



## Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus*

Enikő Gyuris<sup>a,\*</sup>, Orsolya Feró<sup>a,b</sup>, Zoltán Barta<sup>a</sup>

<sup>a</sup> Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Debrecen, Hungary

<sup>b</sup> Computational Group, Institute of Nuclear Research, Hungarian Academy of Sciences, Debrecen, Hungary

### ARTICLE INFO

#### Article history:

Received 2 December 2011  
 Initial acceptance 4 January 2012  
 Final acceptance 21 March 2012  
 Available online 12 May 2012  
 MS. number: 11-00962R

#### Keywords:

animal personality  
 ecdysis  
 firebug  
 larval–adult transition  
 life history  
 ontogeny  
*Pyrrhocoris apterus*  
 sexual maturation

Consistent behavioural differences have long been recognized in animals but it still remains unclear how these traits change over ontogeny. As individuals can face different situations over their lives, and their life history expectation may not be the same in different life stages, one can expect that using different strategies in different life stages would be advantageous. Characteristics of animal personality across ontogeny could be measured at group and individual levels. Since personality alteration across time can be studied from various aspects one should use the following indexes: mean-level, differential, structural and individual consistency. We investigated whether common firebugs behave in the same way through a major life stage transition, namely final ecdysis. We measured activity, boldness and exploration twice in the larval stage and also twice when bugs reached the adult stage. We found that the relative value of behavioural traits was stable across ontogeny and the correlation structure among behavioural traits remained constant over time. Nevertheless, larvae differed from adults in general in that they were bolder, explored their environment more thoroughly and seemed to be more active before final ecdysis. These results indicate that personality could change differently across major life stage transitions; therefore this important factor needs to be considered in further research.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Studying animal personalities may furnish an answer to the question of why individuals of the same sex and age within a population differ consistently in their behaviour in the same context, or to put it more generally, why persistent behavioural variation exists in populations (Sih et al. 2004; Bell 2007; Réale et al. 2007; Wolf et al. 2007). The most studied personality traits in animals are boldness, activity, aggressiveness, exploratory tendency and sociability (Réale et al. 2007). Consistent behavioural traits appear as the result of developmental pathways that are determined by an individual's genes, its developmental environment and the interactions between them (Sinn et al. 2008).

Although animal personality has been intensively studied for a long time (reviewed in Dall et al. 2004; Sih et al. 2004; Dingemanse & Réale 2005; Bell 2007; Réale et al. 2007; Biro & Stamps 2008), the effect of ontogeny on personality development in animals has just started to be explored (Stamps & Groothuis 2010). Circumstances experienced during early life can have important effects on subsequent life stages (Lindstrom 1999; Lummaa & Clutton-Brock 2002). Long-term fitness consequences of early life experiences were demonstrated, for instance, in European rabbits, *Oryctolagus cuniculus* (Rödel et al. 2009). In addition, Rödel

& Meyer (2011) suggested that early development alters ontogeny of personality traits in laboratory rats, *Rattus norvegicus*: the heavier newborns were braver and more explorative. On the other hand, the life of an individual is usually composed of several markedly different life stages (e.g. larval/adult, or sexually immature stage/sexually mature stage) and one might expect an individual's personality to change during the fundamental transitions from one life stage to the other (e.g. during morphogenesis, sexual maturation or moult).

Individuals undergo extensive hormonal changes in the course of sexual maturation, which is obviously a period of behavioural reorganization. Edenbrow & Croft (2011) demonstrated in killifish, *Kryptolebias marmoratus*, that individuals were braver and more explorative in their early developmental stage, which, after sexual maturity, was followed by a lowered expression of such personality traits. Consequently, the developmental change in personality is a characteristic of this species.

As selection pressures can vary throughout life (McNamara et al. 2009), different behavioural traits can be advantageous at different ontogenetic stages. For instance, traits related to acquisition of food, and hence contributing to productivity (growth and/or fecundity), are expected to be expressed differently over an individual's lifetime (Biro & Stamps 2008). Therefore, we suggest that, because they are in different life stages with different fitness potentials (i.e. the juvenile must first grow, while the adult can immediately

\* Correspondence: E. Gyuris, Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, H-4010 Debrecen, Hungary.

E-mail address: [eniko.gyuris@vocs.unideb.hu](mailto:eniko.gyuris@vocs.unideb.hu) (E. Gyuris).

reproduce), juveniles and adults might respond differently to the same situation.

A sexually mature cricket, for instance, should be risk averse because it has successfully collected the costly resources that can be invested in reproduction but, at the same time, can easily be lost (Niemelä et al. 2011). As the cricket's case illustrates, a phenotype, despite being beneficial in an early period of life, does not necessarily match well with the conditions of later life stages (Roberts & Robins 2004; Taborsky 2006). Hence, it is necessary to examine which personality traits are more advantageous in the juvenile stage and which ones in the adult. A recent study in field crickets, *Gryllus integer*, indicated that in spite of predation risk, larvae are selected for feeding intensively to grow large because body size is fixed after the final moult in adults (Hedrick & Kortet 2012). Consequently, juvenile stages may be adapted to maximize growth, survival and dispersal while adults maximize reproductive output (McNamara 1996; Roff 2002). As these studies suggest, investigating personality around life stage transitions can reveal important aspects of personality development and life history as well.

The temporal changes of personality through ontogeny can be studied at two levels: individual and group (Stamps & Groothuis 2010). 'Individual stability' characterizes the extent of temporal consistency in an individual's behaviour, that is, whether a given behavioural trait in a given context will be similar later in time. At the group level we can use the following indexes: differential consistency, mean-level consistency and structural consistency (Stamps & Groothuis 2010). 'Differential consistency' describes the extent to which the scores of individuals are maintained over time compared to the scores of others in the group. 'Mean-level consistency' assesses the extent of change in the mean score of behaviour in a given group in the same context from one time to another. 'Structural consistency' describes the changes in the correlation structure among behaviours, that is, the extent to which the relations among behavioural traits are preserved over time. Structural consistency and differential consistency can change independently. For example, aggressiveness and boldness in a population of three-spined sticklebacks, *Gasterosteus aculeatus*, were positively correlated in juveniles and adults but those that had high aggressiveness and high boldness scores as juveniles were not necessarily bolder and more aggressive as adults (Bell & Stamps 2004).

Recently, we have shown that adult firebugs possess consistent behaviour across contexts and time (Gyuris et al. 2011). It is still unknown, however, how the bugs' personality changes around a major life history transition, the final ecdysis (moult) into adulthood during which they reach sexual maturation. To address this gap in knowledge, we investigated the following questions. (1) Do individuals show any consistency in terms of variation in their behaviour? (2) Does the relative performance of individuals change during sexual maturity, that is, will the bugs that are bolder than the majority as larvae be bolder as adults too? (3) How do average scores of different behavioural traits change during the transition, that is, are larvae bolder or more exploratory than adults? (4) Finally, do the relations between the different behavioural traits alter during the transition? In other words, we investigated individual stability, differential, mean-level and structural consistencies (Stamps & Groothuis 2010) across the final ecdysis in the firebug.

## METHODS

### Keeping Conditions

*Pyrrhocoris apterus* is one of the most common species of Pyrrhocoridae in Europe, and can usually be found at the base of linden

(*Tilia* spp.) trees, the seeds of which are its main food. The development of the firebug is hemimetabolous, which means there are five larval stages without a pupa and the adult emerges after the fifth ecdysis (Socha 1993). Brachypterous firebugs were taken from laboratory stock cultures which originated from a wild population in Debrecen, northeast Hungary (47.52°N, 21.63°E; 130 m above sea level; subcontinental climate), and have been kept in the laboratory from 24 September 2010. Food (sunflower and linden tree seeds) and water were provided ad libitum and temperature was consistently  $25 \pm 1$  °C. The behavioural tests (hereafter runs) were carried out in January and February 2011.

### Experimental Animals

Forty individuals in the fifth larval stage were selected and kept individually in separate jars between the runs. They were tested twice during their fifth larval stage and, after their final moult, twice again. 'Run a' was carried out on the third day after the bugs had moulted into the fifth larval stage and we repeated this run after 1 or 2 days (referred to as 'run b'), while the bugs were still in their fifth larval stage. Of the 40 bugs, 32 moulted successfully: nine females and 23 males. Because sex determination is very difficult in the larval stages we could not ensure a more balanced sex ratio. On the second or third day after the bugs moulted to adult we tested them again (hereafter 'run c'). 'Run d' was carried out on the 2nd or 3rd day after the third one (Fig. 1).

### Behavioural Tests and Walking Path Analysis

We used the same series of tests as those in Gyuris et al. (2011), which are briefly summarized below. The runs were carried out in a circular arena of 55 cm in diameter where four plugs as novel objects were set on the floor. We used different plugs with different sizes (all plastic plugs were circular ranging from 1.5 to 5 cm in diameter) and colours (to ensure they would be treated as novel). In each series of runs every plug touched was replaced before the next individual's test (to avoid uncontrolled olfactory cues). The floor of the arena was covered with white filter paper, which was replaced before each test.

Behavioural tests consisted of two 10 min sessions. In the first test, we measured boldness while in the second we performed an open field test. The bug was put into a vial covered with paper (to prevent the bug leaving the vial) and to let it get used to its environment we waited for 1 min. After this time, we flicked the vial once (to ensure that the bug was in the bottom of the vial), removed the paper and laid it on its side. The bug had 10 min to emerge from its refuge. We registered the appearance of the antennae (hereafter 'emergence') and the time until the bug left the refuge (since the bugs left the vial in only 10 of 118 cases we omitted this variable in the rest of the study). The bugs that left the vial were put back into it immediately, while those that did not leave within 10 min were left in it. Again, 1 min habituation was allowed before the second test. In the second test, the open field test, we flicked the vial (to make sure the bug was at the bottom of the vial), then we shook the bug into the centre of the arena. In this test we measured the bug's response to a startling stimulus after it entered the new environment, referred to as 'walking latency'. Then we measured exploration, that is, how thoroughly the bug explored its environment, by recording (1) the time it took to reach the arena wall (hereafter 'wall time') and (2) the number of novel objects visited (hereafter 'number of novel objects'). Activity was also measured in the open field test by recording the pathway of the bug at 1 s intervals until it reached the wall within a 10 min period, and by calculating the following variables: (1) the mean and (2) the variance of step size

(the distance between two consecutive positions), and (3) the mean and (4) variance of turning angles.

### Statistical Analyses

To measure individual stability for each variable we calculated the ISS (individual stability statistic) scores as in [Sinn et al. \(2008\)](#). The ISS score is a measure of the difference between an individual's trait responses at two points and therefore a relative measure of the individual's developmental change. As we measured behaviour at four points in time during ontogeny we were able to investigate how ISS scores changed over ontogeny. We calculated these scores between the first and the second, the second and the third and the third and the fourth runs, then compared the scores with a Friedman test because individual scores are not independent of each other.

To test the consistency of behaviour across ontogeny, which can be defined as differential consistency or broad-sense repeatability, we measured all the behavioural variables of the bugs four times (twice in the fifth larval stage and twice as adult, [Fig. 1](#); see above). Then we assessed the consistency across runs by computing the Kendall's  $W$  coefficient of concordance for each measured behavioural variable separately ([Legendre 2005](#)). We also calculated a composite rank variable for each run as the sum of the individuals' ranks for each variable, and computed Kendall's  $W$  coefficient of concordance for these four composite rank variables as an overall measure of differential consistency. Kendall's  $W = 1$  means that there is complete concordance among the individuals' scores at different times (across four runs); conversely, if  $W$  equals 0, there is no concordance. Since we tested the same statistical hypotheses several times we corrected for familywise errors with [Holm's \(1979\)](#) procedure. We also analysed the behavioural consistency between the consecutive runs with Spearman rank correlations on both the original and the composite variables.

To investigate mean-level consistency, we fitted mixed-effects models with the individuals' IDs as a random factor and run ID as a fixed factor. To control the effect of sex and moulting time (i.e. the time between moulting to the fifth larval stage and to adult) we entered these two variables as fixed effects. We fitted separate models for each behavioural variable entered as the response variable. Since the distributions of most of the behavioural variables were skewed, these variables were dichotomized (e.g. 'slow' and

'fast' emergence) and binomial mixed-effects models were fitted to them ([Gyuris et al. 2011](#)). The effect of a given explanatory variable was assessed by a likelihood ratio test ([Crawley 2007](#)).

We also investigated whether the correlation structure among the behavioural variables changed across time. We first computed a Spearman rank correlation matrix among the variables for each run. Then we compared all matrices with a Mantel randomization test in a pairwise manner ([Manly 1997](#)) with [Holm's \(1979\)](#) correction. If the correlation structure did not change between two runs, we expected a significant relation between the two correlation matrices representing this structure. We also computed the mean of the correlation matrices and used this average matrix, after taking one minus the absolute values of its entries, as a distance matrix to calculate a summarized clustering of the behavioural variables ('agnes' function of cluster package of the R statistical environment, Ward's clustering method).

All statistical analyses were carried out in the R interactive statistical environment ([R Development Core Team 2008](#)) with cluster ([Maechler et al. 2005](#)), ade4 ([Dray & Dufour 2007](#)), vegan ([Oksanen et al. 2009](#)) and lme4 ([Bates & Maechler 2010](#)) packages.

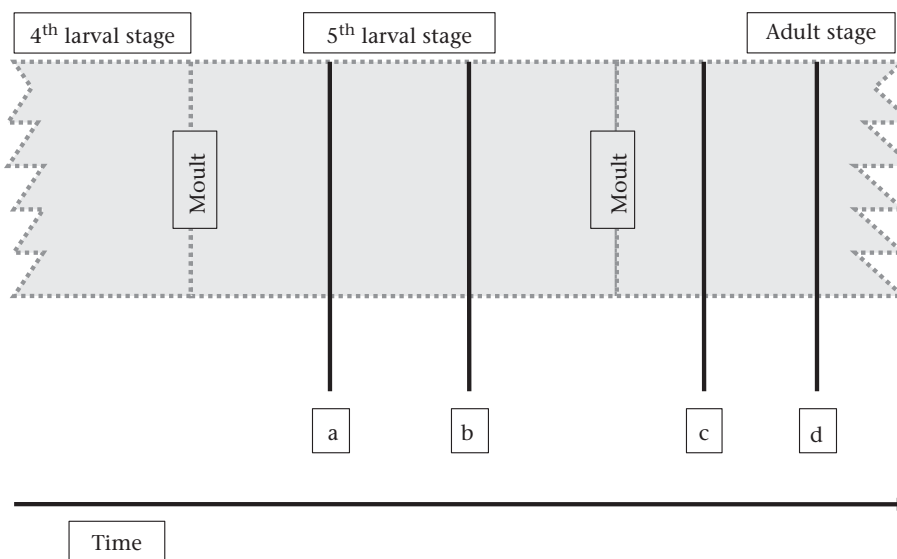
## RESULTS

### Individual Stability

We measured the individual's developmental change after calculating the ISS scores between each consecutive run and we found no significant difference between them ([Table 1](#)). This result indicates that the magnitude of possible behavioural changes over time did not differ between the life stages.

### Differential Consistency (Repeatability)

Of the eight measured behavioural variables five were significantly consistent ([Table 1](#)). All of these five consistent variables measure some aspect of the movement pattern of the firebugs. For the consistency of the overall behaviour we found that the composite rank variables were also consistent between runs ( $W = 0.407$ ,  $P = 0.011$ ). In seven of the eight behavioural variables correlation coefficients were largest between runs c and d ([Fig. 2](#); binomial test against the null hypothesis that the probability of the largest coefficients being between runs c and d is  $1/3$ ;  $P = 0.003$ ).



**Figure 1.** The timing of behavioural tests, marked here as runs, over a period of a firebug's life. Vertical continual lines labelled from 'a' to 'd' indicate the runs.

**Table 1**  
Different aspects of developmental effects on personality

Indexes		Variables							
		Emergence	Walking latency	Wall time	Number of novel objects	Mean step size	Variance of step size	Mean turning angle	Variance of turning angle
Individual stability	$\chi^2_2$	0.724	0.311	3.111	4.741	2.551	7.103	0.482	0.482
	<i>P</i>	1	0.855	1	0.653	1	1	0.229	1
Differential consistency	<i>W</i>	0.211	0.325	0.454	0.262	0.544	0.521	0.488	0.382
	<i>P</i>	0.687	0.115	<b>0.001*</b>	0.414	<b>0.001*</b>	<b>0.001*</b>	<b>0.001*</b>	<b>0.015</b>
Mean-level consistency	$\chi^2_3$	1.086	16.662	3.001	18.781	8.813	6.887	3.860	3.194
	<i>P</i>	0.780	<b>0.0008*</b>	0.391	<b>0.0003*</b>	<b>0.031</b>	0.075	0.277	0.362

'Individual stability' characterizes temporal consistency in an individual's behaviour (results of Friedman tests are shown). 'Differential consistency' describes how scores of individuals are maintained over time relative to others in the group (Kendall's *W* coefficients of concordance are given). 'Mean-level consistency' assesses the change in the mean score of behaviour in a given group in the same context from one time to another (likelihood ratio tests of mixed-effect models are given). *P* values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.

Correlation coefficients calculated between the composite rank variables of consecutive runs supported this result: we found a significant correlation only between runs c and d (between a and b:  $r_s = 0.165$ ,  $P = 0.366$ ; b and c:  $r_s = 0.188$ ,  $P = 0.300$ ; c and d:  $r_s = 0.381$ ,  $P = 0.031$ ; all  $N = 32$ ). These results show that behaviour was more consistent during adulthood than during development.

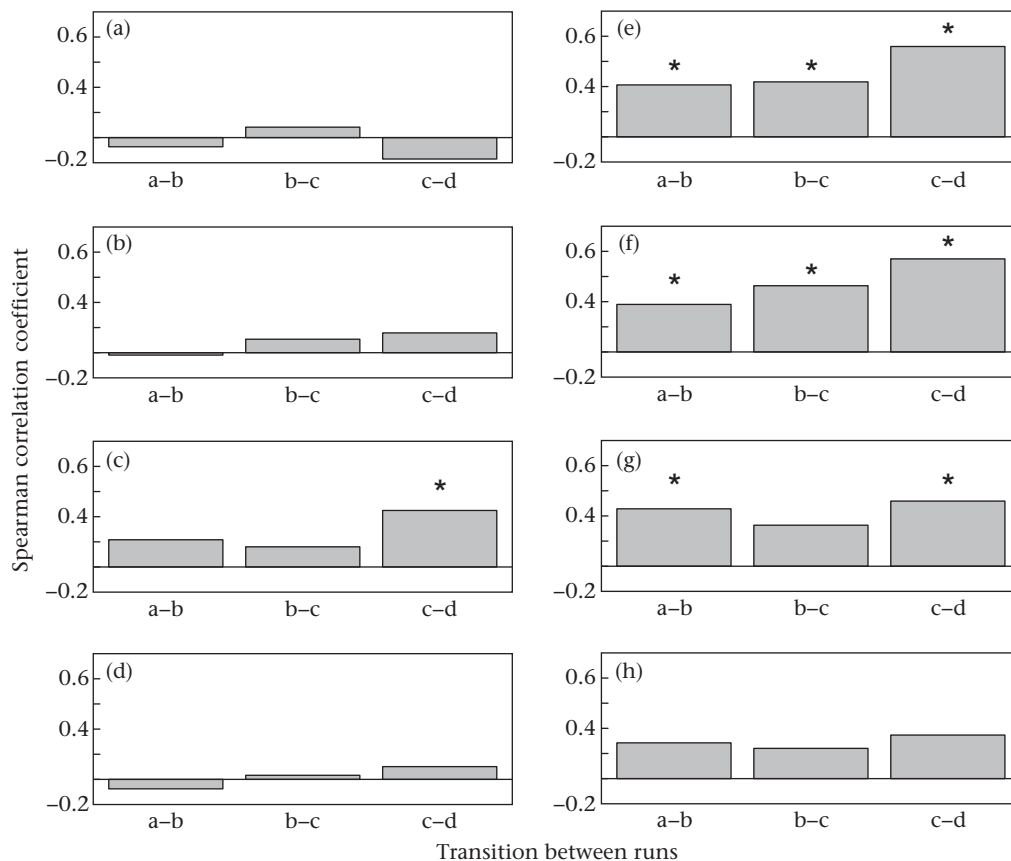
#### Mean-level Consistency

Neither the effect of sex nor the moulting time was significant (all  $P > 0.078$  for sex and all  $P > 0.138$  for moulting time). By analysing the effect of runs we found that the mean values differed strongly across runs for the following behavioural

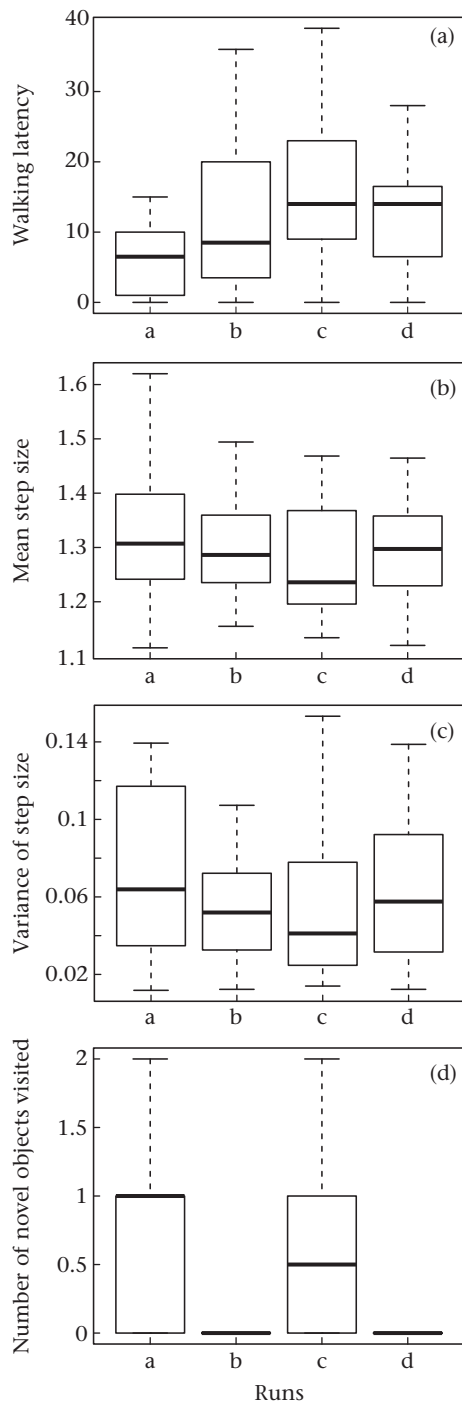
variables: walking latency, number of novel objects, mean step size; in addition, the variance of step size was nearly significantly affected (Table 1). Walking latency was largest after the moult, while the mean and variance of step size were smallest at the same time but later they increased (Fig. 3). The number of novel objects visited peaked immediately after moulting again (Fig. 3).

#### Structural Consistency

All the pairwise Mantel's tests between the correlation matrices were significant (Table 2). This result means that the correlational structure of the measured variables was similar across the runs.

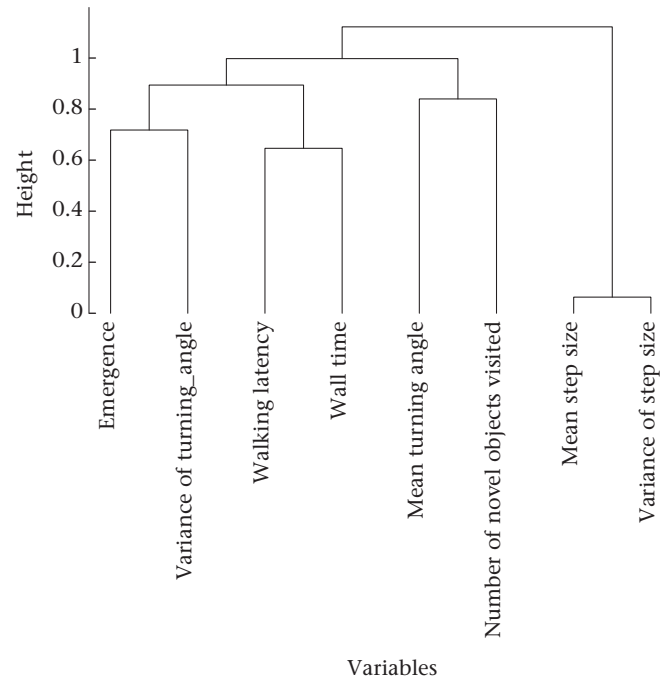


**Figure 2.** Extent of behavioural consistency between consecutive runs for each variable based on Spearman correlations between pairs of consecutive runs. Variables: (a) emergence, (b) walking latency, (c) wall time, (d) number of novel objects visited, (e) mean step size, (f) variance of step size, (g) mean turning angle and (h) variance of turning angle. Letters from 'a' to 'd' on the horizontal axes mark the runs. Runs 'a' and 'b' were carried out in the final larval stage while 'c' and 'd' were carried out in the adult stage. Asterisks mark significant correlations between runs at  $P < 0.05$ . The figure is based on the behavioural analyses of 32 firebugs.



**Figure 3.** Effect of runs ('a', 'b': in larval stage, 'c', 'd': in adult stage) on different behavioural traits. (a) Walking latency, (b) mean step size, (c) variance of step size, (d) number of novel objects visited. The box plots show the median and 25th and 75th percentiles; the dashed lines indicate the range. The figure is based on the behavioural analyses of 32 firebugs. For further details see text.

Based on the summarized cluster dendrogram, our variables can be divided into the following groups (Fig. 4). The first group consisted of emergence, variance of turning angle, walking latency and wall time, which can be considered as proxies for the shy–bold personality axis. The second group consisted of mean turning angle and number of novel objects, which can indicate the individual's tendency for exploration. The third group contained mean



**Figure 4.** Dendrogram showing the relation between the measured behavioural traits, calculated from the average correlation matrix of the four runs. The figure is based on the behavioural analyses of 32 firebugs. For further details see text.

step size and the variance of step size, which can be interpreted as variables of general activity.

## DISCUSSION

The final ecdysis, during which firebugs reach sexual maturity, is thought to be a major life stage transition in this insect. In this study we found that firebugs behaved consistently through this transition. The relative value of the individuals' behavioural traits, compared to each other, did not change across ontogeny (differential consistency). The correlation structure of behavioural variables also remained the same during this transition (structural consistency). Rödel & Meyer (2011) similarly found in laboratory rats that personality traits within contexts at different ages are consistent. Niemelä et al. (2011) have also shown in field crickets that personality can change around maturity, but the rank order repeatability between individuals can remain. Our results show that behaviour in firebugs is most consistent during adulthood. This finding is in accordance with human studies, which find that personality changes less over time with greater level of maturity (Roberts et al. 2001).

By investigating the absolute value of the behavioural traits, however, we found that some of them changed across metamorphosis (mean-level consistency). Larvae seemed to be bolder (i.e. they started to explore the new environment sooner), explored their environment more thoroughly (visited more novel objects in the first runs) and seemed to be more active before the final transition (Fig. 3). Hedrick & Kortet (2012) found similar results, with boldness changing across ontogeny in field crickets.

Consistent differences between individuals can be explained by the integrative pace-of-life syndrome (POLS, Réale et al. 2010). This is based on the growth–mortality trade-off (Stamps 2007), which means individuals with a 'slow lifestyle' are expected to have low metabolic rate and to be less aggressive, facilitating risk-averse behaviour (Mathot et al. 2009). Consequently, they have a long



**Table 2**  
Structural consistency of the relations among behavioural traits in firebugs

Distance matrices	$r_s$	$P$
a vs b	0.665	0.031
a vs c	0.709	0.010
a vs d	0.808	0.010
b vs c	0.647	0.031
b vs d	0.676	0.031
c vs d	0.787	0.002

Pairwise Mantel tests between rank correlation matrices ( $r_s$ ) of behavioural scores and their significance ( $P$  value). 'a'–'d' represent the runs. All of these  $P$  values remained significant after Holm's (1979) correction.

life and long developmental time in contrast to those with a 'fast lifestyle'. Accordingly, one may expect that bugs with a more active, exploratory personality may develop faster. We examined whether the length of the fifth larval stage has any effect on personality traits but found no correlation between any of the behavioural variables and the duration of the fifth stage. Further investigations are needed because we observed only a given life period of the bugs. Another explanation for interindividual differences might be the different life history expectations in different life stages (Roff 2002; Wolf et al. 2007; McNamara et al. 2009). By sexual maturity, the rate of growth decreases or becomes zero in many species and therefore we expect maturity to change the value of different behaviours and hence their level of expression (Niemelä et al. 2011). Weed et al. (1997) reported that home cage activity of male rhesus monkeys, *Macaca mulatta*, declined during their early adulthood. Human studies have shown that the greatest decrease in physical activity occurs during adolescence rather than during adulthood and is related to sexual maturation (Bijnen et al. 1998). Several studies (e.g. Wirth-Dziedziolowska et al. 1996; Walsh et al. 2006; Johnson & Sih 2007) have found that juvenile growth rate correlates positively with adult size and thereby with fecundity (Anholt et al. 1991; Plaistow & Siva-Jothy 1996, 1999). Consequently, larvae should first feed, while for an adult reproduction might be more relevant (Roff 1992), that is, larvae might tolerate a higher risk of predation than adults. Therefore, different behaviours or different levels of the same behaviour could be beneficial in different life stages (Wolf et al. 2007). Accordingly, we found that firebug larvae show more risk-prone behaviour than adults and, similarly, nymphs of field crickets use different strategies from adults, as they are bolder (Hedrick & Kortet 2012). However, Hedrick & Kortet (2012) proposed an alternative explanation for the differences between larval and adult behaviour: they assumed that the two forms differ because they are often challenged by different predators. Note, however, that adult variability of phenotype may not always be an adaptive strategy for the current circumstances; it can be a behavioural 'carryover' which remains from an early life stage (Stamps 2003; West et al. 2003; Taborsky 2006).

By comparing which variables showed differential consistency and mean-level consistency, we could infer that the measured personality traits changed in different ways. Age had a strong effect on all variables that identified activity traits: bugs' activity decreased immediately after the final moult, but later it seemed to increase again (Fig. 3). One may argue that this is simply the effect of the physiological changes induced by the final moult. When bugs were tested after moult, however, they always had fully hardened exoskeletons. Therefore we presume that moult-induced changes were over by the time of the tests.

In conclusion, we found that different behaviours changed differently across a major life stage transition in the firebug. To catch this complexity fully we need the indexes proposed by Stamps & Groothuis (2010). It is still a mystery how and why personality changes during this important transition. To answer the

former question, studying hormonal reorganization at sexual maturity (O'Dor & Wells 1978) may be useful. For the latter, detailed study of personality changes during the final ecdysis in individuals with different life history expectations, that is, the winged and unwinged forms of the firebug (Gyuris et al. 2011), could be a promising direction.

## Acknowledgments

We are indebted to V. Bókony, M. Földvári, N. Jánosik, A. Tartally, J. Tökölyi and two anonymous referees for their useful comments and suggestions that helped to improve the manuscript. Our work was partially supported by the Hungarian Scientific Research Fund (OTKA, no. K75696) and by the TAMOP 4.2.1./B-09/1/KONV-2010-0007 project. The project is implemented through the New Hungary Development Plan, cofinanced by the European Social Fund and the European Regional Development Fund. The publication is supported by the TÁMOP-4.2.2./B-10/1-2010-0024 project. The project is cofinanced by the European Union and the European Social Fund.

## References

- Anholt, B. R., Marden, J. H. & Jenkins, D. M. 1991. Patterns of mass gain and sexual dimorphism in adult dragonflies (Insecta, Odonata). *Canadian Journal of Zoology*, **69**, 1156–1163.
- Bates, D. & Maechler, M. 2010. lme4: Linear mixed-effects models using Eigen and R package version 0.999375-36. <http://CRAN.R-project.org/package=lme4>.
- Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B*, **274**, 755–761. doi:10.1098/rspb.2006.0199.
- Bell, A. M. & Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **68**, 1339–1348. doi:10.1016/j.anbehav.2004.05.007.
- Bijnen, F. G., Feskens, E. J., Caspersen, C. J., Mosterd, W. L. & Kroanhout, D. 1998. Age, period, and cohort effects on physical activity among elderly men during 10 years of follow-up; the Zutphen Elderly Study. *Journal of Gerontology A*, **53**, M235–M241.
- Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361–368. doi:10.1016/j.tree.2008.04.003.
- Crawley, M. J. 2007. *The R book*. Chichester: J. Wiley.
- Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.
- Dingemans, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.
- Dray, S. & Dufour, A. B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.
- Edenbrow, M. & Croft, D. P. 2011. Behavioural types and life history strategies during ontogeny in the mangrove killifish, *Kryptolebias marmoratus*. *Animal Behaviour*, **82**, 731–741.
- Gyuris, E., Ferő, O., Tartally, A. & Barta, Z. 2011. Individual behaviour in firebugs (*Pyrrhocoris apterus*). *Proceedings of the Royal Society B*, **278**, 628–633. doi:10.1098/rspb.2010.1326.
- Hedrick, A. V. & Kortet, R. 2012. Sex differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology*, **66**, 407–412. doi:10.1007/s00265-011-1286-z.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.
- Johnson, J. C. & Sih, A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour*, **74**, 1131–1138. doi:10.1016/j.anbehav.2007.02.006.
- Legendre, P. 2005. Species associations: Kendall coefficient of concordance revisited. *Journal of Agricultural, Biological, and Environmental Statistics*, **10**, 226–245.
- Lindstrom, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343–348.
- Lummaa, V. & Clutton-Brock, T. 2002. Early development, survival and reproduction in humans. *Trends in Ecology & Evolution*, **17**, 141–147.
- McNamara, J. M. 1996. Risk-prone behaviour under rules which have evolved in a changing environment. *American Zoologist*, **36**, 484–495.
- McNamara, J. M., Houston, A. I., Barta, Z., Scheuerlein, A. & Fromhage, L. 2009. Deterioration, death and the evolution of reproductive restraint in late life. *Proceedings of the Royal Society B*, **276**, 4061–4066.
- Maechler, M., Rousseeuw, P., Struyf, A. & Hubert, M. 2005. *Cluster Analysis Basics and Extensions*. <http://cran.r-project.org/web/packages/cluster/citation.html>.
- Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. London: Chapman & Hall.

- Mathot, K. J., Godde, S., Careau, V., Thomas, D. W. & Giraldeau, L.-A. 2009. Testing variance-sensitive foraging using individual differences in basal metabolic rate. *Oikos*, **118**, 545–552.
- Niemelä, P. T., Vainikka, A., Hedrick, A. V. & Kortet, R. 2011. Integrating behaviour with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology*. Published online 23 November 2011. doi:10.1111/j.1365-2435.2011.01939.x.
- O'Dor, R. K. & Wells, M. J. 1978. Reproduction versus somatic growth: hormonal control in *Octopus vulgaris*. *Journal of Experimental Biology*, **77**, 15–31.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Sölymos, P., Henry, M., Stevens, H. & Wagner, H. 2009. Vegan: community ecology package, R package version 1.15-3. <http://vegan.r-forge.r-project.org/>, <http://cran.r-project.org/>.
- Plaistow, S. & Siva-Jothy, M. T. 1996. Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proceedings of the Royal Society B*, **263**, 1233–1239.
- Plaistow, S. & Siva-Jothy, M. T. 1999. The ontogenetic switch between odonate life history stages: effects on fitness when time and food are limited. *Animal Behaviour*, **58**, 659–667.
- R Development Core Team 2008. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318, doi:10.1111/j.1469-185X.2007.00010.x.
- Réale, D., Garant, D., Humbries, M. M., Bergeron, P., Careau, V. & Montiglio, P. E. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B*, **365**, 4051–4063.
- Roberts, B. W. & Robins, R. W. 2004. Person-environment fit and its implications for personality development: a longitudinal study. *Journal of Personality*, **72**, 89–110.
- Roberts, B. W., Caspi, A. & Moffitt, T. E. 2001. The kids are alright: growth and stability in personality development from adolescence to adulthood. *Journal of Personality and Social Psychology*, **81**, 670–683, doi:10.1037/0022-3514.81.4.670.
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. London: Chapman & Hall.
- Roff, D. 2002. *Evolution of Life Histories*. Cambridge, Massachusetts: Sinauer.
- Rödel, H. G. & Meyer, S. 2011. Early development influences ontogeny of personality types in young laboratory rats. *Developmental Psychobiology*, **53**, 601–613.
- Rödel, H. G., Holst, von D. & Kraus, C. 2009. Family legacies: short- and long-term fitness consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*, **78**, 789–797.
- Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277, doi:10.1086/422893.
- Sinn, D. L., Gosling, S. D. & Moltchanivskyj, N. A. 2008. Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. *Animal Behaviour*, **75**, 433–442.
- Socha, R. 1993. *Pyrrhocoris apterus* (Heteroptera): an experimental model species: a review. *European Journal of Entomology*, **90**, 241–286.
- Stamps, J. A. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. *Animal Behaviour*, **66**, 1–13.
- Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, **10**, 355–363.
- Stamps, J. & Groothuis, T. G. G. 2010. The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, **85**, 301–325, doi:10.1111/j.1469-185X.2009.00103.x.
- Taborsky, M. 2006. The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B*, **273**, 741–750.
- Walsh, M. R., Munch, S. B., Chiba, S. & Conover, D. O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters*, **9**, 142–148.
- Weed, J. L., Lane, M. A., Roth, G. S., Speer, D. L. & Ingram, D. K. 1997. Activity measures in rhesus monkeys on long-term calorie restriction. *Physiology & Behavior*, **62**, 97–103.
- West, M. J., King, A. P. & White, D. J. 2003. The case for developmental ecology. *Animal Behaviour*, **66**, 617–622.
- Wirth-Dziedziolowska, E., Czumińska, K., Reklewska, B. & Katkiewicz, M. 1996. Life time reproductive performance and functional changes in reproductive organs of mice selected divergently for body size over 90 generations. *Animal Science Papers and Reports*, **14**, 187–198.
- Wolf, M., van Doorn, C. S., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–585, doi:10.1038/nature05835.