



Intra-individual variation in exploration behaviour in a largely aquatic frog: effects of sex and personality traits

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Behavioural plasticity is important for survival and to adapt to a dynamic environment. However, it is known that many animals exhibit fixed behavioural responses termed behavioural syndromes. That said, even when exhibiting such fixed behavioural responses, animals still show variability in their behaviour. We here evaluate the variability in exploration behaviour in the frog *Silurana (Xenopus) tropicalis* by quantifying two different metrics of variability: the absolute difference between two sets of measurements, and the individual stability statistic. Our results show differences in the intra-individual variability between groups of frogs that can be assigned to different behavioural syndromes. Marked differences in variability also occur between males and females, with males being more stereotyped in their responses. Frogs identified as belonging to different behavioural groups (i.e. shy, intermediate, and bold) differed in the variability of the expression of these strategies, with bold individuals being more stereotypic in the exploration of an identical, novel environment. These observations may have implications for the evolution of behaviour in natural populations.

Key words: locomotion, amphibian, variability, behaviour, exploration

INTRODUCTION

Behaviour is a major component of life and is related to fitness and population survival (Smith & Blumstein, 2008; Wolf & Weissing, 2012). Behaviour impacts feeding and locomotion (Sustaita et al., 2013), hunting (Steele & Anderson, 2006), reproductive success (Moore et al., 2005), territory defence (Wells, 1977), the exploration of novel environments (Simmons & Thomas, 2004), as well as anti-predator responses (Millot et al., 2009). Although behaviour was initially considered to be highly variable, research over the past few decades has shown that fixed individual behavioural strategies exist, typically termed personality traits or behavioural syndromes (Briffa & Weiss, 2010). These behavioural syndromes describe the persistence of a behavioural strategy across time and behavioural contexts. Behavioural syndromes are of interest because they have been documented across the entire animal kingdom and suggest a genetic basis of behaviour (Sih et al., 2004). Despite the fact that individuals may have fixed behavioural strategies, behavioural responses are not invariant and variability exists even within a given behavioural strategy.

This variability in behavioural response is directly linked to the adaptive nature of behaviour in contexts such as predation or predator avoidance (Niemelä et al., 2012;

Furtbauer et al., 2015). Phenotypic plasticity characterises the component of a behavioural response that is context dependent, and reaction norms describe the behavioural shift occurring due to behavioural plasticity. These are two key elements describing potential variability in behaviour. Depending on individuals, reaction norms can be different and illustrate dynamic responses to variable environmental contexts (Dingemanse & Wolf, 2013). Behavioural plasticity has been observed in several species (Dingemanse et al., 2009) and is intimately linked to the evolutionary responses of animals in variable environments (Foster & Sih, 2013; Snell-Rood, 2013). In this context, understanding behavioural plasticity and the complexity of behavioural responses to variable and changing environments is of interest given the major and global modifications of natural habitats due to anthropogenic factors, including global warming and habitat fragmentation and destruction.

Here, we analyze exploration behaviour in the frog *Silurana (Xenopus) tropicalis* (Gray, 1864). Exploration behaviour is a complex behaviour that is fitness relevant (Smith & Blumstein, 2008). Previously, we (Videlier et al., 2014) characterised three distinct and repeatable exploration syndromes in this species: shy, intermediate and bold. Moreover, we demonstrated significant differences between the sexes, with males being bolder than females (Videlier et al., 2015) and similar

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exploration syndrome clusters within the sexes. Yet, the variability in the behavioural responses within each sex or exploration syndrome in a fixed behavioural context has not been explored. Here, we use two different metrics to analyse the variability shown by individuals in the expression of behavioural syndromes: the absolute difference between two or more sets of measurements (Diff-values) and a more complex indicator of variability termed the individual stability statistic (ISS) (Dingemanse et al., 2009). We use these to quantify variability in behaviour between sexes and individuals that show stable exploration syndromes.

MATERIALS AND METHODS

Animals

Silurana tropicalis ($N = 86$) were caught in the wild in Cameroon in 2009 (permit number 000117/MINRESI/B00/C00/C10/C13). Species identification was confirmed through genetic analysis (V. Gvoždík, personal communication). An additional ten individuals that were bred in captivity were added to the data set. As no qualitative differences were observed in exploration behaviour between the captive bred and wild-caught individuals we decided to pool them for further analyses. Animals were housed by sex in groups of 8 to 12 individuals at the Muséum National d'Histoire Naturelle (MNHN) in Paris and maintained in 21-L tanks mounted on three-shelf stand-alone frog racks (Aquaneering, Inc., San Diego, CA, USA) with the water temperature set at 24 °C. This temperature is close to the optimal performance temperature of *S. tropicalis* (Herrel & Bonneaud, 2012) and similar to temperatures measured under field conditions in ponds in the forest (Careau et al., 2014). Animals were fed with beef heart and mosquito larvae twice weekly. All individuals were pit-tagged (Nonatec, Rodange, Luxembourg) for unique identification. Fifty nine females and thirty seven males were used for the present study, which was performed in 2014. All experiments were performed in accordance with European ethical and legal regulations related to animal welfare and experimentation. Behavioural recordings were approved by the local institutional ethics committee at the MNHN (#68-25). All individuals were in good condition and alive at the end of the experiments with no signs of weight loss.

Behavioural analyses

All frogs were maintained in the laboratory under identical conditions for four years before testing, and had not been used for behavioural tests prior to these experiments. For each trial, animals were released in a rectangular container (height: 40 cm, length: 100 cm, width: 20 cm) with a water level of 20 cm maintained at a temperature of 24 ± 2 °C (Videliér et al., 2014). Water was changed with water from the home cages between recordings. Animals were introduced in a clean tank and left quietly for 5 min before the onset of the recordings. Shelters (opaque ceramic 'turtle huts' of 12 x 12.5 x 5.5 cm; ZooMed, San Luis Obispo, CA, U.S.A.) were placed at the two extremities. Frogs were filmed for 60 minutes

with a Quickcam Pro 500 (Logitech, Inc. at Romanel-sur-Morges, Switzerland) set at 15 frames per second. Each individual was tested three times at different times of the day (morning: 09:00 am to 12:00 pm; early afternoon: 12:00–04:00 pm; late afternoon: 04:00–08:00 pm) in a randomised way. This allowed us to test the repeatability of behaviour across different activity periods and also to test the variability in behaviour. Videos were analysed using the ProAnalyst software (Xcitex, Inc., Cambridge, MA, USA) by tracking all movements of frogs during their exploration of the environment. Coordinates of the snout-tip as a marker of individuals were extracted and used to quantify the movements of each individual from which a number of variables were extracted: the total distance moved in 60 minutes (cm); the number of all movements and complete roundtrips; the maximal, minimal, and average speed of movement (cms-1); the latency of the first, the second and the last movement (s); the average, minimal, and maximal duration of a roundtrip with pauses (s); the entire duration of exploration with and without pauses(s); the total and average duration spent hidden between two roundtrips(s); the average number of pauses and the number of roundtrips away from the wall of the aquarium. See Videliér et al. (2014, 2015) for a definition of the variables.

Measures of variability

Two methods were used to quantify the variability in the behavioural parameters listed higher.

The first is the measure of the absolute difference in the \log_{10} -transformed values between the three trials for each individual (i.e. difference between trials 3 and 1; between trials 3 and 2; and between trials 2 and 1), hereafter named Diff-values; where X is the \log_{10} -transformed value of one of the eighteen behavioural traits and t_1 and t_2 are two of the three recorded trials. The repeatability of these Diff-values was tested across the three possible combinations (the difference between trials 3 and 1; between trials 3 and 2; and between trials 2 and 1) using Pearson correlations (Pearson, 1909). Low Diff-values indicate a stable behaviour and high Diff-values indicate more labile traits with high variability.

$$\text{Diff-values } X_{t_1-t_2} = X(t_1) - X(t_2)$$

The second method used was the ISS (individual stability statistic) proposed by Asendorp (1990) and reviewed by Dingemanse and collaborators (2009); where X is the standardized \log_{10} -transformed value of one of the eighteen behavioural traits and t_1 and t_2 are two of the three trials. If the ISS value is close to one, the behavioural parameter is stable and shows little variability. To test the repeatability of the ISS we also used Pearson correlations between all possible combinations.

$$\text{ISS } X_{t_1-t_2} = 1 - ([X(t_1) - X(t_2)]^2 / 2)$$

Diff and ISS values were tested for normality and homoscedascity before further statistical testing. ANOVAs and Tukey HSD post-hoc tests were performed using Diff-values and ISS values to test for differences

between the sexes and between individuals categorised into different behavioural syndromes within each sex (Tables 2 and 3). All analyses were performed in R (R Development Core Team, 2010). Bonferroni corrected results are indicated in Tables 1-3 by an asterisk.

RESULTS

Absolute differences in trait values

The Diff-values (trial 3 vs. trial 2, trial 3 vs. trial 1, trial 2 vs. trial 1, further referred to as 3-2, 3-1, 2-1) for each behavioural parameter were significantly correlated (all $P < 0.05$; Table 1) with correlations between these behavioural parameters ranging from 0.38 to 0.68 (Table 1). Absolute Diff-values showed a difference between sexes (Table 2). For the Diff-set composed of the first two observations (2-1), speed (maximal, minimal and average), the duration of a roundtrip (maximal, minimal and average), the latency of the last movement, the total time of exploration, and the total distance traveled during the exploration showed significant differences between the sexes, with females scoring significantly higher than males (i.e. being more variable). When considering the other difference sets (3-1 and 3-2), the number of behavioural parameters showing a sex difference decreased, with only the variability of parameters linked to speed remaining significantly different between the sexes.

Each sex can be divided into three behavioural groups or syndromes as demonstrated previously (Videlier et al., 2015). For females, behavioural groups show differences in all Diff-values except for the minimal speed (Table 3). For males, syndromes are different with the exception of Diff set 2-1. Male differences were observed for most variables except for the number of complete roundtrips, the duration of exploration without pauses, the average number of pauses, and the number of movements away from the walls. For both males and females, the Diff-values were greater for shy individuals relative to those for other behavioural groups (Table 3) indicating that individual behavioural variability was greater for shy frogs.

Individual Stability Statistics

All ISS parameters show a correlation between at least two of the three sets calculated ($P < 0.05$; see Table 1). The correlation coefficients varied between 0.16 and 0.55. As observed with the Diff-values, the ISS between the first two measures (2 vs. 1) for speed (average, maximal and minimal), the duration of a roundtrip (maximal, average and minimal), the latency of the first movement and the last movement, the duration of the total exploration, and the distance explored are different between sexes (Table 2). We also observe a decrease over time in the number of variable behavioural parameters that differs significantly between sexes, with only the variability

Table 1. Results of the Pearson correlations testing for the repeatability of the Diff and ISS values

	Diff-values		ISS									
	Diff3-1vs-Diff2-1	Diff3-2vs-Diff2-1	Diff3-1vsDiff3-2				Diff3-1vsDiff2-1		Diff3-2vsDiff2-1		Diff3-1vsDiff3-1	
			F	P	F	P	F	P	F	P	F	P
number of complete roundtrips	0.47	<.0001*	-0.53	<.0001*	0.47	<.0001*	0.34	<.0001*	0.24	0.02	0.18	0.08
number of movements	0.44	<.0001*	-0.52	<.0001*	0.53	<.0001*	0.24	0.02	0.22	0.03	0.29	<.01
total distance moved	0.41	<.0001*	-0.48	<.0001*	0.60	<.0001*	0.25	0.01	0.27	0.01	0.58	<.0001*
average speed	0.41	<.0001*	-0.48	<.0001*	0.60	<.0001*	0.32	<.01	0.55	<.0001*	0.29	<.01
minimal speed	0.44	<.0001*	-0.45	<.0001*	0.60	<.0001*	0.21	0.04	0.11	0.29	0.68	<.0001*
maximal speed	0.44	<.0001*	-0.45	<.0001*	0.60	<.0001*	0.31	<.01	0.52	<.0001*	0.30	<.01
number of movements away from the wall	0.53	<.0001*	-0.44	<.0001*	0.52	<.0001*	0.26	0.01	0.16	0.01	0.08	0.11
average number of pauses	0.43	<.0001*	-0.68	<.0001*	0.37	0.0002*	0.23	0.02	0.6	<.0001*	0.13	0.19
average duration of a roundtrip	0.44	<.0001*	-0.49	<.0001*	0.56	<.0001*	0.35	<.0001*	0.26	0.01	0.46	<.0001*
minimal duration of a roundtrip	0.46	<.0001*	-0.55	<.0001*	0.48	<.0001*	0.45	<.0001*	0.29	<.01	0.42	<.0001*
maximal duration of a roundtrip	0.45	<.0001*	-0.44	<.0001*	0.60	<.0001*	0.21	0.04	0.29	<.01	0.49	<.0001*
latency of the first movement	0.44	<.0001*	-0.50	<.0001*	0.56	<.0001*	0.42	<.0001*	0.28	<.01	0.29	<.01
latency of the second movement	0.45	<.0001*	-0.51	<.0001*	0.53	<.0001*	0.26	0.01	0.36	<.0001*	0.39	<.0001*
latency of the last movement	0.44	<.0001*	-0.42	<.0001*	0.63	<.0001*	0.31	<.01	0.27	<.01	0.62	<.0001*
duration of all movements with pauses	0.41	<.0001*	-0.48	<.0001*	0.60	<.0001*	0.18	0.09	0.27	<.01	0.57	<.0001*
duration of exploration without pauses	0.40	<.0001*	-0.53	<.0001*	0.56	<.0001*	0.08	0.41	0.35	<.0001*	0.38	<.0001*
total time spent hidden	0.42	<.0001*	-0.53	<.0001*	0.55	<.0001*	0.25	0.01	0.24	0.02	0.46	<.0001*
average time spent hidden	0.43	<.0001*	-0.53	<.0001*	0.54	<.0001*	0.27	<.01	0.29	<.01	0.38	<.0001*

bold values are significant. * significant after Bonferroni correction.

Table 2. Results of the ANOVAs testing for differences between the sexes in behavioural plasticity (Diff and ISS values). Bold values indicate significant *P*-values and highlighted cells indicate variables with significant differences. d.f. = 1,95 for all tests.

	Set 2 vs. set 1						Set 3 vs. set 1						Set 3 vs. set 2					
	Diff-Values			ISS			Diff-Values			ISS			Diff-Values			ISS		
	F	P		F	P		F	P		F	P		F	P		F	P	
number of complete roundtrips	1.13	0.29	m=f	1.32	0.25	m=f	0.57	0.45	m=f	0.27	0.60	m=f	1.64	0.20	m=f	2.37	0.13	m=f
total number of movements	3.17	0.08	m=f	3.04	0.08	m=f	0.49	0.49	m=f	0.52	0.47	m=f	0.95	0.33	m=f	1.96	0.17	m=f
average speed	23.49	<0.001*	f>m	13.36	<0.001*	m>f	6.85	0.01	f>m	4.07	0.05	m>f	11.76	<0.001*	f>m	6.78	0.01	m>f
maximal speed	22.18	<0.001*	f>m	14.38	<0.001*	m>f	6.18	0.01	f>m	4.08	0.05	m>f	14.51	<0.001*	f>m	10.00	<0.01	m>f
minimal speed	22.96	<0.001*	f>m	13.39	<0.001*	m>f	14.97	<0.001*	f>m	8.30	<0.01	m>f	10.84	<0.01	f>m	6.86	0.01	m>f
average duration of a roundtrip	11.74	<0.001*	f>m	9.86	<0.01	m>f	2.47	0.12	m=f	3.23	0.08	m=f	1.94	0.17	m=f	2.49	0.12	m=f
maximal duration of a roundtrip	8.72	<0.001*	f>m	8.70	<0.01	m>f	1.56	0.22	m=f	2.50	0.12	m=f	1.90	0.17	m=f	2.78	0.10	m=f
minimal duration of a roundtrip	6.06	0.02	f>m	5.89	0.02	m>f	1.37	0.25	m=f	3.27	0.07	m>f	2.57	0.11	m=f	2.33	0.13	m=f
latency of the first movement	4.38	0.04	f>m	5.96	0.02	m>f	3.27	0.07	m=f	4.33	0.04	m>f	1.44	0.23	m=f	2.35	0.13	m=f
latency of the second movement	2.31	0.13	m=f	3.15	0.08	m=f	0.21	0.65	m=f	0.70	0.41	m=f	0.27	0.61	m=f	0.47	0.49	m=f
latency of the last movement	9.85	<0.01	f>m	8.56	<0.01	m>f	2.69	0.10	m=f	2.31	0.13	m=f	2.91	0.09	m=f	2.57	0.11	m=f
duration of all movements with pauses	9.83	<0.01	f>m	8.29	<0.01	m>f	2.44	0.12	m=f	1.41	0.24	m=f	1.92	0.17	m=f	1.20	0.28	m=f
duration of exploration without pauses	1.50	0.22	m=f	1.50	0.22	m=f	0.14	0.71	m=f	0.01	0.93	m=f	0.01	0.93	m=f	0.21	0.65	m=f
total time spent hidden	2.95	0.09	m=f	2.50	0.12	m=f	0.54	0.47	m=f	0.35	0.56	m=f	0.55	0.46	m=f	0.38	0.54	m=f
average time spent hidden	3.39	0.07	m=f	3.61	0.06	m=f	0.05	0.82	m=f	0.00	0.95	m=f	0.23	0.64	m=f	0.06	0.81	m=f
average number of pauses	2.09	0.15	m=f	1.92	0.17	m=f	0.00	0.99	m=f	0.09	0.77	m=f	1.46	0.23	m=f	1.70	0.20	m=f
number of movements away from the wall	0.35	0.55	m=f	0.07	0.79	m=f	0.08	0.77	m=f	0.27	0.60	m=f	0.48	0.49	m=f	0.24	0.63	m=f
total distance moved	6.51	0.01	f>m	6.54	0.01	m>f	2.57	0.11	m=f	2.09	0.15	m=f	3.08	0.08	m=f	3.32	0.07	m=f

* significant after Bonferroni correction for multiple testing. m = male; f = female

in speed remaining different in all cases (Table 2). In addition, the ISS also differs between behavioural groups. As observed with Diff-values, there was no significant difference in minimal speed, the number of complete roundtrips, the total number of movements, and the number of movements away from the wall for female behavioural groups. For males ISS, all syndromes show differences except for the set 2-1 as observed for the Diff-values. However, for both females and males, the shy group has lower ISS values compared to the bold or intermediate group (Table 3) suggesting again a greater variability for shy frogs.

DISCUSSION

Sex differences in individual variation in behaviour

Sexual dimorphism is observed across the entire animal kingdom and is a direct response to the optimisation of reproduction in the two sexes (Lande, 1980; Hedrick & Temeles, 1989). Although sexual dimorphism in morphological traits is well documented, other phenotypic traits including behaviour, metabolism, and performance can also be sexually dimorphic (Shine, 1979; Payne, 1984; Post et al., 1999; Shillington, 2005; Labus et al., 2013; Tomlinson & Phillips, 2015). In

frogs, sexual dimorphism in body size, morphology, and performance has been documented (Le Galliard & Ferrière, 2008; Herrel et al., 2014; Gordon et al., 2015). Moreover, distinct differences in the behaviour of the two sexes has been demonstrated in frogs (Kelley, 1988). *Silurana tropicalis* is no exception with females being larger than males, but males having relatively longer limbs and a relatively greater endurance capacity (Herrel et al., 2012). Moreover, females of this species are shy than males (Videliier et al., 2015).

Our analyses (Table 2) also show that females display larger differences between the first two sets of measurements and generally lower ISS values than males. Surprisingly this suggests that females show a greater variability in the expression of their behaviour than males. Shy individuals are averse to risk taking and explore their environment less. Yet, despite restricting their movements, females show more intrinsic variability in the way they explore their environment. Interestingly, over time the difference between the sexes is reduced to variables relating to differences in the variability in the speed of their exploration. Locomotor speed often differs between the sexes, including in snakes (Shine et al., 2003), lizards (Lailvaux et al., 2003), and frogs (Herrel & Bonneaud, 2012; Herrel et al., 2012). However, these

Table 3. ANOVAs testing for differences in behavioral plasticity between behavioural groups. Both sexes were tested separately. Bold values indicate significant *P*-values and highlighted cells indicate variables with significant differences. d.f. = 2,95 for all tests.

MALE // Diff values	Set 2 vs. set 1			Set 3 vs. set 1			Set 3 vs. set 2		
	F	P		F	P		F	P	
number of complete roundtrips	2.15	0.13	Bold=Interm=Shy	0.12	0.89	Bold=Interm=Shy	0.80	0.46	Bold=Interm=Shy
total number of movements	1.22	0.31	Bold=Interm=Shy	5.20	0.01	(Bold=Interm)<Shy	2.95	0.07	Bold=Interm=Shy
average speed	1.86	0.16	Bold=Interm=Shy	13.65	<0.001*	(Bold=Interm)<Shy	21.51	<0.001*	(Bold=Interm)<Shy
maximal speed	0.87	0.43	Bold=Interm=Shy	10.64	<0.001*	(Bold=Interm)<Shy	15.39	<0.001*	(Bold=Interm)<Shy
minimal speed	2.15	0.13	Bold=Interm=Shy	6.11	<0.01	(Interm<Shy)=Bold	8.46	<0.01	(Bold=Interm)<Shy
average duration of a roundtrip	0.57	0.57	Bold=Interm=Shy	9.87	<0.001*	(Bold=Interm)<Shy	24.77	<0.001*	(Bold=Interm)<Shy
maximal duration of a roundtrip	0.28	0.75	Bold=Interm=Shy	8.76	<0.001*	(Bold=Interm)<Shy	27.55	<0.001*	(Bold=Interm)<Shy
minimal duration of a roundtrip	1.42	0.25	Bold=Interm=Shy	4.36	0.02	(Interm<Shy)=Bold	10.29	<0.001*	(Bold=Interm)<Shy
latency of the first movement	2.00	0.15	Bold=Interm=Shy	2.07	0.14	Bold=Interm=Shy	4.49	0.02	(Bold<Shy)=Interm
latency of the second movement	1.52	0.23	Bold=Interm=Shy	7.71	<0.01	(Bold=Interm)<Shy	2.22	0.12	Bold=Interm=Shy
latency of the last movement	0.29	0.75	Bold=Interm=Shy	19.29	<0.001*	(Bold=Interm)<Shy	17.05	<0.001*	(Bold=Interm)<Shy
duration of all movements with pauses	2.79	0.08	Bold=Interm=Shy	27.56	<0.001*	(Bold=Interm)<Shy	35.75	<0.001*	(Bold=Interm)<Shy
duration of exploration without pauses	4.11	0.02	(Interm<Shy)=Bold	2.10	0.14	Bold=Interm=Shy	4.08	0.02	(Bold<Shy)=Interm
total time spent hidden	2.21	0.13	Bold=Interm=Shy	15.71	<0.001*	(Bold=Interm)<Shy	7.03	<0.01	(Bold=Interm)<Shy
average time spent hidden	22.45	0.10	Bold=Interm=Shy	11.89	<0.001*	(Bold=Interm)<Shy	7.67	<0.01	(Bold=Interm)<Shy
average number of pauses	0.27	0.77	Bold=Interm=Shy	0.26	0.77	Bold=Interm=Shy	0.25	0.78	Bold=Interm=Shy
number of movements away from the wall	0.90	0.42	Bold=Interm=Shy	0.17	0.85	Bold=Interm=Shy	1.07	0.35	Bold=Interm=Shy
total distance moved	2.02	0.15	Bold=Interm=Shy	17.60	<0.001*	(Bold=Interm)<Shy	26.90	<0.001*	(Bold=Interm)<Shy

* significant after Bonferroni correction for multiple testing.

MALE // ISS values	Set 2 vs. set 1			Set 3 vs. set 1			Set 3 vs. set 2		
	F	P		F	P		F	P	
number of complete roundtrips	0.87	0.43	Bold=Interm=Shy	0.18	0.84	Bold=Interm=Shy	0.43	0.66	Bold=Interm=Shy
total number of movements	1.19	0.32	Bold=Interm=Shy	4.21	0.02	Bold=Interm=Shy	1.71	0.20	Bold=Interm=Shy
average speed	2.35	0.11	Bold=Interm=Shy	18.59	<0.0001*	Shy<(Bold=Interm)	16.95	<0.0001*	Shy<(Bold=Interm)
maximal speed	1.89	0.17	Bold=Interm=Shy	16.73	<0.0001*	Shy<(Bold=Interm)	14.17	<0.0001*	Shy<(Bold=Interm)
minimal speed	1.15	0.33	Bold=Interm=Shy	6.93	<0.01	Shy<(Bold=Interm)	10.26	<0.001*	Shy<(Bold=Interm)
average duration of a roundtrip	0.91	0.41	Bold=Interm=Shy	10.07	<0.001*	Shy<(Bold=Interm)	24.70	<0.0001*	Shy<(Bold=Interm)
maximal duration of a roundtrip	0.47	0.63	Bold=Interm=Shy	11.00	<0.001*	Shy<(Bold=Interm)	30.50	<0.0001*	Shy<(Bold=Interm)
minimal duration of a roundtrip	1.05	0.36	Bold=Interm=Shy	3.20	0.05	Bold=Interm=Shy	6.20	0.01	Shy<(Bold=Interm)
latency of the first movement	2.68	0.08	Bold=Interm=Shy	2.07	0.14	Bold=Interm=Shy	6.36	<0.01	Shy<(Bold=Interm)
latency of the second movement	2.11	0.14	Bold=Interm=Shy	7.05	<0.01	Shy<(Bold=Interm)	2.52	0.0953	Bold=Interm=Shy
latency of the last movement	0.47	0.63	Bold=Interm=Shy	21.56	<0.0001*	Shy<(Bold=Interm)	20.60	<0.0001*	Shy<(Bold=Interm)
duration of all movements with pauses	2.46	0.10	Bold=Interm=Shy	28.80	<0.0001*	Shy<(Bold=Interm)	46.52	<0.0001*	Shy<(Bold=Interm)
duration of exploration without pauses	3.13	0.06	Bold=Interm=Shy	1.07	0.35	Bold=Interm=Shy	3.10	0.06	Bold=Interm=Shy
total time spent hidden	2.66	0.08	Bold=Interm=Shy	18.71	<0.0001*	Shy<(Bold=Interm)	8.31	<0.01	Shy<(Bold=Interm)
average time spent hidden	3.03	0.06	Bold=Interm=Shy	17.24	<0.0001*	Shy<(Bold=Interm)	11.69	<0.001*	Shy<(Bold=Interm)
average number of pauses	0.29	0.75	Bold=Interm=Shy	0.14	0.87	Bold=Interm=Shy	0.31	0.732	Bold=Interm=Shy
number of movements away from the wall	0.69	0.69	Bold=Interm=Shy	0.03	0.97	Bold=Interm=Shy	0.61	0.55	Bold=Interm=Shy
total distance moved	1.21	0.31	Bold=Interm=Shy	20.56	<0.0001*	Shy<(Bold=Interm)	25.59	<0.0001*	Shy<(Bold=Interm)

* significant after Bonferroni correction for multiple testing.

FEMALE // Diff values	Set 2 vs. set 1			Set 3 vs. set 1			Set 3 vs. set 2		
	F	P		F	P		F	P	
number of complete roundtrips	3.67	0.03	(Shy<Interm)=Bold	4.50	0.01	Shy<(Bold=Interm)	4.12	0.02	(Shy<Bold)=Interm
total number of movements	3.61	0.03	(Bold<Interm)=Shy	1.54	0.22	Bold=Interm=Shy	0.56	0.58	Bold=Interm=Shy
average speed	7.31	<0.001*	Bold<(Interm=Shy)	4.44	0.02	(Bold<Interm)=Shy	4.88	0.01	(Bold<Interm)=Shy
maximal speed	5.81	<0.001*	(Bold<Interm)=Shy	4.56	0.01	(Bold<Interm)=Shy	7.89	<0.001*	(Bold<Interm)=Shy
minimal speed	1.53	0.022	Bold=Interm=Shy	0.22	0.8	Bold=Interm=Shy	0.25	0.78	Bold=Interm=Shy
average duration of a roundtrip	15.00	<0.001*	Bold<Interm<Shy	9.93	<0.001*	Bold<Interm<Shy	5.19	<0.01	(Bold<Interm)=Shy
maximal duration of a roundtrip	12.56	<0.001*	Bold<(Interm=Shy)	5.71	<0.01	(Bold<Shy)=Interm	3.44	0.04	(Bold<Interm)=Shy
minimal duration of a roundtrip	16.55	<0.001*	Bold<Interm<Shy	10.72	<0.001*	(Bold=Interm)<Shy	3.15	0.05	Bold=Interm=Shy
latency of the first movement	10.01	<0.001*	(Bold=Interm)<Shy	10.41	<0.001*	Bold<Interm<Shy	3.07	0.05	Bold=Interm=Shy
latency of the second movement	6.89	<0.01	(Bold=Shy)<Interm	7.89	<0.001*	Shy<Bold<Interm	6.26	<0.01	Shy<Bold<Interm
latency of the last movement	9.64	<0.001*	Bold<Interm<Shy	8.70	<0.001*	Bold<(Interm=Shy)	5.79	<0.01	(Bold<Interm)=Shy
duration of all movements with pauses	10.45	<0.001*	Bold<(Interm=Shy)	6.13	<0.01	Bold<(Interm=Shy)	4.01	0.02	(Bold<Interm)=Shy
duration of exploration without pauses	5.81	<0.01	Bold<(Interm=Shy)	2.27	0.11	Bold=Interm=Shy	1.99	0.15	Bold=Interm=Shy
total time spent hidden	9.64	<0.001*	(Bold=Shy)<Interm	9.18	<0.001*	(Bold=Shy)<Interm	5.20	<0.01	(Bold=Shy)<Interm
average time spent hidden	9.08	<0.001*	(Bold=Shy)<Interm	8.38	<0.001*	(Bold=Shy)<Interm	5.58	<0.01	(Bold=Shy)<Interm
average number of pauses	7.75	<0.01	Bold<(Interm=Shy)	5.37	<0.01	Shy<(Bold=Interm)	5.01	<0.01	(Bold<Shy)=Interm
number of movements away from the wall	4.55	0.01	(Shy<Interm)=Bold	3.74	0.03	(Shy<Bold)=Interm	3.58	0.03	(Shy<Bold)=Interm
total distance moved	4.84	0.01	(Bold<Interm)=Shy	3.56	0.03	Bold=Interm=Shy	2.43	0.10	Bold=Interm=Shy

* significant after Bonferroni correction for multiple testing.

FEMALE // ISS values	Set 2 vs. set 1			Set 3 vs. set 1			Set 3 vs. set 2		
	F	P		F	P		F	P	
number of complete roundtrips	1.06	0.35	Bold=Interm=Shy	1.87	0.16	Bold=Interm=Shy	2.54	0.09	Bold=Interm=Shy
total number of movements	2.54	0.09	Bold=Interm=Shy	2.44	2.44	Bold=Interm=Shy	0.56	0.58	Bold=Interm=Shy
average speed	3.58	0.03	Bold=Interm=Shy	3.30	0.04	(Interm<Bold)=Shy	2.57	0.09	Bold=Interm=Shy
maximal speed	2.59	0.08	Bold=Interm=Shy	4.0	0.02	(Interm<Bold)=Shy	4.66	0.01	(Interm<Bold)=Shy
minimal speed	0.94	0.39	Bold=Interm=Shy	0.12	0.89	Bold=Interm=Shy	0.32	0.73	Bold=Interm=Shy
average duration of a roundtrip	15.88	<0.0001*	Shy<Interm<Bold	13.55	<0.0001*	Shy<Interm<Bold	5.49	0.01	(Shy<Bold)=Interm
maximal duration of a roundtrip	10.43	<0.001*	Shy<Interm<Bold	5.85	<0.01	Shy<Interm<Bold	3.70	0.03	Bold=Interm=Shy
minimal duration of a roundtrip	24.76	<0.0001*	Shy<(Bold=Interm)	17.33	<0.0001*	Shy<(Bold=Interm)	5.12	0.01	Shy<(Bold=Interm)
latency of the first movement	17.3	<0.0001*	Shy<(Bold=Interm)	16.72	<0.0001*	Shy<(Bold=Interm)	4.96	0.01	(Shy<Bold)=Interm
latency of the second movement	4.96	0.01	(Interm<Bold)=Shy	7	<0.01	Interm<Bold<Shy	5.98	<0.01	(Interm<Bold)=Shy
latency of the last movement	8.56	<0.001*	Shy<Interm<Bold	8.56	<0.001*	Shy<Interm<Bold	5.31	0.01	(Interm<Bold)=Shy
duration of all movements with pauses	8.2	<0.001*	(Interm=Shy)<Bold	4.88	0.01	(Bold<Shy)=Interm	3.53	0.04	(Interm<Bold)=Shy
duration of exploration without pauses	4.5	0.02	(Interm<Bold)=Shy	1.83	0.17	Bold=Interm=Shy	2.06	0.14	Bold=Interm=Shy
total time spent hidden	7.53	<0.01	(Interm<Bold)=Shy	5.98	<0.01	(Interm<Bold)=Shy	3.33	0.04	Bold=Interm=Shy
average time spent hidden	6.57	<0.01	(Interm<Bold)=Shy	5.88	<0.01	(Interm<Bold)=Shy	4.24	0.02	(Interm<Bold)=Shy
average number of pauses	4.89	0.01	(Interm=Shy)<Bold	2.35	0.11	Bold=Interm=Shy	8.05	<0.001*	Shy<(Bold=Interm)
number of movements away from the wall	2.6	0.08	Bold=Interm=Shy	1.82	0.17	Bold=Interm=Shy	1.95	0.15	Bold=Interm=Shy
total distance moved	3.42	0.04	(Interm<Bold)=Shy	4.00	0.02	(Interm<Bold)=Shy	0.15	0.05	Bold=Interm=Shy

* significant after Bonferroni correction for multiple testing.

are typically measured as maximal locomotor capacity. Here, variability in the voluntary speeds selected during the exploration of a novel environment differed, with males selecting higher speeds that differ less from one trial to the next (Videli er et al., 2015). Voluntary speed can be different from maximal speed and be dependent on condition, on season, and on sex as observed in salamanders (Finkler et al., 2003). Male *S. tropicalis* showed a more stereotyped movement speed across trials. Females, in contrast, adapt their movement speed more based on their experience with the experimental condition. This suggests that both sexes show a different level of flexibility in their behavioural response, even under stable environmental conditions. Whereas behaviour in males thus appears more 'hard-wired', females show evidence of a more dynamic response in the expression of their behaviour.

Variability within behavioural syndromes

In *S. tropicalis* three different behavioural syndromes have been observed: bold, shy, and intermediate (Videli er et al., 2014). These three syndromes were moreover identified for both sexes (Videli er et al., 2015). Our two measures of behavioural variability (Diff and ISS) showed similar results when comparing the three syndromes within each sex. In both sexes, shy frogs show greater differences between two sets of measurements and lower ISS values compared to bold and intermediate frogs. Part of this greater variability may have been caused by the fact that shy frogs move very little. Consequently, any additional movement from one trial to another may impact the Diff or ISS scores to a greater degree than for animals that already move much more, such as intermediate or bold individuals. Bold individuals have been described as more proactive (Sih et al., 2004; Bell, 2007; Frost et al., 2007) with a curiosity to explore (Von Merten & Siemers, 2012) and are generally more aggressive (Kralj-Fi er & Schneider, 2012) compared to shy individuals. Despite the consistency of individuals in their behavioural response, intra-individual variation can be observed (Dingemans et al., 2007; Highcock & Carter, 2014). Bold individuals appear more rigid in their behavioural pattern and show less variability from one trial to the next. This observation is pertinent and this has also been documented in mice and fish (Benus et al., 1990; Sih et al., 2004; Kareklas et al., 2016). To conclude, in general, proactive (bold) individuals appear more stereotyped than reactive (shy) ones. Interestingly, for males, differences between syndromes appear only when comparing the third set of measurements to sets one and two, contrary to females which show consistent differences across all sets of measurements. This further highlights the conservative nature of males showing more stereotyped movements and exploration behaviours.

Habitat fragmentation is known to strongly affect the tropical West-African rainforest belt which is the native home of these frogs (Achard et al., 2002; Wright, 2005). Habitat fragmentation is likely to act on exploration behaviour. Indeed, bold individuals may be selected for to counter the effect of an increase in the distance between isolated fragments (Berg et al., 2010; Buckley

et al., 2013). Consequently natural selection may erode the variability in exploration behaviours observed if exploration behaviour is indeed heritable (Falconer, 1961). Several previous studies have highlighted the heritable nature of exploration behaviour (Dingemans et al., 2002; Van Oers et al., 2004) suggesting that this may also be the case in *S. tropicalis*. The link between boldness and aggression (Quinn & Cresswell, 2005; Wilson & Godin, 2009; Thomson et al., 2011) could constitute another selective advantage of bold individuals, especially in the context of male-male competition and anti-predator behaviour. This may over time induce more stereotyped exploration behaviours in populations, resulting in an overall behavioural specialisation. However, in the context of global change resulting in more variable climatic contexts, generalist individuals may have higher fitness than specialists (Berg et al., 2010; Sih, 2013). Moreover, it has been suggested that generalists maintain gene flow more and can adapt faster to change (Simmons & Thomas, 2004). Thus, our laboratory study of the intra-individual variability of exploration behavioural in *S. tropicalis* highlights how habitat fragmentation could potentially impact this species in the wild. More stereotyped and specialised responses, in addition to the multiple problems already induced by habitat fragmentation, may impact the resilience of a population to environmental change leading possibly to reduced gene flow (Dixo et al., 2009), an increase in local adaptation (Huey et al., 2009), and possibly even species extinction (Hilliers et al., 2008).

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REFERENCES

- Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.P. (2002). Determination of deforestation rates of the world's humid tropical forests. *Science* 297, 999–1002.
- Asendorp, J. (1990). The measurement of individual consistency. *Methodika* 4, 1-23.
- Bell, A.M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B* 274, 755-761.
- Benus, R.F., Den Daas, S., Koolhaas, J.M. & Van Oortmerssen, G.A. (1990). Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. *Behaviour* 112, 176-193.
- Berg, M.P., Kiers, E.T., Driessen, G., Van der Heidjen, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A. & Ellers, J. (2010).

- Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16, 587-598.
- Briffa, M. & Weiss, A. (2010). Animal personality. *Current Biology* 20, 912-914.
- Buckley, L.B., Tewksbury, J.J. & Deutsch, C.A. (2013). Can terrestrial ectotherms escape the heat of climate change by moving? *Proceedings of the Royal Society B* 280, 20131149.
- Careau, V., Biro, P.A., Bonneaud, C., Fokam, E.B. & Herrel, A. (2014). Individual variation in thermal performance curves: swimming burst speed and jumping endurance in wild-caught tropical clawed frogs. *Oecologia* 175, 471-480.
- Dingemanse, N.J. & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Animal Behavior* 85, 1031-1039.
- Dingemanse, N.J., Both, C., Drent, P.J., Van Oers, K. & Van Noordwijk, A.J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behavior* 64, 929-938.
- Dingemanse, N.J., Kazem, A.J.N., Réale, D. & Wright, J. (2009). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution* 25, 81-89.
- Dingemanse, N.J., Wright, J., Anahita, J.N., Thomas, D.K., Hickling, R. & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* 76, 1128-1138.
- Dixo, M., Metzger, J.P., Morgante, J.S. & Zamudio, K.R. (2009). Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. *Biological Conservation* 142, 1560-1569.
- Falconer, D.S. (1961). *Introduction to Quantitative Genetics*. Person, Essex, U.K.
- Finkler, M.S., Sugalski, M.T. & Claussen, D.L. (2003). Sex-related differences in metabolic rate and locomotor performance in breeding spotted salamanders (*Ambystoma maculatum*). *Copeia* 2003, 887-893.
- Foster, S.A. & Sih, A. (2013). Behavioural plasticity and evolution. *Animal Behavior* 85, 1003.
- Frost, A.J., Winrow-Giffen, A., Ashley, P.J. & Sneddon, L.U. (2007). Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings Biological Sciences* 274, 333-339.
- Fürtbauer, I., Pond, A., Heistermann, M. & King, A.J. (2015). Personality, plasticity and predation: linking endocrine and behavioural reaction norms in stickleback fish. *Functional Ecology* 29, 931-940.
- Gordon, S.P., Chen, Y.Y., Yamashita, K., Bejar, C., Wilshire, A. & Cheung, V. (2015). Sex-specific genetic differences in endurance swimming of Trinidadian guppies. *Ecology and Evolution* 5, 5318-5328.
- Hedrick, A. V & Temeles, E.J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* 4, 136-138.
- Herrel, A. & Bonneaud, C. (2012). Temperature dependence of locomotor performance in the tropical clawed frog, *Xenopus tropicalis*. *Journal of Experimental Biology* 215, 2465-2470.
- Herrel, A., Gonwouo, L.N., Fokam, E.B., Ngundu, W.I. & Bonneaud, C. (2012). Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *Journal of Zoology* 287, 311-316.
- Herrel, A., Vasilopoulou-kampitsi, M. & Bonneaud, C. (2014). Jumping performance in the highly aquatic frog, *Xenopus tropicalis*: sex-specific relationships between morphology and performance. *Peer J* 2:e661.
- Highcock, L. & Carter, A.J. (2014). Intraindividual variability of boldness is repeatable across contexts in a wild lizard. *PLoS One* 9, e95179
- Hilliers, A., Veith, M. & Rodel, M.-O. (2008). Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conservation Biology* 22, 762-772.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Álvarez Pérez, H.J. & Garland, T.J. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B* 276, 1939-1948
- Kareklas, K., Arnott, G., Elwood, R.W. & Holland, R.A. (2016). Plasticity varies with boldness in a weakly-electric fish. *Frontiers in Zoology* 13, 22.
- Kelley, D.B. (1988). Sexually dimorphic behaviors. *Annual Reviews in Neuroscience* 11, 225-251.
- Kralj-Fišer, S. & Schneider, J.M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behavior* 84, 197-204.
- Labus, N., Cvijanovic, M. & Vukov, T. (2013). Sexual size and shape dimorphism in *Salamandra salamandra* (Amphibia Caudata, Salamandridae) from the central Balkans. *Archives of Biological Sciences Belgrade* 65, 969-975.
- Lailvaux, S.P., Alexander, G.J. & Whiting, M.J. (2003). Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiological and Biochemical Zoology* 76, 511-521.
- Lande, R. (1980). Sexual Dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34, 292-305.
- Le Galliard, J-F. & Ferrière, R. (2008). Evolution of maximal endurance capacity: natural and sexual selection across age classes in a lizard. *Evolutionary Ecology Research* 10, 157-176.
- Millot, S., Bégout, M. & Chatain, B. (2009). Exploration behaviour and flight response toward a stimulus in three sea bass strains (*Dicentrarchus labrax* L.). *Applied Animal Behavior Science* 119, 108-114.
- Moore, F.L., Boyd, S.K. & Kelley, D.B. (2005). Historical perspective: Hormonal regulation of behaviors in amphibians. *Hormones and Behavior* 48, 373-383.
- Niemelä, P.T., Dirienzo, N. & Hedrick, A. V. (2012). Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behavior* 84, 129-135.
- Payne, R.B. (1984). Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithological Monographs* 33, 1-52.
- Pearson, K. (1909). Determination of the coefficient of correlation. *Science* 30, 23-25.
- Post, E., Langvatn, R., Forchhammer, M.C. & Stenseth, N.C. (1999). Environmental variation shapes sexual dimorphism in red deer. *Proceedings of the National Academy of Sciences U.S.A.* 96, 4467-4471.
- Quinn, J.L. & Cresswell, W. (2005). Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour* 142, 1383-1408.
- R Development Core Team. (2010). *R: A Language and*

- Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Shillington, C. (2005). Inter-sexual differences in resting metabolic rates in the Texas tarantula, *Aphonopelma anax*. *Comparative Biochemistry and Physiology A* 142, 439-445.
- Shine, R. (1979). Sexual selection and sexual dimorphism in the Amphibia. *Copeia* 1979, 297-306.
- Shine, R., Cogger, H.G., Reed, R.R., Shetty, S. & Bonnet, X. (2003). Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). *Journal of Zoology* 259, 261-268.
- Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behavior* 85, 1077-1088.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavior Syndromes: an integrative overview. *Quarterly Review of Biology* 79, 241-277.
- Simmons, A.D. & Thomas, C.D. (2004). Changes in dispersal during species' range expansions. *American Naturalist* 164, 378-395.
- Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19, 448-455.
- Snell-Rood, E.C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behavior* 85, 1004-1011.
- Steele, M.A., & Anderson, T.W. (2006). Predation. In: *Ecology of marine fishes: California and adjacent waters* (Allen, L.G. Horn, M.H & Pondella D.J.III, eds.). University of California Press, Berkeley, p. 428-448.
- Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Hertel, F. & Herrel, A. (2013). Getting a grip on tetrapod grasping: form, function, and evolution. *Biological Reviews* 88, 380-405.
- Thomson, J.S., Watts, P.C., Pottinger, T.G. & Sneddon, L.U. (2011). Physiological and genetic correlates of boldness : Characterising the mechanisms of behavioural variation in rainbow trout , *Oncorhynchus mykiss*. *Hormones and Behavior* 59, 67-74.
- Tomlinson, S. & Phillips, R.D. (2015). Differences in metabolic rate and evaporative water loss associated with sexual dimorphism in thynnine wasps. *Journal of Insect Physiology* 78, 62-68.
- Van Oers, K., Drent, P.J., de Goede, P. & van Noordwijk, A.J. (2004). Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B* 271, 65-73.
- Videllier, M., Bonneaud, C., Cornette, R. & Herrel, A. (2014). Exploration syndromes in the frog *Xenopus (Silurana) tropicalis*: correlations with morphology and performance? *Journal of Zoology* 294, 206-213.
- Videllier, M., Cornette, R., Bonneaud, C. & Herrel, A. (2015). Sexual differences in exploration behavior in *Xenopus tropicalis*? *Journal of Experimental Biology* 218, 1733-1739.
- Von Merten, S. & Siemers, B.M. (2012). Exploratory behaviour in shrews: fast-lived *Sorex* versus slow-lived *Crocidura*. *Animal Behavior* 84, 29-38.
- Wells, K.D. (1977). The social behavior of anuran Amphibians. *Animal Behaviour* 25, 666-693.
- Wilson, A.D.M. & Godin, J.J. (2009). Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology* 231-237.
- Wolf, M. & Weissing, F.J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution* 27, 452-461.
- Wright, S.J. (2005). Tropical forests in a changing environment. *Trends in Ecology and Evolution* 20, 553-560.

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