein et al. 2016), we also predicted that behavioural consistency will be strongest in the high food × vitamin D_3 supplementation treatment and lowest in the low food × placebo treatment. We also expected our treatments to affect behavioural types (mean behaviour). Here, different predictions could be drawn based on different well-established hypotheses. According to the asset protection principle (e.g. Clark 1994), individuals with high state (and thus having high potential future reproductive success) should decrease their behavioural activity to protect their asset by avoiding risk. In contrast, following the state-dependent safety principle (e.g. Dingemanse and Wolf 2010), individuals with high state are expected to express high behavioural activity for its benefits, because their high state allows them to deal with the increased risk. In addition, the terminal investment principle (e.g. Engqvist et al. 2015) predicts that individuals with low state (and thus with low expected survival) should increase their behavioural activity to maximise their current reproductive output, accepting the associated increase in risk.

Methods

Study animals

We captured 60 adult *I. cyreni* males by noosing during the mating season (between May 31 and June 3) in 2014 at the 'Alto del Telégrafo' peak (Sierra de Guadarrama, Madrid prov., Spain, 1900 m asl). The habitat is characterized by a relatively dense vegetation of shrubs (*Cytisus* and *Juniperus*) and grassy meadows with a large number of granite rock boulders, which provide basking spots and shelter for the lizards. The animals were transported to the 'El Ventorrillo' field station of the Museo Nacional de Ciencias Naturales, 5 km from the capture site. The animals were housed individually outdoor in grey opaque boxes (57 cm × 37 cm × 30 cm; length, width, height, respectively). In the boxes, we used a layer of coconut fibres as substrate (2–3-cm thick, approximately) and we provided shelters (one per box) made of fibreboards (20 cm × 15 cm × 1 cm; length, width, height, respectively). The shelters were made without bottom and were open from the front, providing a suitable hiding place for the lizards, but the shelters could be also quickly removed with minimal disturbance to the animals. Between the assays (see below), we covered the boxes with fine metal mesh to protect animals from bird predators. Individuals spent at least 3 days in the boxes used for the experiment to habituate before the treatments started. During habituation, treatments and assays (see below) water was provided ad libitum. Amount of food (house crickets, *Acheta domestica*) differed between treatment groups (see below). At the end of the experiment, all lizards were released at their original capture points, without any sign of injury.

Treatments

Treatments were applied for a 17-day period, between June 7 and 23, including the days of behavioural assays. We applied two treatments with two levels in each in a factorial design (i.e. there were 15 lizards in each treatment combination). Lizards were randomly assigned to the low ($N = 30$) and high food treatments ($N = 30$). Low food males were provided with four house crickets every second afternoon (ca. 14.00 pm [UTC + 02.00]) for 3 h. After this time window, all remaining crickets were removed from the home cages. In contrast, high food males were fed daily (with the same amount starting at the same time), uneaten crickets being removed only 5 h later. This translates to 3 h per 2-day foraging possibility in the low food, and 10 h per 2-day foraging possibility in the high food treatment. In the high food treatment, there was always food left, while in the low food treatment, all food was eaten in the vast majority of time. Thus, the amount of food lizards encountered during a 2-day timeframe was twice for the high food treatment lizards with foraging time being more than threefold. Similar manipulations affect body condition of lacertid lizards considerably (Bajer et al. 2012; GeH et al. unpublished). The timing of food provision (afternoon) ensured that at the time of the behavioural assays (ending ca. 2 h before food provisions), all lizards were already hungry, actively searching for food (GeH personal observation).

Within each food treatment, males were also randomly assigned to the vitamin D_3 supplementation treatment ($N = 30$) and control treatment ($N = 30$). Supplemented males were provided with a dietary dose of 0.25-ml vitamin D_3 supplement specially developed for reptiles (Tetra ReptoSol, Tetra GmbH, Melle, Germany) diluted (1:1) in soybean oil (Sigma-Aldrich Chemicals Co., St. Louis, MO, USA) every 2 days on the afternoon between June 7 and 23. The applied vitamin supplement is a liquid solution containing 67.85 IU ml^{-1} of vitamin D_3 (manufacturer's description). Hence, each male was provided approximately 8.48 IU (= 0.21 μg) vitamin D_3 per dose approximately, an amount that evidently raises the secretory provitamin D_3 levels (Martín and López 2006b). To ensure that all males ingested the same amount of vitamin solution, we gently handled the lizards and used a sterile syringe to slowly deliver the solution into their mouth. Lizards were released back to their cages when we ensured that they had swallowed the entire dose. Control males were treated the same way (including handling), but we provided them with 0.25 ml of soybean oil alone, without the vitamin D_3 solution. Note that soybean oil contains no vitamin D_3.

Behavioural assays

The behaviour assays took place between June 16 and 23 after 9 days from the start of treatments. Activity and risk taking of lizards were tested four times, on sunny, low-wind days in the animals' home cages. Observations took place every second day so animals had time to recover from the handling related to treatments.

Activity of lizards was video-recorded between 11:15 a.m. and 12:15 p.m. (UTC + 02.00) using car cams (ConCorde RoadCam HD10, CONCORDE, ConCorde Elektronik Ltd., Budapest, Hungary). We assessed movement activity of animals in their home boxes based on a 30-min sample from every 1-h video footage (sum of three 10-min intervals, distributed equally: 0–10, 25–35, 50–60 min) using MATLAB (MathWorks, Natick, MA, USA) to calculate the total distance moved (in mm) and number of movement periods. We also evaluated the time (s) the animals spent under the shelter during the observation period to get another measure of activity. As Spearman's rank correlation tests indicated high positive correlations between these three measures (all $|r_s| > 0.49$, all $P < 0.001$), we ran a principal component (PC) analysis on them resulting two PCs. The first PC strongly correlated with all three original variables (proportion of variation explained = 75 %; factor loadings: distance moved = 0.93, number of movements = 0.93; shelter use = −0.73), while the second PC described shelter use independent from movement activity (proportion of variation explained = 20 %; factor loadings: distance moved = 0.28, number of movements = 0.26; shelter use = 0.69). Therefore, the first PC described general activity (hereafter activity) while PC2 described shelter use independent from movement activity (hereafter, shelter use).

Risk taking was also tested in the lizards' home cages, since this approach resembles how animals react in their natural home ranges more than tests done in a new unfamiliar environment (Beckmann and Biro 2013). Tests were done right after the video recording of movement activity. The experimenter (GeH) caught the lizard, briefly removed it from the home cage and then put it back under the lizard's own shelter. Males that were resting under their shelters at the beginning of the assay were also caught, briefly removed and put back under their shelter. Whether a male was under shelter or not at the beginning of the trial was used as a correction factor in the later analyses (see below). Time till the lizards left their refuges (when the lizards' midbody [from head to the cloaca region] emerged from the shelter) after the procedure was used as a proxy for risk taking with individuals emerging quickly seen as risk takers. This was measured from 25-min video records. The test order of the animals was randomized in every assay. Out of the 240 assays, lizards emerged in 107 cases during the 25-min observation period. Excluding the observations where lizards did not emerge from the analyses would lead to considerable loss of information, while giving them maximal score (1500 s) or applying random-rank transformation (see Bajer et al. 2015; Horváth et al. 2016) would mislead us in calculating within-individual variation in risk taking. Hence, we treated risk taking as a binomial variable, giving score 1 to individuals that emerged within 25 min and score 0 to those who stayed under the shelter for longer.

We note that the video evaluation was not blind regarding the test animals' identity, because the identification number of the animals was visible in the video recordings. However, it does not pose a problem since the subjectivity in our methods was minimal. Environmental variation between cages was considered minimal and random; however, we could not affect climatic variation among days in our semi-natural setup. In reptiles, behaviour is highly dependent from body temperature; moreover, there is evidence that individual thermal preferences may correlate with behavioural consistency (Stapley 2006; Stahlschmidt et al. 2016). Hence, to control for body temperature-induced differences, we measured the lizards' body temperature after the behavioural assays every afternoon (ca. 1:00 p.m. (UTC + 02.00), right after the behavioural tests) using a handheld non-contact infrared thermometer (ST80 ProPlus™, Raynger®ST™, Raytek, Santa Cruz, CA, USA). This approach provides body temperature estimates for small lacertids that are highly correlated with cloacal body temperature estimates without the disturbance connected to the latter (Herczeg et al. 2006, 2008). Body temperature measures were made from 20 to 30 cm distance to minimize the disturbance of the focal individuals. Since the assays were done on optimal days for lizards (sunny, low wind) we assumed that lizards could maintain their preferred body temperature during the assays and at the time of the temperature measurement.

Statistical analyses

Analyses were performed using the *R* statistical environment (R Developmental Core Team 2016). To estimate repeatability in the pooled sample and treatment groups for activity and shelter use, we ran linear mixed models (LMM) separately with behavioural variable of interest as the dependent variable and individual as the random factor. Confidence intervals were calculated by nonparametric bootstrapping, while significance is provided by random permutation, both sampled at each 1000th iteration. We applied a generalized linear mixed model (GLMM) to calculate repeatability for the binomial risk-taking data provided by the rptR add-on package following the methods of Nakagawa and Schielzeth (2010). This method utilizes a multiplicative overdispersion GLMM with a logit-link and using penalized quasi likelihood (PQL) estimation for repeatability on the original scale. Significance was estimated by randomization tests. 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).

Non-parametric Spearman rank order correlations were used on individual mean behaviours to explore behavioural syndromes. We note that a test for 'true' behavioural syndromes should be based on decomposing within- and between-individual correlations (Dingemanse and Dochtermann 2013). However, since our risk-taking data was binary, decomposition was not possible. Therefore, we could only test for phenotypic behavioural correlation.

To test whether the treatments affected the mean behaviour expressed in the different groups, we ran LMMs on activity and shelter use and binomial GLMM with logit link on risk taking. In our mixed-effect models the behaviours were the response variables, the treatments, their interaction and body temperature as fixed effects. Random effects were estimated using likelihood ratio tests. Models were run with the lme4 and lmerTest packages (Bates et al. 2015; Kuznetsova et al. 2016). In a pilot GLMM, we introduced position (under shelter or not) at the beginning of the assay as a correction variable to test its effect on risk taking, but since it did not have an effect ($z = 0.82$, $P = 0.41$) we excluded this variable from our final model. We tested potential habituation effects by including the *z*-transformed order of trials both as a single fixed effect and random slopes (i.e. the interaction with individual) to our mixed-effect models. Random-intercept (random effect: individual) and random-slope (random effects: individual, individual × order of trials) models were compared using chi-squared tests. We report marginal and conditional R^2 estimations for our models available in MuMIn package (Bartoń 2016) based on the method of Nakagawa and Schielzeth (2013).

Results

Animal personality and behavioural syndrome

All behaviours were repeatable in the pooled sample; however, repeatability of shelter use was rather low (Table 1). Repeatability estimates for all treatment groups revealed statistically significant, low to moderate repeatabilities ($0.21 < R < 0.34$) for activity (Table 1). Repeatabilities of shelter use proved to be significant only in males from the high food × vitamin D_3 supplemented treatment ($R = 0.28$) (Table 1). In risk taking, repeatabilities can be considered as low to moderate again ($0.23 < R < 0.36$), with randomization tests indicating significant risk-taking repeatabilities in all groups except in low food × placebo males (Table 1). Confidence intervals for the repeatability estimates between the groups and the pooled sample highly overlapped in all behavioural variables (Table 1). According to Spearman's rho, there was a weak, but significant phenotypic correlation between activity and risk taking in the pooled sample; however, there were no significant correlations between these behaviours in any of the treatment groups separately (Table 2). Between shelter use and risk-taking, there were no phenotypic correlations neither in the pooled sample nor in any of the treatment groups (Table 2).

Behavioural types

Our LMM revealed significant habituation in activity ($F_{1,177.45} = 79.93$, $P < 0.001$), lizards getting less active with time. However, individual trends did not differ ($\chi^2 < 0.001$, df = 1, $P > 0.99$). LMM showed that food treatment had a significant effect on activity (Food: $F_{1,58.1} = 4.8$, $P = 0.03$; vitamin D_3: $F_{1,57.1} = 0.28$, $P = 0.59$; food × vitamin D_3: $F_{1,56.14} = 0.04$, $P = 0.84$; body temperature: $F_{1,212} = 2.04$,

Table 1 Repeatability estimates for activity, shelter use and risk-taking of adult male *Iberolacerta cyreni* in the pooled sample (all) and in the different treatment groups (*HF* high-food treatment, *LF* low-food treatment, *P* vitamin D_3 placebo treatment, *V* = vitamin D_3 supplement treatment). Estimates are based on Linear Mixed Models (LMMs) for activity and shelter use, while on generalized linear mixed models (GLMMs) using penalized quasi likelihood (PQL) for risk-taking. Repeatabilities (R) and 95 % confidence intervals (CI) are shown. Significance (*P*) estimates are based on randomization tests

Behaviour	All ($N = 60$)	HF/P ($N = 15$)	LF/P ($N = 15$)	HF/V ($N = 15$)	LF/V ($N = 15$)
Activity	$R = 0.25$ $P < 0.001$ CI = 0.11–0.39	$R = 0.34$ $P = 0.005$ CI = 0.04–0.57	$R = 0.246$ $P = 0.024$ CI = 0–0.5	$R = 0.21$ $P = 0.026$ CI = 0–0.46	$R = 0.21$ $P = 0.026$ CI = 0–0.47
Shelter use	$R = 0.1$ $P = 0.037$ CI = 0–0.22	$R < 0.001$ $P = 0.99$ CI = 0–0.22	$R < 0.001$ $P = 0.98$ CI = 0–0.25	$R = 0.28$ $P = 0.009$ CI = 0–0.54	$R = 0.1$ $P = 0.16$ CI = 0–0.32
Risk taking	$R = 0.34$ $P = 0.001$ CI = 0.12–0.45	$R = 0.36$ $P = 0.006$ CI = 0–0.62	$R = 0.23$ $P = 0.1$ CI = 0–0.56	$R = 0.27$ $P = 0.02$ CI = 0–0.54	$R = 0.26$ $P = 0.03$ CI = 0–0.54

$P = 0.16$): lizards being less active in the high food treatment (Fig. 1). R^2 estimates revealed that fixed effects explained 22 %, while the entire model explained 49 % of the total variation in activity.

We found significant habituation in shelter use as well ($F_{1,178.25} = 12.63$, $P < 0.001$), lizards using shelter less with time. But again, individual trends did not differ ($\chi^2 = 0.4$, df = 1, $P = 0.5$). LMM revealed that males with vitamin D_3 treatment spent significantly more time under their shelters than males in other groups (Food: $F_{1,57.54} = 0.002$, $P = 0.9$; vitamin D_3: $F_{1,58.53} = 4.9$, $P = 0.03$; food × vitamin D_3: $F_{1,56.73} = 0.02$, $P = 0.88$; body temperature: $F_{1,232.63} = 0.12$, $P = 0.74$; Fig. 2). R^2 estimates revealed that fixed effects explained 7 %, while the entire model explained 16 % of the total variation in shelter use.

Our GLMM revealed significant habituation in risk-taking ($z = 2.41$, $P = 0.02$), lizards taking more risk with time; however, individual trends did not differ ($\chi^2 < 0.001$, df = 1, $P > 0.99$). The GLMM revealed a significant interaction between the treatments (food: $z = -1.6$, $P = 0.1$; vitamin D_3: $z = 0.66$, $P = 0.51$; food × vitamin D_3: $z = 2.2$, $P = 0.03$; body temperature: $z = 1.44$, $P = 0.15$); individuals receiving low amount of food but supplemented with vitamin D_3 took higher risk than their conspecifics (Fig. 3).

Discussion

We examined the effects of quantity and quality of the diet, as two different ecologically relevant factors, on behavioural consistency and behavioural type of adult male *I. cyreni* during their short mating season. Numerous studies claimed recently that various, labile state-dependent traits are linked to different components of behavioural consistency (see Careau and Garland 2012; Hammond-Tooke et al. 2012; Bajer et al. 2015; Horváth et al. 2016; Mell et al. 2016). Further, social and environmental conditions during early life seem to have a fundamental role in the emergence of behavioural consistency during early stages of ontogeny (Dingemanse et al. 2007; DiRienzo et al. 2012, 2015, 2016; Urszán et al. 2015a, b). However, effects of short-term differences in internal state or environmental conditions on behavioural consistency during late ontogeny are not obvious (Garamszegi et al. 2012b; Dosmann et al. 2014; McEvoy et al. 2015; Seaman and

Table 2 Spearman rank correlations between individual mean behaviours (*ACT* activity, *SHU* shelter use, *RT* risk-taking) of adult male *Iberolacerta cyreni* in the pooled sample (all) and in the different treatment groups (*HF* high-food treatment, *LF* low-food treatment, *P* vitamin D_3 placebo treatment, *V* vitamin D_3 supplement treatment). Spearman correlation coefficients (r_s) and 95 % confidence intervals (CI) are shown. Since ACT and SHU are represented by principal components from the same principal component analysis, there is zero correlation between them by definition

Behaviours	All ($N = 60$)	HF/P ($N = 15$)	LF/P ($N = 15$)	HF/V ($N = 15$)	LF/V ($N = 15$)
ACT-RT	$r_s = 0.16$ CI = 0.03–0.28 $P = 0.01$	$r_s = 0.18$ CI = −0.62–0.41 $P = 0.18$	$r_s = 0.05$ CI = −0.19–0.3 $P = 0.71$	$r_s = 0.22$ CI = −0.03–0.5 $P = 0.1$	$r_s = 0.16$ CI = −0.1–0.38 $P = 0.24$
SHU-RT	$r_s = -0.1$ CI = −0.23–0.03 $P = 0.14$	$r_s = -0.13$ CI = −0.4–0.1 $P = 0.32$	$r_s = -0.17$ CI = −0.42–0.1 $P = 0.2$	$r_s = -0.18$ CI = −0.5–0.06 $P = 0.18$	$r_s = -0.1$ CI = −0.31–0.18 $P = 0.46$

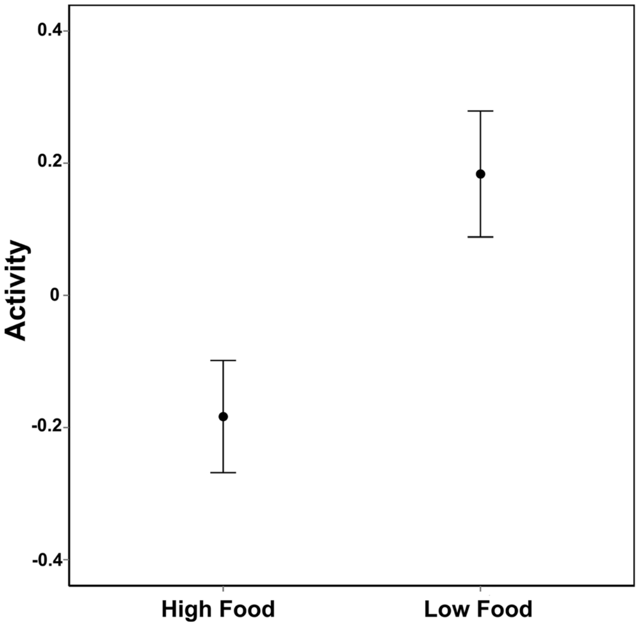

Fig. 1 Differences in activity induced by the food treatment in adult male Carpetan rock lizards (*Iberolacerta cyreni*). Activity is represented by a principal component positively correlated to 'distance moved', 'movement frequency' and negatively to 'shelter use', describing activity in general. In our model (see text) analysing activity, only the food effect was significant. Means and standard errors are shown

Briffa 2015). Whether state-dependence of behavioural consistency exists during adulthood and the strength of behavioural consistency could change during short time periods are still among the unresolved questions of personality studies (Sinn and Moltschaniwskyj 2005; David et al. 2012; Dosmann et al. 2014; Sih et al. 2015). In our study, by manipulating the quantity and quality of diet for more than 2 weeks during the short and highly synchronized mating season of *I. cyreni* (Martín and Salvador 1992), we could not affect the consistency of activity, but the presence/absence of animal personality in shelter use and risk taking was environment-dependent. Behavioural types of all studied behaviours responded to the treatments. Although we found significant habituation in all behaviours (animals got less active, spent less time under their shelter and took more risk by time), consistent between-individual differences were detected irrespective of general trends of habituation. Thus, we believe that our assays give a good estimate of individual behavioural differences (Biro 2012). We discuss our findings in two steps. First, we consider what the short-term environmental effects on animal personality could add to our knowledge about the development of behavioural consistency, and second, we discuss how do the different treatment effects on behavioural types fit to the existing theories.

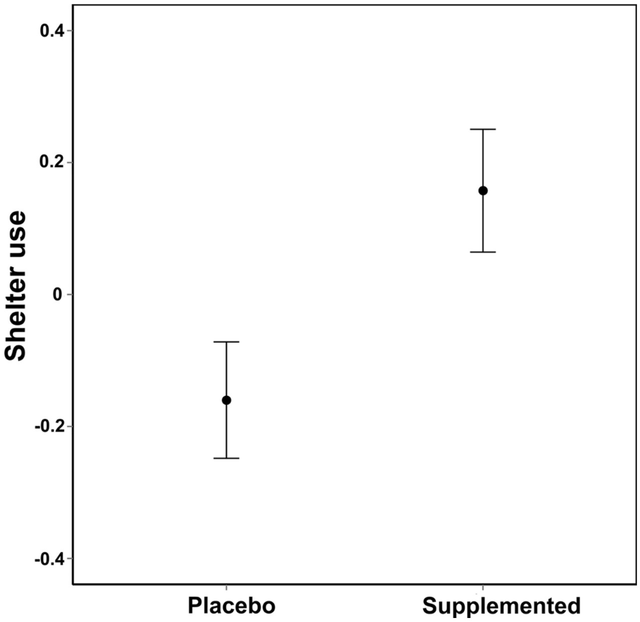

Fig. 2 Differences in shelter use induced by vitamin D_3 supplementation in adult male Carpetan rock lizards (*Iberolacerta cyreni*). Shelter use is represented by a principal component correlated positively to 'shelter use' only, describing shelter use independent of 'distance moved' and 'movement frequency'. In our model (see text) analysing shelter use, only the vitamin D_3 effect was significant. Means and standard errors are shown

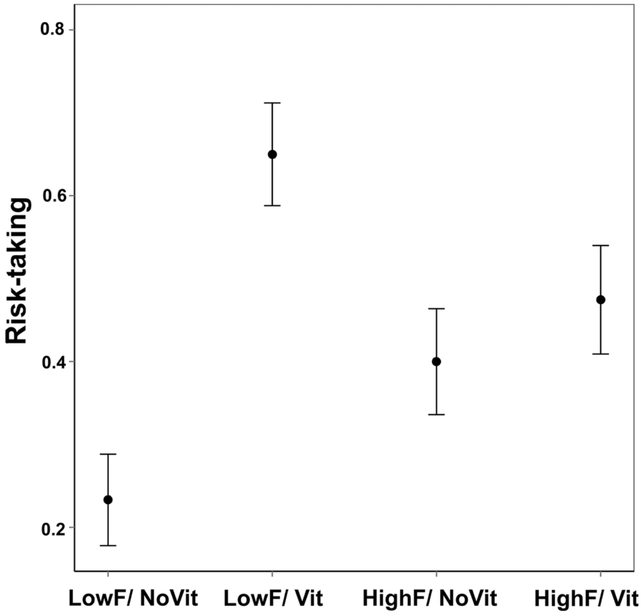

Fig. 3 Differences in risk-taking induced by the food and vitamin D_3 treatments in adult male Carpetan rock lizards (*Iberolacerta cyreni*). Risk-taking is estimated by the binary variable of emerging (= 1) or not (= 0) from the shelter after a simulated predator attack. In our model (see text) analysing risk-taking only the food treatment × vitamin D_3 treatment interaction was significant. Means and standard errors are shown. *HighF* high-food treatment, *LowF* low-food treatment, *NoVit* only placebo supplemented, *Vit* vitamin D_3 supplemented

Behavioural consistency

In both the pooled sample and the different treatment groups, activity proved to be low to moderately repeatable (Table 1), as our values overlap with the mean estimate for repeatability (0.37) reported in the meta-analysis of Bell et al. (2009).

Group-specific confidence intervals widely overlapped with that of the pooled sample; thus, repeatability estimates did not differ between treatment groups and the whole sample. Therefore, in the case of activity, we could not support either of our hypotheses regarding short-term environmental effects on behavioural consistency.

On the other hand, repeatability of shelter use was negligible, except in the high food × vitamin D_3 group where it was moderately repeatable and in the pooled sample where it was weak (see Bell et al. 2009) (Table 1). This suggests that the emergence of 'shelter use personality' is environment-dependent as between-individual variation increased under the best conditions offered by our treatments. Basically, shelter use can be seen as describing general activity (see Koolhaas et al. 1999; Réale et al. 2007), individuals spending more time under their shelter regarded inactive. We can only speculate about the biology behind the emergence of animal personality in the optimal treatment group (or the absence in others). For instance, it is plausible that individuals under favourable environmental conditions can allow 'extreme' behavioural strategies, which increases the between-individual component of variance. This assumption is supported by a recent experimental study (Lichtenstein et al. 2016). Environmental effects on yearly variation in presence/absence/strength of behavioural consistency have been also supported in different wild bird populations (Dingemanse et al. 2004; Garamszegi et al. 2015). There was no indication of higher repeatability in the pooled sample compared to the treatment groups; therefore, we reject the hypothesis about lowered environmental variation weakening shelter use personality.

For risk taking, randomization tests showed highly significant low to moderate repeatabilities (see Bell et al. 2009) in all groups except in the low food × placebo males. As randomization test gives robust measures of statistical significance in the case of non-Gaussian data (Nakagawa and Schielzeth 2010), we consider risk-taking personality being present in three out of the four treatment groups and also in the pooled sample. Such pattern could be explained similarly to the pattern seen in shelter use: individuals under unfavourable environmental conditions tend to shift their behaviour towards a general strategy, resulting in decreased between-individual variation (Lichtenstein et al. 2016). However, since the actual risk taking repeatability estimates were quite close to each other in the four treatment groups, this pattern should be regarded rather as a trend than a pattern. Again, there was no indication of higher repeatability in the pooled sample compared to the treatment groups; therefore, we reject the hypothesis about lowered environmental variation weakening risk-taking personality.

Non-parametric correlation coefficients indicated a weak, but significant phenotypic correlation between activity and risk taking in the pooled sample, but phenotypic correlations between these two behaviours within treatment groups were all nonsignificant (Table 2). This pattern is congruent with our hypothesis at first sight: behavioural consistency across two behaviours was only observed in a sample of individuals covering maximum environmental variation. However, we note that phenotypic behavioural correlations cannot be seen as true behavioural syndromes, because behavioural syndrome is the between-individual correlation by definition (Dingemanse et al. 2010, 2012), while we were not able to separate the within- and between-individual components of the phenotypic behavioural correlation. It has been shown recently that even strong phenotypic correlations can be based on within-individual correlations alone (Brommer et al. 2014; Urszán et al. 2015a). Further, the significant correlation in the pooled sample had similar correlation coefficient to coefficients from non-significant correlations in three out of the four groups; hence, the presence/absence patterns are likely resulted from sample size variation (i.e. statistical power) and not biological variation. There were no significant correlations between shelter use and risk-taking.

These results indicate that our treatments had influence on the strength of animal personality in adult male *I. cyreni*, supporting our hypothesis about the importance of short-term environmental conditions in maintaining behavioural consistency. Our study species is known to have a short and highly synchronized mating season starting right after the emergence from hibernation; hence, males do not have much time to spend on foraging before reproduction (Martín and Salvador 1993; Salvador et al. 2008). Consequently, short-term shifts in environmental conditions and individual state are expected to strongly affect fitness, and eventually, behaviour. The role of energetic constraint is evident, simply because all behaviours have energetic needs (Mathot et al. 2014; Mathot and Dingemanse, 2015). Further, as the amount of supplementary vitamin D_3 might affect reproductive success during mating season, quality of diet is also expected to shape behaviour. We suggest that behavioural consistency is—on some level—affected by short-term ecological conditions in the studied population of adult male *I. cyreni* during the mating season. Hence, environmental conditions are likely responsible not only for the long-term development, but also for the short-term maintenance of individual behavioural variation. Within our treatments, important environmental variables were not only modified but also standardised compared to the natural variation. Still, we found no support for the hypothesis that the level environmental variation per se is important in the short-term maintenance of behavioural consistency.

Behavioural types

Our treatments did not only affect behavioural consistency, but also affected activity, shelter use and risk-taking behavioural types. Males under food shortage were more active than their conspecifics, which is in line with starvation avoidance and could be seen as an aspect of asset protection principle (Clark 1994; McElreath et al. 2007; Luttbeg and Sih 2010; Dosmann et al. 2014; DiRienzo and Montiglio 2016). By being more active, individuals with low energy reserves potentially obtain more food and thus increase their state, while well-fed individuals can protect their reproductive asset by decreasing activity. Males treated with supplementary vitamin D_3 spent more time under their shelter, which can also be linked to the asset protection principle (Clark 1994). It is known that provitamin D_3 is the main chemical signal in male *I. cyreni* femoral secretion, correlating positively with individual quality (Allen et al. 1994; Laing and Fraser 1999; Griffin et al. 2003; Hayes et al. 2003) and being under positive female choice (Martín and López 2006a). Further, males with more vitamin D in their secretions have increased immune response (López et al. 2006). Therefore, vitamin-supplemented males are attractive with high potential reproductive success, and in the sense of asset protection principle, they have to secure their reproductive asset. It was also shown recently that *I. cyreni* females prefer places with scent marks from vitamin D_3-supplemented males (Martín and López, 2006b). Hence, one would expect males with low-scent quality to be more active and take higher risk to find mates, while attractive males should become more risk-averse. By spending less time outside their shelters, chemically attractive males can reduce predation threat directly by (i) avoiding predators and also indirectly by (ii) avoiding aggressive conspecifics as conspicuous agonistic interactions between them would again increase predation risk (Engqvist et al. 2015), while still successfully attracting females to their territory.

Males with supplementary vitamin D_3 but under food restriction took more risk than their conspecifics. The type of interaction between the two treatments on risk taking contradicts both asset protection and state-dependent safety principles (Clark 1994; Luttbeg and Sih 2010, respectively), since maximum risk taking was observed in lizards with high state in one but low state in the other aspect. Basically, vitamin-supplemented but food-deprived males can be seen as attractive, high-quality males with lowered survival possibilities. The pattern that attractive males took more risk than others only under energy-poor conditions can be explained as a special case of terminal investment principle (e.g. Clutton-Brock 1984; Massot et al. 2011; Nielsen and Holman 2012; González-Tokman et al. 2013; Lee et al. 2014). If low food availability translates to low future reproductive success (note that lizards in our population reproduce once a year), it makes sense to otherwise attractive males to take more risk for the immediate reproductive benefits. On the other hand, males facing food shortage without increased attractiveness were the most risk-averse, probably because they might not realize the benefits of increased risk- aking, and thus they only increased their general activity for foraging without taking more risk under actual threat. However, there is an alternative explanation. If vitamin D_3 supplementation has a positive effect on antipredator success (e.g. better sprint speed due to increased bone health; Laing and Fraser 1999; Griffin et al. 2003), it is plausible that food-deprived lizards accept the higher predatory risk to increase their foraging time. This can be seen as a combination of the starvation avoidance and state-dependent safety principles, where high state in one aspect allows lizards to face higher risk to increase another aspect of their state.

Conclusions

Taken together, our ecologically relevant short-term treatments affected both the level of behavioural consistency and the behavioural types of adult *I. cyreni* males during the reproductive season. Studies show that behavioural carryovers over a short period have ecological significance (Sih et al. 2003; Luttbeg and Sih 2010). As our behavioural assays covered an 8-day interval, we cannot claim that we report 'true' personalities that are consistent over long periods. However, considering the ecological context (the short and synchronized mating season), we think that the phenomenon is biologically significant. By showing that differences in environmental conditions cannot only shift the mean behaviour in animal groups during a short timeframe, but it might affect the level of between-individual variation too, we demonstrated the liability of behavioural consistency. This is not only relevant from a methodological aspect for researchers studying animal personality in the wild or under laboratory settings, but also demonstrates how a certain behavioural trait can be or be not under selection (note that selection operates on between-individual phenotypic variation) depending on some simple environmental factors.

Acknowledgements We are highly grateful for two anonymous reviewers whose comments and advice helped us to improve our manuscript. Our sincere thank goes to Roberto García-Roa for his assistance in noosing lizards. We thank 'El Ventorrillo' Field Station of Museo Nacional de Ciencias Naturales for use of their facilities. Our work was funded by the Hungarian Scientific Research Fund (# OTKA-K 105517 for GH). LZG was supported by funds from The Ministry of Economy and Competitiveness (Spain) (CGL2015-70639-P) and The National Research, Development and Innovation Office (Hungary) (K-115970). PL and JM were supported by the Ministerio de Economía y Competitividad project MINECO CGL2014-53523-P. The research also received support from the SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Research Infrastructure Action under the FP7 "Capacitie" Program.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The experiment was performed under licence (permit number: 10/024398.9/13) from the Environmental Agency of Madrid Government ("Consejería de Medio Ambiente de la Comunidad de Madrid", Spain).

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