Moderate consistency in smooth newt behaviour

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Behavioural consistency (i.e., personality) is a novel field of research in amphibians. Current published studies often address only one or two aspects of personality and therefore cannot assess more complex relationships and behavioural syndromes. This is the first study focusing on all relevant behavioural traits and their relationships in urodele amphibians. Based on the three trials of the experiment, we examined the consistency of activity (time spent moving), boldness (latency of the first movement and time spent escaping) and exploration (number of visited segments of testing arena) of 43 smooth newts (*Lissotriton vulgaris*). Individual consistency, calculated through the intraclass correlation coefficient (ICC), was low in newt activity (ICC = 0.192) and moderate in boldness (0.491) and exploration (0.412). Activity was moderately consistent for each trial (0.425), indicating a possible habituation that was supported by a decrease of mean activity throughout the trials. Correlation of the behavioural traits studied suggests the presence of a behavioural syndrome, which potentially shaped the

traits together. Our findings suggest the need for a complex approach to the study of amphibian personality and the need for standardized methodology, which would solve the current difficulties in comparing published results.

Introduction

Behavioural consistency (i.e., personality) is a well-known phenomenon studied in many taxa[1–3] and recently studied in amphibians[4–10]. Consistency in the expression of behavioural traits over time and in different situations, as well as the correlation of those traits, i.e., behavioural syndrome[3], is often linked to survival in predator-prey situations[11,12] (but see Carlson & Langkilde[4]), reproductive success[13,14], disease risk[9] and dispersal tendencies[6,8,15,16]. Therefore, animal personality plays an important part in individual life histories and should be inspected and carefully considered when dealing with most aspects of animal ecology.

Amphibian personality research, however, is limited and includes mostly studies performed on anurans, especially their larvae (see Table 1). In contrast, there are considerably fewer studies for urodeles[10,17] and none for caecilians. Existing amphibian studies most commonly address the consistency of activity, boldness and exploration (Table 1). Most of these studies (none of which consider urodeles), however, address only one or two of these behavioural traits (axis of personality) and usually cover some specific problem, not personality *per se*. There are also differences in approaches to behavioural consistency because some studies cover differences across time[5–8], while others consider differences across situations[9,10,17,18].

Therefore, the aim of our study was to measure the consistency of main behavioural traits—activity, exploration and boldness—in one experiment to examine the main types of behavioural responses and to focus only on temporal consistency while

reducing other factors. Furthermore, we wanted to assess the correlations between these behaviour types (i.e., the existence of behavioural syndrome).

Results

Activity

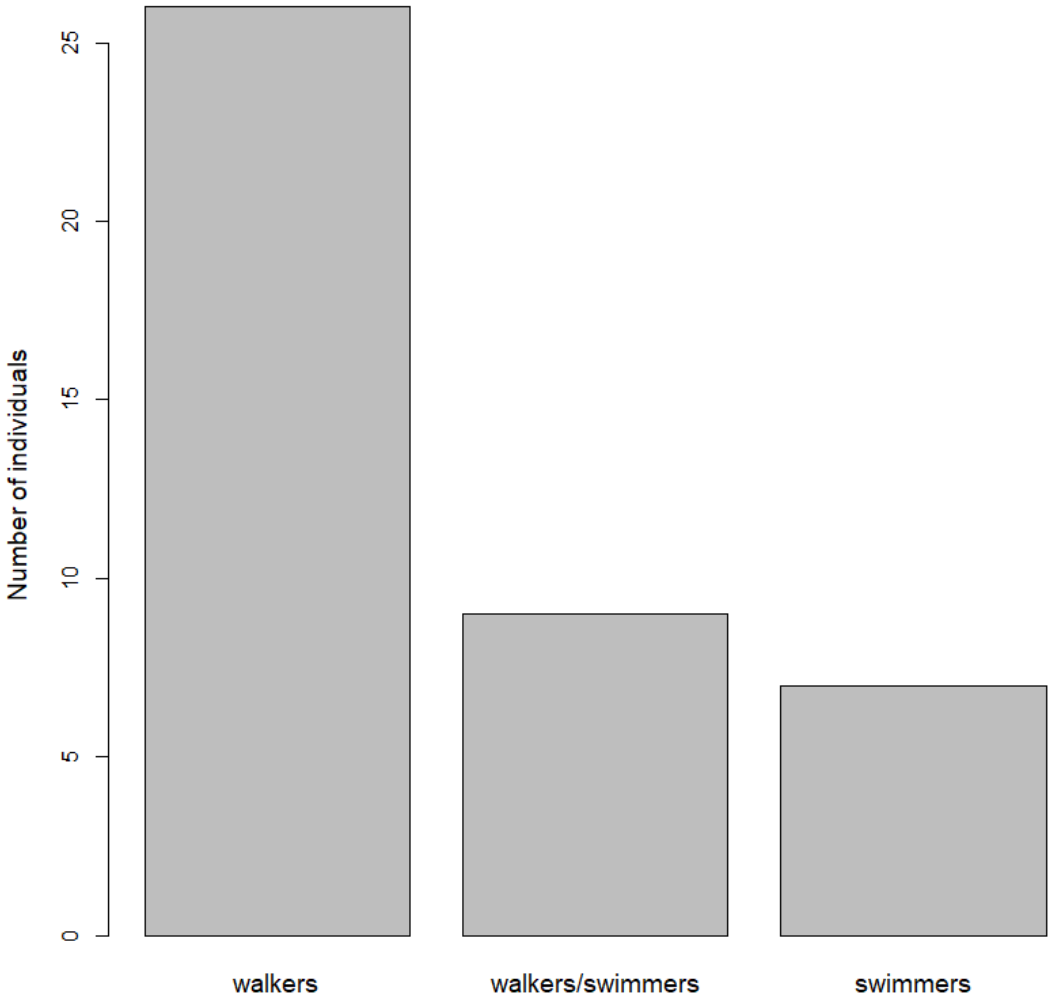
The sex of newts (X^2 = 0.31, P = 0.58) and the time of day (X^2 = 0.49, P = 0.48) had no significant effect on their activity. There were, however, significant differences in mean activity between each trial (X^2 = 76.57, $P < 10^{-6}$). The initial mean activity of 309.9 seconds decreased by 32 % in the second trial and by 20 % in the third trial. Although the activity had a low ICC (*ICC* = 0.192, *CI* = [0.089, 0.361]), the activity was significantly repeatable for each newt. The activity among the newts was also repeatable during each trial of the experiment (*ICC* = 0.425, *CI* = [0.298, 0.477]).

When the activity was divided into walking and swimming, walking was the preferred type of locomotion with the ratio of 1.8:1 with respect to swimming (X^2 = 816.09, $P < 10^{-6}$). As with the total activity, sex and time of day had no influence on the amount of walking (sex: X^2 = 0.35, P = 0.55; day time: X^2 = 0.97, P = 0.33) or swimming (sex: X^2 = 0.66, P = 0.42; day time: X^2 = 2.63, P= 0.10). Both the amount of walking (X^2 = 9.68, $P < 0.01$) and swimming (X^2 = 19.92, $P < 10^{-4}$) differed significantly between the trials of the experiment, but their ratio remained unchanged, with sex and time of day having no effect (sex: X^2 = 0.43, P = 0.51; day time: X^2 = 0.86, P = 0.35; trial: X^2 = 0.87, P = 0.65). Albeit significant, the repeatability of walking was relatively low for each newt (*ICC* = 0.273, *CI* = [0.073, 0.474]) and non-significant for the trial (*ICC* = 0.066, *CI* = [0, 0.247]). Swimming was more repeatable than walking and was significant for each individual (*ICC* = 0.434, *CI* = [0.229, 0.635]) but not each trial (*ICC* = 0.116, *CI* = [0, 0.338]). The walking to swimming ratio was moderately consistent for each individual

(*Kendall's W* = 0.597, *P* = 0.002) but, although significant, was practically inconsistent for each trial (*Kendall's W* = 0.107, *P* = 0.015).

Figure 1. Number of newts according to their prevalent type of movement

Walkers – walking to swimming time ratio >2, walkers/swimmers –ratio 0.5–2, swimmers –ratio < 0.5.



Exploration

The sex of the newt (X^2 = 0.50, *P* = 0.48) and the time of day (X^2 = 0.17, *P* = 0.68) did not affect the number of squares explored by newts. As with the first activity, there was a significant difference between each trial of the experiment (X^2 = 9.64, *P* = 0.01). The

initial mean of 27.8 explored squares decreased by 2.5 % in the second and by 18 % in the third trial. Exploration was significantly repeatable for each newt with a moderate ICC (*ICC* = 0.412, *CI* = [0.225, 0.593]). In contrast to activity, there was no repeatability for the exploration in each trial (*ICC* = 0.053, *CI* = [0, 0.215]).

Boldness

Boldness was measured as the latency to move and the time spent with an escape response. Latency to move was not dependent on any tested variables (sex: X^2 = 0.03, P = 0.86; day time: X^2 = 0.24, P = 0.63; trial: X^2 = 0.61, P = 0.74). Time spent with an escape response was also independent of sex (X^2 = 0.04, P = 0.85) and time of day (X^2 = 0.93, P = 0.33) and marginally independent of the trial (X^2 = 5.64, P = 0.06). The initial mean time spent with the escape response of 226.9 seconds decreased by 5.5 % in the second trial and then rose by 30 % in the third trial. The repeatability of latency and time spent escaping was similar for each trial of the experiment, but not for individual newts. Latency was not repeatable for both newt (*ICC* = 0.128, *CI* = [0, 0.339]) and trial (*ICC* = 0, *CI* = [0, 0.065]). Time spent escaping was, on the other hand, moderately repeatable for each newt (*ICC* = 0.491, *CI* = [0.312, 0.659]) and not repeatable for each trial (*ICC* = 0.024, *CI* = [0, 0.111]).

Correlated behaviour

The similarity in mean activity, exploration and time spent escaping of individuals was relatively high (*Kendall's W* = 0.694, P = 0.0001). Pairwise correlations showed a strong positive relationship between activity and time spent escaping (r = 0.734, $P < 10^{-6}$) and a moderate correlation between activity and exploration (r = *0*.539, P = 0.0002) and between time spent escaping and exploration (r = 0.405, P = 0.0078).

Discussion

106 Observed behavioural responses of studied newts were moderately consistent for
107 swimming activity, walking to swimming ratio, exploration and escape response.
108 Repeatability of activity as a whole was lower because of the less repeatable walking
109 activity that was more prevalent than swimming. The consistency of walking to
110 swimming ratio, i.e., the choice of locomotion type, however, suggests at least some
111 degree of individuality. Boldness was consistent only if measured as thigmotaxis (i.e.,
112 time spent with escape response), not as latency of the first movement. Studied
113 behaviour responses also did not differ between sexes and were unaffected by the time
114 of day that experiment started.
115 We expected the results of our study to be similar to *Lissotriton boscai*[10] which is, out
116 of studied urodeles, the closest relative to our model species. In the study of *Lissotriton*
117 *boscai*, however, there was a significant difference in individual activity between sexes,
118 with higher consistency in males ($r = 0.77$, $P < 0.001$) and no consistency in females (r
119 $= 0.05$, $P > 0.84$). On the other hand, the consistency was measured between different
120 situations—in the presence of none and conspecifics' odour, and thus the different
121 outcomes may be due to the different experimental design. Additionally, there was no
122 distinction between walking and swimming activity, nor any mention of their ratio.
123 In terms of anuran research, the overall activity of *Lithobates catesbeianus* was not
124 found to repeatable in time for Carlson & Langkilde[5] ($ICC = 0.12$) but was slightly
125 repeatable in different environments for Smith & Doupnik[18] ($r_1 = 0.355$, $r_2 = 0.151$, $r_3 =$
126 0.219). Wilson & Krause[7] reported consistent activity in time for both tadpoles ($r = 0.8$,
127 $P < 0.0001$) and froglets ($r = 0.91$, $P < 0.0001$) of *Pelophylax ridibundus*. There are
128 either no tests of consistency of activity in other studies (Table 1), or the results are
129 incomparable due to the use of different statistical methods.

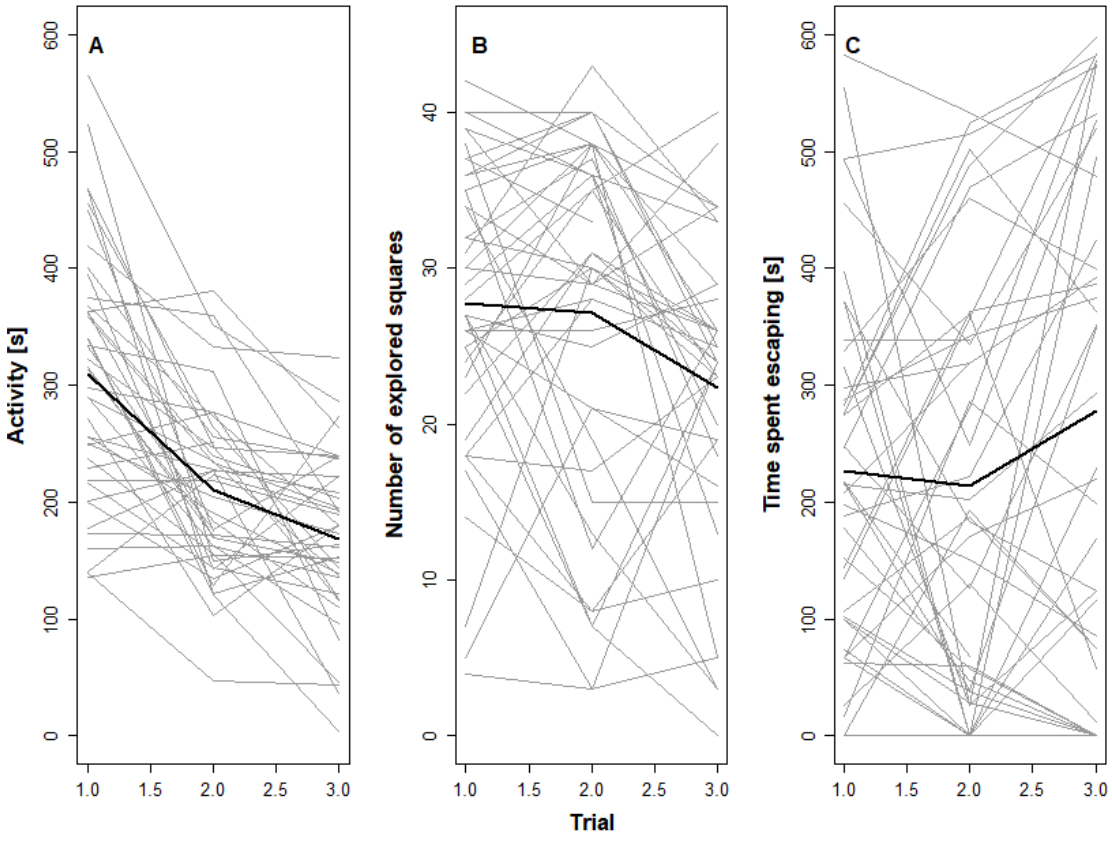
Multiple behaviour patterns were observed for exploration as well. Most of the newts started the trial with a quick escape response and then commenced with the exploration of the outer ring of the arena, rarely visiting the inner parts. A smaller group was startled at first and then explored the inner parts of the arena, eventually reaching the outer ring. Compared to *Rana temporaria*, for which Brodin et al.[8] tested the repeatability between life stages ($r = 0.25$, $P > 0.05$), our consistency of exploration was higher but was less than in *Lithobates catesbeianus*[5] (*ICC* = 0.68, *CI* = [0.46, 0.93]). The higher consistency in bullfrogs was, however, accompanied by short (24 h) intervals between trials. Furthermore, both studies differed in the definition of exploratory behaviour; the first study used a four cm buffer around the trajectory of the individual and the second counted the sides of the squares crossed by individuals including those already visited.

The repeatability of boldness was present only for the escape response (*ICC* = 0.491, *CI* = [0.312, 0.659]), which is a similar measure to that of Carlson & Langkilde[5], who counted the number of square sides on the inner portion of the test arena crossed by an individual and which is also a measure of thigmotaxis. Their results (*ICC* = 0.25, CI = [0–0.57]) are less precise, and the estimated coefficient is lower even though measured with the shorter 24 h breaks between trials. The accuracy of latency of the first movement, as the measure of boldness, was impaired for our study by the inability to consistently raise the glass dome in the centre of the arena at the start of the experiment. We suspect this to be issue in other studies as well, deeming this method impractical. This problem can be mitigated by changing the first movement to a movement longer than one body length[7], but in our opinion, it is better to choose a different option, e.g., shelter use, escape initiation distance or thigmotaxis.

Moderate correlation of shelter use in the presence and absence of predator cues in urodeles was reported by Sih et al.[17] for *Ambystoma barbouri* (r = 0.5, P < 0.001) and *A. texanum* (r = 0.64, P = 0.02), whose shelter use was also consistent between day and night (without predator cues: r = 0.8, P < 0.001; with predator cues: r = 0.617, P < 0.001). Brodin et al.[8] reported weak consistency of time, needed for the escape from the starting zone for *R. temporaria* tadpoles (r = 0.34, P = 0.012), which prevailed even after metamorphosis (r = 0.25, P > 0.05). Maes et al.[6] (r = 0.24, P > 0.05) and Carlson & Langkilde[5] (*ICC* = 0.25, *CI* = [0, 0.57]) reported similar magnitudes of correlation for latency of the first movement and thigmotaxis, while Wilson & Krause[7] found a much stronger correlation in tadpoles (r = 0.85, P < 0.0001) and froglets (r = 0.96, P < 0.0001) between latency of the first movement and escape initiation distance (tadpoles EID: r = 0.56, P = 0.0003; froglets EID: r = 0.42, P = 0.04).

Activity and exploration significantly decreased with each trial of the experiment, which suggests that habituation may have taken place (but see Carlson & Langkilde[5]). Except for activity, no behavioural trait was repeatable for each trial of the experiment. This could mean that the magnitude of habituation varied individually, i.e., individuality was stronger than habituation (see Fig. 2). For activity, its repeatability for each trial of the experiment was, unexpectedly, followed by low repeatability of both walking and swimming. Other than habituation, another less likely explanation is that the decrease in the expression of behaviour traits could have been caused by insufficient time between the trials of the experiment, allowing newts to remember the last trial. Unfortunately, it was not possible to allow more time between the trials because we feared that newts might switch to the terrestrial phase and change their behaviour. Nevertheless, most amphibian personality studies had a less than four-day gap between repeated

178 measurements (but see[6,8]). Habituation recovery time is unknown for the studied
179 species. For the common toad, however, Ewert & Kehl[26] stated that 6–24 h is long
180 enough for recovery from habituation to an artificial rectangular-shaped prey dummy.
181
182 **Figure 2. Individuality *vs.* habituation**
183 A – activity between trials, B – exploration between trials, C – escape response between trials.



184
185 Behavioural syndromes are referred to as suites of correlated behaviours[3]. In
186 amphibians, activity has been found to correlate with exploration[6,9] and boldness[6,7].
187 Boldness has also been found to correlate with exploration[6] (but see Brodin et al.[8]).
188 Maes et al.[6] divided the behaviours, using a PCA analysis, into two axes, the first
189 containing activity and exploration, while the second contained only latency of the first
190 movement. Contrary to their findings, our results show a correlation of activity,

191 exploration and time spent escaping, potentially creating only one axis (*Kendall's W* =
192 0.694, *P* = 0.0001). More active individuals tended to explore more and were less bold,
193 spending more time escaping. This behaviour might also be a result of a common
194 selective pressure, favouring individuals with a greater insight on the situation in their
195 home pond. The predation rate in the pond was, however, low (pers. obs.), and thus the
196 pressure might be of a reproductive nature. Increase in locomotion activity has been
197 found to benefit in mate searching[27], but we are not aware of any studies researching the
198 other two axes. Because of the absence of behavioural differences between sexes, this
199 pressure might be beneficial for both males and females or at least not harmful for
200 either. Whatever the cause, correlated behaviours, i.e., behaviours that are part of a
201 syndrome should not be studied in isolation because they develop as a group[3]. To study
202 behaviour syndrome completely, it would also be beneficial to test if the correlations
203 persist in different situations and ecological contexts.
204 In conclusion, amphibian personality research is very sparse, and findings differ
205 considerably in both approach and results. Behavioural consistency is often studied on a
206 small scale in relatively specific conditions, and behavioural correlations are sometimes
207 neglected. We believe that a more complex approach (measuring more types of
208 behaviour) and similar methodologies (i.e., definition of behaviour types, correlation in
209 time and different situations, standard time gap between repeated measurements,
210 number of repeated measurements, duration of experiment and sampling effort, and test
211 arena shape and size) is due. Our study design is easily reproducible with a
212 straightforward statistical evaluation and is applicable to most amphibian species while
213 introducing a novel view on urodele locomotion activity, which makes it a viable
214 contribution to the studied phenomenon.

Methods

Experimental design

The experiment was carried out at the specialized laboratory of the Czech University of Life Sciences in Prague. For a model organism, we chose the urodele that was most abundant locally, the smooth newt (*Lissotriton vulgaris*). At the start of the reproductive season in the beginning of May 2015, 21 males and 21 females were captured by nets in a single pond in the village Stará Lysá in the Central Bohemia region. The newts were housed separately in plastic containers of dimensions 18 × 12 × 14 cm that were filled with aged tap water, and the newts were fed *Daphnia* and Chironomidae larvae *ad libitum*. The air temperature in the laboratory was constant and set to 17°C. Sufficient light intensity in a diurnal cycle was provided by the translucent roof of the laboratory.

The experiment itself was conducted between 13th and 27th May in two experimental arenas made of non-transparent round green water barrels with bottom diameters of 80 cm. Using a non-toxic waterproof marker, a square grid of 7 cm segments was drawn at the bottom to better assess the position of each newt. The arena was filled with 5 cm of cold tap water (10.8–11.2°C), and after each recording, the water was changed, and the arena was thoroughly cleaned with a clean sponge and water pressure and then left to dry to eliminate any potential chemical cues that remained from the previous individual tested.

Each trial of the experiment was 12 minutes long. Behaviour was recorded at 30 frames per second with a full HD camera, positioned approximately 150 cm above the water level. Newts were separately inserted under the transparent glass dome (10 cm diameter) into the centre of the arena and left to calm down for the first two minutes. Then, the dome was carefully removed in a motion perpendicular to the ground, and the

239 recording was initiated. To measure the temporal repeatability of the behaviour, each
240 individual was recorded three times with a six day gap between each recording, which
241 was the longest gap possible before the newts started to shift to the terrestrial phase of
242 the season. Unfortunately, three videos were lost due to technical difficulties in the last
243 trial of the experiment, so the total number of analysed videos was 123.
244 Three types of behaviour (personality traits) were tracked: activity, exploration and
245 boldness. Activity was measured as the amount of time(s) during which the individual
246 moved. Furthermore, the movement activity was divided to walking and swimming to
247 distinguish the role of each in total activity and the consistency of each as well as to
248 determine the consistency of their ratio. Typical walkers tended to move slowly and
249 cautiously, almost never swimming (walking to swimming time ratio > 2). Swimmers
250 often swam the entire time (ratio < 0.5), and walkers/swimmers spent time walking in
251 one part and swimming in other parts of the same trial (ratio 0.5–2; see Fig. 1).
252 Exploration was recorded as the number of grid blocks that an individual entered.
253 Boldness was measured as the latency of the first movement(s) (the most common but
254 imprecise measure of boldness, see Discussion) and as the time(s) spent staying outside
255 the edge of the arena. Staying in its vicinity (thigmotaxis) can be interpreted as an
256 escape response and therefore can also be a valuable measure of shyness[5,19,20].
257 Behaviour was scored manually by the same person using the software Observer XT v.
258 10[21]. The study was carried out in accordance with permit SZ-092744/2012KUSK/3
259 issued by the Regional Office of the Central Bohemian Region of the Czech Republic.
260 *Data analysis*
261 The effect of sex and time of day on the newts' activity, exploration and boldness was
262 tested with separate linear mixed effects models (LMM) fitted by restricted maximum

likelihood (REML) with the random intercepts of individual (1–42) and the trial number (1–3) and was evaluated using Type II Wald Chi-squared tests. Unlike Carlson & Langkilde[5], we considered trial number a random intercept because the estimation of slope from just three measurements would have been too imprecise. The same model was also run separately for walking and swimming activity and for their ratio.

The repeatability of personality traits was calculated using the intraclass correlation coefficient (ICC), computed from the variance components of described models. Confidence intervals (CI) for the ICC were estimated by parametric bootstrapping with 1000 iterations (for details see Nakagawa & Schielzeth[22]). The existence of behavioural syndromes was tested using Kendall's coefficient of concordance, rather than ICC, because the interest lays in the ranks of responses, rather than their absolute value. The presence of zero values for walking and swimming made the use of ICC on their ratio impossible. Therefore, a constant (0.1) was added to each numerator and denominator, and its repeatability was also calculated using the rank-based coefficient of concordance. Pairwise similarities were analysed using Pearson's correlation coefficient. All statistical analyses were performed in R 3.3.1[23] using *lme4*[24] and *car*[25] packages at the level of significance $\alpha = 0.05$.

Data Availability

The datasets generated during and/or analysed during the current study are available in the Open Science Framework repository, https://osf.io/nbfk6/.

Acknowledgements. The study was carried out in accordance with permit SZ-092744/2012KUSK/3 issued by the Regional Office of the Central Bohemian Region of the Czech Republic with the support of Vladimír Vaněk (the mayor of Stará Lysá) and

grants no. 20164234 and 20174216, provided by the Internal Grant Agency of the Faculty of Environmental Sciences, Czech University of Life Sciences Prague.

Author contributions. O. Kopecký captured and cared for newts and together with P. Chajma participated on the execution of the experiment. P. Chajma analysed the data, prepared all figures and tables and together with J. Vojar wrote the main manuscript. All authors reviewed the manuscript.

Competing interests. The author(s) declare no competing interests.

References

1. Gosling, S. D. From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127,** 45–86 (2001).
2. Garamszegi, L. Z., Marko, G. & Herczeg, G. A meta-analysis of correlated behaviors with implications for behavioral syndromes: relationships between particular behavioral traits. *Behav. Ecol.* **24,** 1068–1080 (2013).
3. Sih, A., Bell, A., Johnson, J. & Ziemba, R. Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79,** 241–277 (2004).
4. Carlson, B. E. & Langkilde, T. No evidence of selection by predators on tadpole boldness. *Behaviour* **151,** 23–45 (2014).
5. Carlson, B. E. & Langkilde, T. Personality Traits Are Expressed in Bullfrog Tadpoles during Open-Field Trials. *J. Herpetol.* **47,** 378–383 (2013).
6. Maes, J., Van Damme, R. & Matthysen, E. Individual and among-population variation in dispersal-related traits in Natterjack toads. *Behav. Ecol.* **24,** 521–531 (2012).
7. Wilson, A. D. M. & Krause, J. Personality and metamorphosis: Is behavioral variation consistent across ontogenetic niche shifts? *Behav. Ecol.* **23,** 1316–1323 (2012).
8. Brodin, T., Lind, M., Wiberg, M. & Johansson, F. Personality trait differences between mainland and island populations in the common frog (Rana temporaria). *Behav. Ecol. Sociobiol.* **67,** 135–143 (2013).
9. Koprivnikar, J., Gibson, C. H. & Redfern, J. C. Infectious personalities: behavioural syndromes and disease risk in larval amphibians. *Proc. R. Soc. B Biol. Sci.* **279,** 1544–1550 (2011).
10. Aragón, P. The response to the social environment reveals sex-dependent behavioural syndromes in the Bosca's newt (Lissotriton boscai). *J. Ethol.* **29,** 79–83 (2011).
11. Dingemanse, N. J. & de Goede, P. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav. Ecol.* **15,** 1023–1030 (2004).
12. Carlson, B. E. & Langkilde, T. Predation risk in tadpole populations shapes behavioural responses of prey but not strength of trait-mediated indirect interactions. *Oikos* **123,** 1519–1527 (2014).
13. Cole, E. F. & Quinn, J. L. Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biol. Lett.* **10,** 1–5 (2014).
14. Dingemanse, N. & Réale, D. Natural selection and animal personality. *Behaviour* **142,** 1159–1184 (2005).
15. Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, a. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **365,** 4065–4076 (2010).
16. Cote, J., Fogarty, S., Tymen, B., Sih, A. & Brodin, T. Personality-dependent

dispersal cancelled under predation risk. *Proc. R. Soc. B Biol. Sci.* **280,** 1–9 (2013).

17. Sih, A., Kats, L. B. & Maurer, E. F. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim. Behav.* **65,** 29–44 (2003).

18. Smith, G. R. & Doupnik, B. L. Habitat use and activity level of large American bullfrog tadpoles: Choices and repeatability. *Amphib. Reptil.* **26,** 549–552 (2005).

19. Harris, A. P., D'Eath, R. B. & Healy, S. D. Environmental enrichment enhances spatial cognition in rats by reducing thigmotaxis (wall hugging) during testing. *Anim. Behav.* **77,** 1459–1464 (2009).

20. Burns, J. G. The Validity of Three Tests of Temperament in Guppies (Poecilia reticulata). *J. Comp. Psychol.* **122,** 344–356 (2008).

21. Noldus. *The Observer XT. Reference manual version 10.* (2010).

22. Nakagawa, S. & Schielzeth, H. Repeatability for Gaussian and non-Gaussian data : a practical guide for biologists. *Biol. Rev.* **85,** 935–956 (2010).

23. R Core Team. R: A Language and Environment for Statistical Computing. (2016).

24. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67,** 1–48 (2015).

25. Fox, J. & Weisberg, S. *An R Companion to Applied Regression*. (Sage, 2011).

26. Ewert, J. P. & Kehl, W. Configurational prey-selection by individual experience in the toad Bufo bufo. *J. Comp. Physiol.* **126,** 105–114 (1978).

27. Martin E, Joly, P, Bovet, P. Diel pattern of activity in the alpine newt (Triturus Alpestris, amphibia-urodela) during the aquatic phase. *Biol. Behav.* **14,** 116–131 (1989).

362 **Table 1. Summary of amphibian personality studies**

Study	Species	Stage	Personality traits examined		
			Activity	Boldness	Exploration
Urodeles					
Aragón[10]	*Lissotriton boscai*	adults	yes	no	No
Sih et al.[3]	*Ambystoma barbouri*, *A. texanum*	larvae	no	yes	No
Anurans					
Brodin et al.[8]	*Rana temporaria*	tadpoles, froglets	no	yes	Yes
Carlson & Langkilde[5]	*Lithobates catesbeianus*	tadpoles	yes	yes	Yes
Koprivnikar et al.[9]	*Lithobates sylvaticus*	tadpoles	yes	no	Yes
Maes et al.[6]	*Epidalea calamita*	froglets	yes	yes	Yes
Smith & Doupnik[18]	*Lithobates catesbeianus*	tadpoles	yes	no	No
Wilson & Krause[7]	*Pelophylax ridibundus*	tadpoles, froglets	yes	yes	Yes

363 Stage – stage of individual development (tadpoles, larvae – pre-metamorphosis; froglets – post-
364 metamorphosis; adults – post-metamorphosis, capable of reproduction)

365 Yes/no – the study did (not) measure activity/boldness/exploration

366