Plasticity and flexibility in the flower bat *Glossophaga commissarisi*

Sabine Wintergerst[1], Vladislav Nachev[1*§], York Winter[1*§]

[1] Institute of Biology, Humboldt University, Berlin, Germany

*For correspondence: vladislav.nachev@charite.de, york.winter@charite.de

Present Address: §Dept. of Biology, Humboldt University, Philippstr. 13, 10099 Berlin, Germany

Abstract

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1. Introduction

Individuals of the same species when exposed to the same set of environmental stimuli can consistently differ in their behavioural responses. When such individual differences remain stable with time and across contexts they can be referred to as animal personalities [1] and have been well-documented in a variety of species ranging from insects to mammals [2–4]. Consistent individual differences in behaviour imply that an individual does not express the full range of behavioural trait values present in its population [5] and therefore does not always behave optimally [6]. Despite these limitations, behaviour is usually plastic to some extent and animals can adapt their behaviour in response to changes in environmental stimuli. Individuals thus can also differ at this level of responsiveness to environmental conditions. One approach to conceptualize this is the behavioural reaction norm, which is the set of behaviours exhibited by an individual in a given set of environments [5]. Usually the behavioural reaction norm can be visualized as a line which gives the strength (or presence) of a behaviour at different levels along a continuous environmental gradient like food availability, temperature or time. With linear reaction norms individuals may differ in their intercepts, which correspond to the overall response and in the slopes of the reaction norms, which correspond to the plasticity of the response [7]. Non-plastic individuals exhibit the same (strength of) behaviours regardless of the levels of the environment and have horizontal reaction norms.

When individuals have behavioural reaction norms with non-zero slopes they are also said to exhibit contextual plasticity [8]. Individual differences in contextual plasticity have been described in several species in the wild. For example, red knots differ in how much they adjust their vigilance during foraging to perceived predation risks [9] and Namibian rock agamas differ in how strongly they adjust the time they spent conspicuous depending on the season [10].

- Many different labels for behavioural plasticity and Poorly understood what the underlying mechanisms are and to what extent the different types of behavioural plasticity are independent

- A task that lies ahead is to bring together the mostly disparate scientific fields of behavioural ecology, evolutionary biology, personality research and behavioural neuroscience in their common interest regarding individual, flexible responding.

- Behavioural flexibility is an ill-defined concept.

- Behavioural neuroscience does not use the concept of behavioural reaction norm. In this field of science, behavioural flexibility includes a range of behavioural control functions of an animal aimed to directly respond and adjust its behaviour to environmental stimuli.

- We feel that the terminology used to describe the dimensions of animal personalities should somehow be consistent with the behavioural control function of the underlying brain structures.

Relevant findings and ideas in previous studies:

1. Plasticity:

- (Stamps 2016) "contextual plasticity" :The extent to which the phenotype of an agent varies as an immediate response to variation in external stimuli [11].

- (Snell-Rood 2013) "activational plasticity" : "The external context results in the expression of a particular behaviour such that an individual expresses different behaviours as it encounters different environments or conditions. Activational (i.e. contextual) plasticity refers to the differential activation of an underlying network" [12].

- (Mery and Burns 2010) "innate behavioural plasticity" : "Innate behavioural response occurs when the modification of behaviour in response to environmental factors is the result of evolution at the population scale over multiple generations; that is, a predetermined phenotypic trait is produced in response to a predetermined environmental stimulus."

- (Ducatez et al. 2020) on extinction risk in birds, a very different definition: "Behavioural plasticity determines the ability of animals to formulate behavioural responses to cope with new or unusual challenges such as food shortages or extreme climatological events"

- (Gibelli & Dubois 2017) on Zebra finches: "Specifically, we measured neophobia by quantifying the latency of the birds to eat near a novel object in two different environments across a social gradient and assessed their learning performance on two discriminant tasks and a reversal task. In agreement with our expectation, we found that less neophobic individuals were less plastic in their responses compared to more neophobic ones. Less neophobic individuals were also faster to reach the learning criterion but only in the less difficult discriminant task they performed first. On the contrary, although we found evidence for individual consistency in learning performances, differences among individuals in the number of trials needed to pass the task in both the more difficult discriminant and reversal tasks were not associated with individual differences in neophobia. Thus, our findings indicate that **individual differences in contextual plasticity do not necessarily result from some individuals being more sensitive to environmental changes**. Instead, we suggest that differences among individuals in their level of plasticity might result from differences in the number of suitable habitats they may occupy." [13]

- (Grace & Anderson 2014) on Nazca boobies: "**Low covariance between individual contextual plasticity scores for different behaviours suggests that plasticity in this system is not a 'meta-personality' trait** (Stamps & Groothuis, 2010). Contextual plasticity in a behaviour was positively correlated with the elevation of response in that behaviour" [14]

- (Gomes & Cardoso 2020) "Our work predicts that **complex behaviours whose performance may be constrained by learning and memory limitations are more likely to be individually fixed** (e.g. individual bower birds consistently building the same type of bower [59,60]), rather than changing frequently (e.g.the same individual building different types of bowers) and thus having to be learned multiple times. By contrast, **simple behaviours that can be learned very fast, or that depend less on learning, may more easily be expressed plastically in unstable environments**... Our work indicates that for such complex behaviours, where high performance requires continued practice, the lag-time constraint should cause the evolution of specialized and relatively fixed strategies in unstable environments. By comparison, simpler behaviours that require minimal practice to reach and maintain maximum performance are expected to be used more plastically. For example, even **if the relative abundance of different food sources fluctuates through time, our model predicts higher specialization in species using behaviourally complex foraging techniques (e.g. predators of highly mobile prey) than for species using simpler foraging (e.g.scavengers)**." [15]

- (Wright & Turko 2016) on evolution of amphibious fishes: "Phenotypic plasticity: Biochemical, physiological, behavioural, morphological or life-history traits that change in response to the en-

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vironment. Phenotypic flexibility : Reversible phenotypic plasticity in response to environmental changes,acclimation/acclimatization responses."

2. Flexibility:

- (Coppens et al. 2010) : "Behavioural flexibility is defined as the ability of an individual to directly respond and adjust its behaviour to environmental stimuli" "individual differentiation in behavioural flexibility emerges as a function of underlying variability in the activation of a brain circuitry that includes the prefrontal cortex and its key neurochemical signalling pathways" [16].

- (Lim et al. 2019) on mice: "[Our tests requires animals to] exhibit behavioural flexibility by inhibiting a response driven by a previously learned stimulus-reward association while simultaneously learning a new association. [our second test] requires animals to inhibit a previouslylearned response behaviour, but this occurs without any need to simultaneously learn a new stimulus-reward association." "analyzing the rate of continuous responses provides a measure of the animal's tendency to perseverate".

- (Gapp et al. 2014) : "we next tested the animals on a behavioural sequencing task (BST) using IntelliCages, a task assessing response flexibility. For BST, each animal is first trained to alternatively visit two opposite diagonal corners of an arena to obtain a drink reward. Corners assignment is then switched (reversal) to the other diagonal, and the animal has to shift shuttling from corners in one diagonal to corners in the other diagonal while maintaining a goal-directed strategy."

- (Kosaki & Watanabe 2012): "Ibotenic acid lesions of the medial prefrontal cortex impaired acquisition of each discrimination task by increasing errors specifically in the early phase of each task. These errors were characterised by perseveration to the previously correct lever. By contrast, lesions of the anterior cingulate cortex resulted in the impairment of discrimination in general without inducing perseveration; the impairment was instead characterised by disruption of general error-correction processes. Hippocampal lesions severely impaired learning by increasing perseverative tendencies that were present throughout the learning stages in each task. These results extend our understanding of **the contributions of the different nodes of the limbic cortico-striatal circuit to different aspects of behavioural flexibility.**" [17]

- (Longo et al. 2018) on mice: "Reversal learning, a form of behavioural flexibility, depends on OFC functional integrity. Deletion of Npy1r gene in Y5R neurons increases inflexibility and OFC neuronal activity. Deletion of Npy1r gene in Y5R neurons decreases 5-HT fibers in OFC. SSRI treatment rescues reversal learning impairment and OFC hyperactivity of Npy1rY5R-/- mice. NPY-Y1R transmission in OFC plays a role in behavioural flexibility that is impaired in OCD."

- (Kinnavane et al. 2019) on rats: "Behavioural flexibility, or **the ability to update responding as environmental contingencies change, is a key executive function mediated by the rodent prefrontal cortex** [20, 21]. However, behavioural flexibility encompasses a range of different cognitive processes that are in turn supported by diverse frontal, corticostriatal and corticothalamic systems [22-25]. For example, reversal learning by rats is sensitive to orbitofrontal cortex damage [26-29], while the ability to switch between different stimulus dimensions or response strategies, as well as the use of high-order rules to guide goal-directed behaviour, depend on the integrity of the medial prefrontal cortex and in particular prelimbic cortex [30-35]." [18]

- (Titulaer et al. 2012) on great tits: "learning performance depended on exploratory behaviour of the bird, yet in opposite ways for males and females and only in the most difficult stage. **Birds needed more trials in the reversal stage compared to the other stages, indicating that reversal learning was more difficult than the intra- and extradimensional shifts. Only in this reversal stage, in which birds had most difficulties, was an effect of exploratory behaviour on learning performance found. In contrast to our expectation, fast-exploring males outperformed slow-exploring males, whereas for females the relationship was in the opposite direction.** " [19]

- (Nilsson et al. 2015) on rats: "Non-rewarded or irrelevant prior associations are important for flexible responding. Associations of reward and non-reward in reversal learning are neurally dissociable. Disruption of prior irrelevant or rewarded associations cause pathological deficits. Experimental paradigms of cognitive flexibility can be improved to aid translation."

- (Homberg et al. 2007) on rats: "our data show that the absence of the SERT affects aggression and inhibitory control, but not behavioural flexibility, characteristics that may reflect the trait-like

143 consequences of constitutive changes in central 5-HT levels"

144 • (Dhawan et a. 2019) on rats: "There was a robust effect of over-training, with over-trained rats perform-
145 ing reversal learning in fewer trials than rats trained to criterion only. The pattern of errors supported
146 the hypothesis that **more rapid reversing results from the formation of an attentional set**.
147 This is the same attentional mechanism that results in less rapid shifting or switching. We conclude
148 that the **behavioural flexibility demonstrated in reversal learning does not provide a scale**
149 **on which cognitive flexibility can be measured**." [20]

150 3. Speed-accuracy trade-off (one framework that predicts a correlation between plasticity and flexibility):

151 • (Sih and Del Giudice 2012) : speed-accuracy trade-off, fast but superficial learning and slow but accurate
152 learning are alternative cognitive styles [21].

153 • (Griffin et al. 2015) a great review titled "Cognition and personality: an analysis of an emerging
154 field" : "**bolder individuals learn a particular contingency faster (i.e. in fewer trials) than**
155 **do shyer individuals either because they recognise such contingencies sooner, lay them**
156 **down in memory more readily, or have lower decision thresholds for association formation,**
157 **although which of these it is may not be clear. It may also be the case, however, that**
158 **animals vary in how they respond to reward (or punishment), perhaps because of their**
159 **physiological state or prior experience**." [22]

160 • (Mazza et al. 2018) on voles: "bolder and more active individuals were fast, inflexible and persistent
161 in the associative learning tasks, whereas shyer and less active individuals were slow and flexible. We
162 also found evidence for a speed-accuracy trade-off: correct choices in the cognitive tasks required more
163 time for all individuals compared to incorrect choices, but bolder, more active voles always made their
164 decisions faster than reactive ones. The difference between the time required for a correct and an
165 incorrect choice was most pronounced in initial learning for shyer and less active individuals, but for
166 bolder, more active individuals it was most pronounced in the reversal learning task." From their
167 Introduction though: "**One subject may consistently look for the rewarded cue ignoring the,**
168 **potentially rewarded, other cues, while the second may keep sampling the other cues as**
169 **well. In an associative task, the first individual will achieve a better performance. In**
170 **a reversal task, a measure of behavioural flexibility, the second individual will perform**
171 **better because of the more complete information acquired through extended sampling**"
172 [This is not supported by our data] [23]

173 • (David et al. 2014) on Zebra finches: "social animals, like solitary foragers, may be affected by perhaps
174 universal constraints when foraging, such as limited attention. These constraints may contribute to
175 promote between-individual variation in foraging tactics within social groups. Second, the existence of
176 a speed-accuracy trade-off suggests that between-individual behavioural differences are more likely to
177 come from differential allocation between speed and accuracy than from differences in general intrinsic
178 abilities to exploit food resources." [24]

179 • (Raine & Chittka 2012) on bumble bees: "These results are inconsistent with a trade-off between learning
180 speed and the reversal of a previously made association. On the contrary, they suggest that **differences**
181 **in learning performance and cognitive (behavioural) flexibility could reflect more general**
182 **differences in colony learning ability**. Hence, this study provides additional evidence to support
183 the idea that rapid learning and behavioural flexibility have adaptive value." [25]

184 • (Moiron et al. 2016) on great tits: "some individuals predictably made relatively slow but accurate
185 decisions, whereas others were predictably faster but less accurate. We did not, however, find evidence
186 for the trade-off at the within-individual level. These level-specific relationships imply that different
187 mechanisms acted across levels."

188 • (Ivanoff et al. 2008) on humans: "[The speed-accuracy trade-off] is neurally implemented by modulating
189 not only the amount of externally-derived sensory evidence used to make a decision, but also the internal
190 urge to make a response. We propose that these processes combine to control the temporal dynamics of
191 the speed-accuracy trade-off in decision-making."

2. Materials and Methods

(a) Subjects and study site

Experiments were conducted with 44 adult, wild-caught, male bats of the species *Glossophaga commissarisi* Gardner at La Selva Biological Station, Province Heredia, Costa Rica. Bats were attracted to trapping locations by sugar water feeders scented with dimethyl disulphide [26]. Bats were weighed and marked with radio frequency identification (RFID) collars. They were kept in a flight cage (4 x 6m) with mesh walls and thus under the climatic conditions of the surrounding rainforest until the experiment started. Bats spent at least four days and not longer than fifteen days in this keeping flight cage. During this time we weighed bats regularly and provided them with *ad libitum* sugar solution (30% sucrose w/w) with added 3.5g/100ml hummingbird food (NektarPlus, Nekton), and added 3.5g/100ml milk powder (Nido 1+, Nestle). Additionally, bats were given local bee-collected pollen and a piece of banana every three days. Three days before the experiment, we installed two artificial flowers in this flight cage to accustom the bats to feed from them. These flowers delivered $50\mu L$ sugar solution (30% sucrose w/w) rewards at each visit. Due to automated data collection no blinding was implemented in any experiment. Animals were randomly assigned to the different groups. Animal experimental procedures were reviewed and permission for animal experimentation and RFID-tagging was granted by Sistema Nacional de Areas de Conservación (SINAC) at the Ministerio de Ambiente y Energía (MINAE) Costa Rica.

(b) Experimental setup

We used two experimental flight cages (4 x 6m), each of which contained a horizontally oriented 2 x 2m rectangular frame (h = 1.5m) on which twelve artificial flowers were mounted, three on each side, with flower heads pointing outwards (Fig. 2). All flowers were connected via valves to a stepping-motor syringe pump [27,28]. Rewards always consisted of $40\mu L$ of nectar with 20% w/w sugar concentration (sucrose: fructose 1:2). Bat visits were detected with infrared light beam sensors at the flower opening and with a circular RFID antenna around the flower head. We only considered as visits events in which the bats were detected for at least 300ms. We recorded visits to all flowers, including non-rewarding flowers, during every experimental night from 18:00h to 06:00h. The reward schedule allowed for individual-specific configurations (PhenoSoft Control, Phenosys, Berlin, Germany).

(c) General experimental procedure

During experiments, twelve male bats were tested at the same time in one flight cage. We tested four cohorts in total, with two cohorts participating simultaneously in two different flight cages. Since we only caught 44 males, four individuals took part in the experiment twice to ensure the same number of individuals in each cohort. We did not analyse data from these non-focal individuals from their second participation. On any given night, each bat only received rewards from two out of the twelve artificial flowers. Every bat had its own selection of two rewarding flowers to prevent social learning and reduce crowding. However, since twelve bats used the flowers simultaneously, every flower was used by two different individuals. Pairs of individuals sharing only one flower changed between the nights. The rewarding flowers of each bat were always on opposite sides of the frame and changed every night to the two other sides of the frame to prevent habituation to specific locations.

Rewards were delivered with three different probabilities (30%, 50% and 83%). This corresponds to the same increase by a factor of 1.67 from 30% to 50% and from 50% to 83% [29]. Rewards were drawn from binary sequences (one sequence for each probability) generated using the `sample` function in R [30]. The first visit of an individual at its rewarding flower was always rewarded. For standardization, the same sequence was used for all bats and flowers of the same probability.
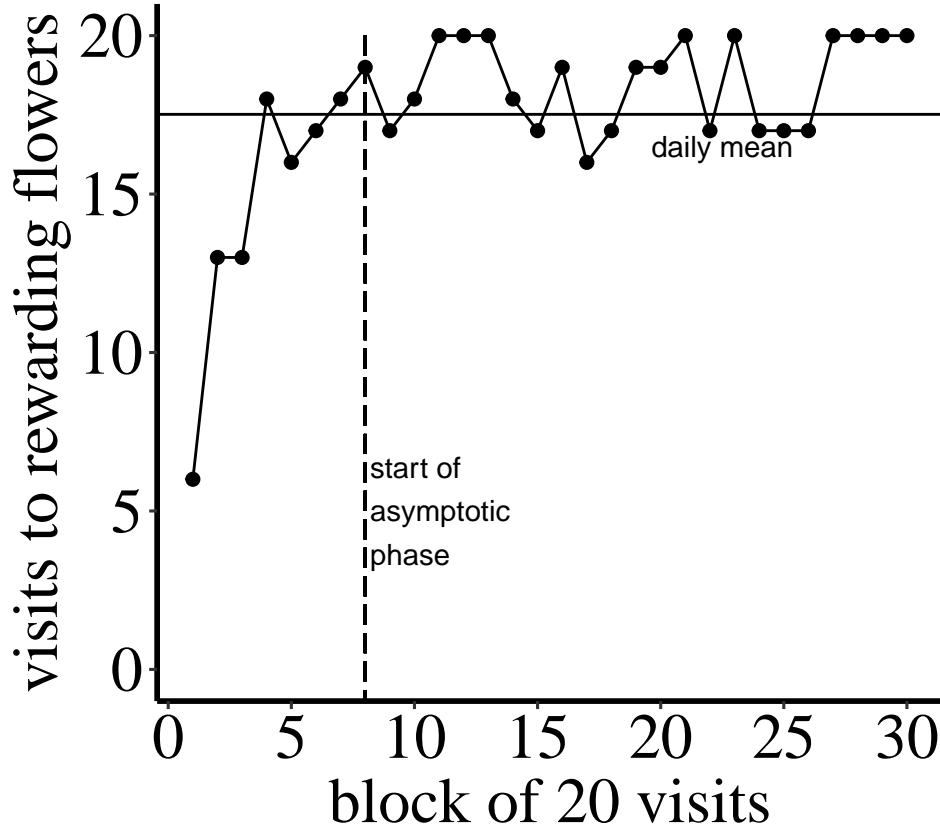
Figure 1: An example of sampling behaviour over the course of one night (bat six on night four, at 50% probability). Flower visits were grouped into blocks of twenty and the number of visits to the two rewarding flowers was determined. The second of two consecutive blocks with more visits to rewarding flowers than the individual daily mean (horizontal line) marked the beginning of the asymptotic phase (vertical dashed line). The sampling rate was calculated as the relative proportion of visits to non-rewarding flowers during the asymptotic phase.

(d) Behavioural plasticity (change in sampling) [a potential criticism could be that we conflate errors with sampling. A potential solution: only count as sampling visits to the two sides where there are no rewarding flowers]

We defined a sampling event as a visit to a non-rewarding flower. Since the positions of rewarding flowers changed every night, bats had to learn the locations of their two rewarding flowers out of the twelve available daily. We performed our main analyses on choice behaviour only after this initial learning phase had been completed, using only the data of the asymptotic phase. We assumed that all visits made to non-rewarding flowers during the asymptotic phase were for exploration and collecting information about the current state of these flowers, i.e. sampling. For the analysis, we grouped individual visits in blocks of 20. The beginning of the asymptotic phase was determined as the second of two consecutive blocks with a number of visits to the rewarding flowers higher than the daily mean (Figure 1).

Since a sampling animal seeks new feeding opportunities, the frequency of sampling may change when overall food availability changes. To investigate how bats adapted their sampling rates to food availability, we set three different probabilities of obtaining a reward (30%, 50%, and 83%) in three different experimental runs. All individuals of one experimental group (12 bats) started with 50% reward probability for five days. For the next eight days, the sequence of probabilities (four days for each probability after 50%) was counter-balanced, so that six bats experienced probabilities in the sequence 50-30-83 and the other six bats

in each cohort experienced 50-83-30. We excluded from analysis the first day of the 50% condition when bats still familiarized themselves with experimental conditions. Thus, for every individual, we obtained four measurements of nightly sampling rates for each reward probability (528 data points over 12 nights). Due to technical problems, some complete nights or time periods within some nights had to be excluded for some bats (67 individual nights in total, including 7 partial exclusions). Between experimental runs at different reward probabilities bats received for one night the same food as in the keeping flight cage.

(e) Behavioural flexibility

This experiment was performed for four consecutive nights immediately after the behavioural plasticity experiment. At the start of the experiment there were two rewarding flowers per bat, both delivering rewards with 50% probability (phase 1). After a bat had made 100 visits to the rewarding flowers, two new flowers became rewarding and the originally rewarding flowers became non-rewarding (phase 2). We chose this number of visits before the phase change since during the previous experiment at 50% reward probability bats had reached asymptotic performance after fewer than 100 visits to the rewarding flowers on 76% of individual nights. After the onset of phase 2 we waited until a bat had first visited and received a reward from one of the two newly rewarding feeders. From then on, a bat was informed of the new, rewarding location. It could choose between visiting the formerly rewarding locations (perseverance) or switching to the newly rewarding location (flexibility). To determine a flexibility score we evaluated the first 60 visits after the bat had encountered one of the newly rewarding flowers in phase 2. The flexibility score was then calculated as 60 minus the number of visits to previously rewarding flowers (perseverance visits). This procedure was repeated for four nights to obtain four measurements per individual, with a different set of flowers on each night. Additionally, we determined the proportion of visits to the rewarding flowers during the last 50 visits in phase 1, since the ratio between flexibility and perseverance might also depend on the sampling exhibited in phase 1. All bats were able to complete the experiment on at least three out of the four nights. Excluded from analysis were nine nights of nine different bats that made fewer than 60 visits after visiting a rewarding flower in phase 2 (seven of these bats failed to find a rewarding flower in phase 2).

(f) Statistical analysis

We used the behavioural reaction norm approach to quantify the plasticity of sampling behaviour for each individual along the gradient of three different reward probabilities [5]. With this approach generalized linear mixed models (GLMM) with random slopes and intercepts are used to fit regression lines for every individual. The slope of such lines is a measure of individual plasticity [31], indicating the degree to which an average behaviour is modified under different environmental conditions. Here we used Bayesian Markov chain Monte Carlo generalized linear-mixed models (`MCMCglmm` [32]) with the binomial error distribution of the `multinomial2` family to fit random intercepts and slopes. The dependent variable for the model was specified as a two-column matrix with the number of visits to non-rewarding flowers and the number of visits to rewarding flowers. Reward probability, weight, and the interaction between cohort and sequence of reward probabilities (50-30-83 or 50-83-30 groups) were included as fixed variables. Only reward probability was mean-centred so that the intercept of the individual regression lines was determined at the middle of the environmental gradient. This was necessary for the calculation of the intercept-slope correlation. Individuals were included as a random effect and the influence of reward probability was allowed to differ between individuals. As priors, we used an inverse-Wishart distribution for the residual variance and a parameter expanded prior for the random effect. From this model, we derived a slope value for every individual, which represents the change in log odds of the individual probability to sample. The latent scale repeatability of sampling at each of the three reward probabilities was quantified by fitting three `MCMCglmms` to the respective data subsets with the same specifications as before but without reward probability as a fixed effect. Since the chosen model had additive over-dispersion the repeatability was calculated by dividing the between-individual variance through the total variance, which is the sum of between-individual variance, within-individual variance, and the distribution specific variance of $\pi 2/3$ [33]. From this model we also estimated the correlation between the individual intercepts and slopes [34,35].

For the analysis of flexibility we used another `MCMCglmm` model with binomial error distribution, with a two-column matrix with the number of flexibility visits and the number of perseverance visits. We included

experimental day number as an independent variable to account for possible habituation to the experimental design. Individuals were included as random effects and we controlled for the influence of sampling in phase 1. Repeatability was calculated as for the repeatability of sampling. Model fits and convergence were assessed by analysis of autocorrelation, effective sample size, and visual inspection of trace plots. For more details about the `MCMCglmm` specification see data repository.

Finally, the correlation between individual behavioural plasticity (the slope for the change of sampling rate as a function of reward probability) and individual flexibility scores (number of visits to newly rewarding flowers) was assessed by combining the two previous models into a two-dimensional `MCMCglmm` model with the matrix of sampling and non-sampling visits (binomial error distribution) and the matrix of flexibility and perseverance scores (binomial error distribution) as the dependent variables. We only took the significant fixed predictors from the previous models - the reward probability for the plasticity estimation and the experimental day for the flexibility estimation. The correlation between the two dependent variables was estimated from the posterior distributions [34,35] and then sign inverted. This last step was made for the ease of interpretation, because the more negative slopes corresponded to the more plastic individuals. The negative correlation thus represented the actual correlation between our measures for contextual plasticity and behavioural flexibility. We also estimated the correlation between the proportion of sampling visits and the flexibility score. All statistical analyses were conducted using R version 4.0.2 [30].

2. Results

(a) Individual differences in contextual plasticity measured as sampling rate

During the three different reward probability conditions bats visited flowers on average (mean $\pm$ SD) 815 ± 279 times at 30%, 603 ± 137 times at 50%, and 342 ± 114 times at 83% probability in one night. In order to quantify individual differences in sampling rate we distinguished between visits to rewarding and non-rewarding flowers and calculated the proportion of visits to non-rewarding flowers. Individuals differed from each other in sampling rate at each of the three reward probabilities (Figure 2). The adjusted repeatabilities were $r = 0.08$, 95% CI = (0, 0.17) at 83%, $r = 0.14$, 95% CI = (0.09, 0.24) at 50%, and $r = 0.17$, 95% CI = (0.1, 0.29) at 30% probability. This means that within a probability condition, individuals behaved similarly on all experimental nights.
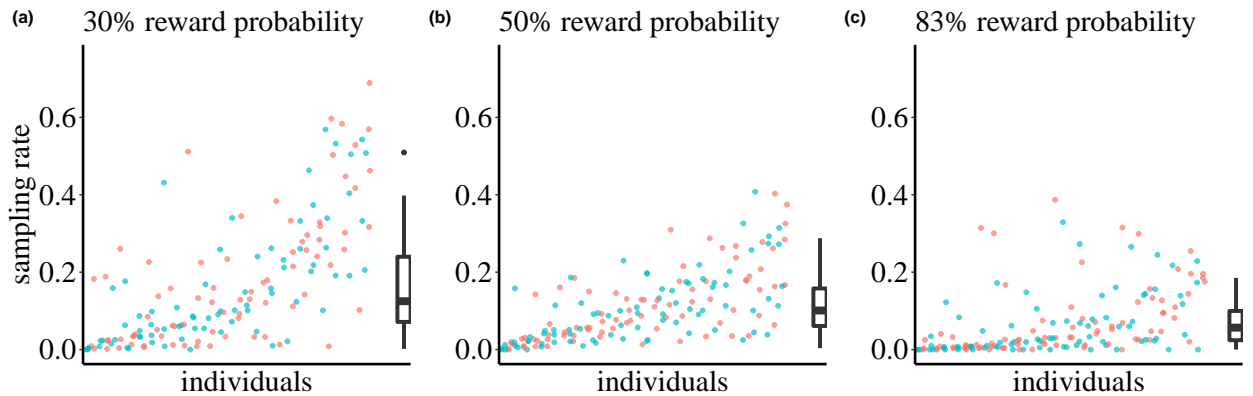

Figure 2: Individual variation in sampling behaviour at the different reward probabilities (30% *a*, 50% *b*, and 83% *c*). Each dot is the sampling rate of one bat on one night and each vertical stack of (up to) four dots of the same colour corresponds to one individual. Neighbouring individuals are shown in alternating different colours, for better visual discrimination. The sampling rate is defined as the proportion of visits to non-rewarding flowers after reaching the performance criterion (Figure 1). In each panel bats are ordered by increasing median sampling rates. The order is not preserved between panels. The boxplot gives the median and interquartile ranges for the 44 individual means at each reward probability.

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329 Reward probability was the only fixed effect that significantly influenced the proportion of visits to non-
330 rewarding flowers (sampling rate) in the random regression model (Table 1). Weight, cohort, and sequence
331 of experienced reward probabilities (group) were not significant. Sampling rate decreased with the increase
332 of reward probability, as indicated by the reaction norms (Figure 3) and the negative slope estimate for
333 reward probability (Table 1). Thus, individuals visited non-rewarding flowers most in the poor environment
334 and reduced visits in a richer environment. The steepness of individual slopes is a measure of the extent of
335 behavioural plasticity. There was a significant between-individual variation in behavioural plasticity for the
336 bats in our sample. This is indicated by the slope variance greater than zero (Table 1, Figure 3b). There was
337 no significant correlation between slope and intercept (Table 1).

Table 1. Summary of fixed and random effects from a generalized linear mixed-effects model of sampling rate.

term	estimate	95% credible interval
(Intercept)	-2.63	(-5.81, 0.6)
reward probability (centered)	**-2.45**	**(-3.21, -1.71)**
weight	-0.10	(-0.46, 0.26)
group50-83-30	1.09	(-0.06, 2.2)
cohort2	0.56	(-0.65, 1.59)
cohort3	0.69	(-0.4, 1.76)
cohort4	0.82	(-0.4, 2.16)
group50-83-30:cohort2	-0.73	(-2.26, 0.84)
group50-83-30:cohort3	-0.93	(-2.48, 0.54)
group50-83-30:cohort4	-0.69	(-2.91, 1.37)
var__(Intercept)	0.76	(0.43, 1.46)
var__reward probability (centered)	2.76	(0.67, 6.28)
var__Observation	1.53	(1.31, 1.82)
cor__(Intercept).reward probability (centered)	-0.26	(-0.75, 0.15)

Note: random effects are prefixed with "var__" for variance estimates and "cor__" for correlation estimates. Fixed estimates whose credible intervals do not span zero are shown in bold
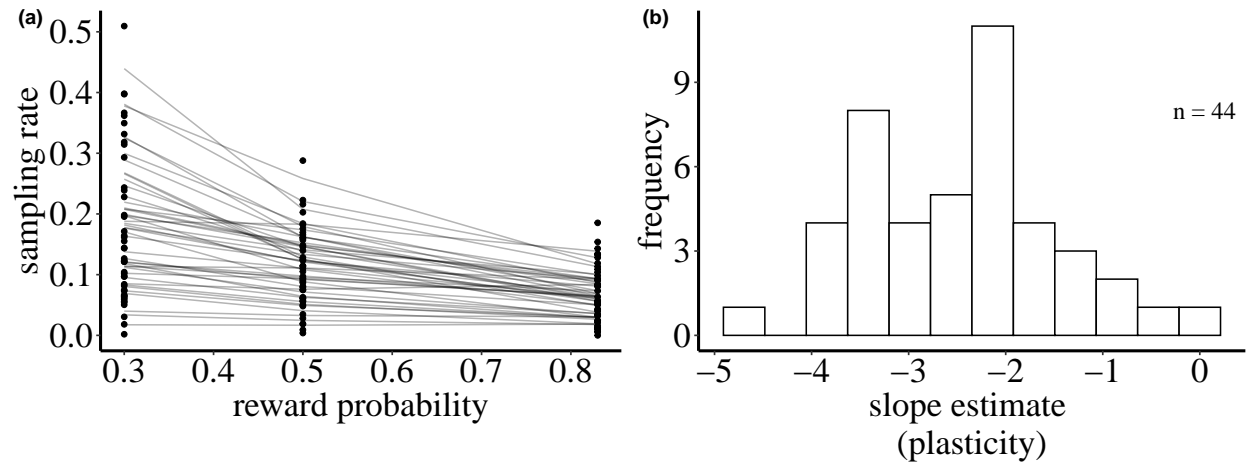
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Figure 3: Behavioural reaction norms for the 44 bats. (*a*) Each dot is the mean sampling rate of one bat over the four experimental days at the same reward probability (abscissa). Each line represents the predicted values (without interpolation) for one individual from the MCMCglmm model (see Results). (*b*) Distribution of the estimated individual reaction norm slopes. A more negative slope corresponds to higher contextual plasticity.

Table 2. Summary of fixed and random effects from a generalized linear mixed-effects model of behavioural flexibility.

term	estimate	95% credible interval
(Intercept)	-2.78	(-5.94, 0.53)
cohort_day	**0.33**	**(0.13, 0.53)**
sampling_before_phase2	-0.84	(-2.57, 0.83)
cohort2	0.56	(-0.34, 1.45)
cohort3	0.30	(-0.6, 1.23)
cohort4	0.52	(-0.61, 1.53)
var__(Intercept)	0.75	(0.26, 1.59)
var__Observation	1.50	(1.07, 2.14)

Note: random effects are prefixed with "var__" for variance estimates. Fixed estimates whose credible intervals do not span zero are shown in bold
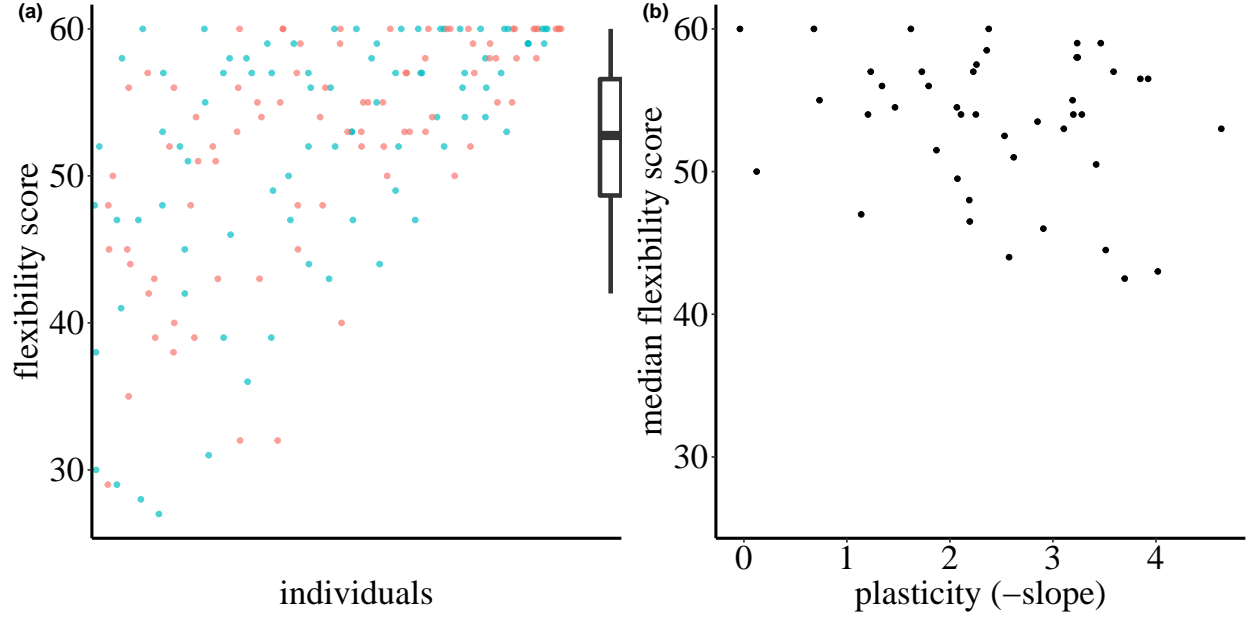
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Figure 4: (*a*) Individual variation in behavioural flexibility. Each dot is the flexibility score of one bat on one night and each vertical stack of (up to) four dots of the same colour corresponds to one individual. Neighbouring individuals are shown in alternating different colours, for better visual discrimination. The flexibility score was calculated as 60 minus the number of visits to previously rewarding flowers during the first 60 visits after the rewarding flowers suddenly stopped giving rewards and the bats encountered one of the new rewarding flowers. The reward probability during this test was 50%. The boxplot gives the median and interquartile ranges for the 44 individual means. Individuals are ordered by median flexibility score. (*b*) Median flexibility score vs. plasticity for 44 bats. The plasticity is represented by the negative best linear unbiased predictor (BLUP) for the slope, so that the more plastic individuals are shown on the right. There was no significant positive correlation between the two measures (see Results).

(b) Individual differences in behavioural flexibility

In order to assess behavioural flexibility between individuals we quantified the number of visits to newly rewarding flowers and to non-rewarding flowers that had previously been rewarding. Over all four experimental nights the most flexible individual had an average flexibility score of 60 (it made 0% perseverative visits), and the least flexible individual had an average score of 42 (30% perseverative visits, Figure 4a). Bats became more flexible over the four experimental days (positive effect for cohort_day in Table 2), however the repeatability of flexibility scores was significant $r = 0.13$, 95% CI = (0.04, 0.24).

(c) No positive correlation between contextual plasticity and flexibility

Behavioural contextual plasticity and behavioural flexibility are both measurements of how an individual responds to changes in the environment. To assess the question whether the two types of responsiveness may be linked to a common underlying mechanism we tested for a correlation between the individual scores for behavioural plasticity and flexibility. In our contextual plasticity experiment the plastic individuals increased their sampling behaviour more strongly as food became less abundant. During our experiment on flexibility the more flexible individuals switched more quickly to the newly rewarding flowers by giving up the formerly rewarding flowers faster. Both behaviours might be expected to be equally dependent on a high level of sensitivity to cues of food availability. Therefore, given that these two traits differed in their strengths between individuals, we would expect that an individual with a strong contextual plasticity would also express a high degree of behavioural flexibility and *vice versa*. However, we did not detect such an effect.

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There was no positive correlation between our two experimental measures of responsiveness (Figure 4b, $\rho =$ -0.47, 95% CI = (-0.86, 0.13)). Similarly, there was no positive correlation between the flexibility scores and the proportions of sampling visits in the first experiment $\rho =$ -0.39, 95% CI = (-0.7, 0.05)), indicating that the bats that sampled more were not also more flexible. Thus, our behavioural analysis on the individual level did not provide any support for the notion that behavioural contextual plasticity and behavioural flexibility share a common underlying mechanism of sensitivity to environmental cues.

3. Discussion

The two choice situations In both experiments, bats were during their active feeding phase motivated by hunger to seek food and active in a well-known foraging environment with its 12 potentially active feeders. During foraging, an animal is motivated to collect food from known feeding locations (exploitation) but it also has a behavioural tendency to search for and explore new opportunities for their current food potential (exploration). This was the case during both of our experiments. While measuring the reaction norm for behavioural plasticity individual bats had already found their feeders that reliably provided food. Feeder visitation provided them with an experience of both positive reinforcements when rewarded but also negative reinforcements when the reward was withheld. Taken together this provided some overall reinforcement value for the food locations and satisfied the bats' motivation to feed which in turn counterbalanced the motivation to explore. During the different experimental conditions, this level of satisfaction differed because the ratio of positive and negative reinforcements at active feeders differed. In turn, the reinforcing effect of visiting active feeders differed and therefore also the counterbalancing effect of the feeding experience on the motivation to explore. In the behavioural flexibility experiment, the situation was on one hand very similar but contained an additional component. An individual had also found its feeders that reliably provided food. In this situation food provisioning suddenly stopped. Each subsequent visit now led to negative reinforcement. However, bats also still carried their fresh memories of successfully feeding at those locations just earlier. While in both experiments bats probably carried the same general tendency to explore their environment for food when they are hungry, their own recent experience of successfully feeding at a specific location also affected choice. In the flexibility experiment, the tendency to retain a recently successful routine obviously differed between individuals. Some tended to stay with the former routine while others adopted more quickly a new opportunity. Thus, in the first experiments individuals differed in their balancing of exploitation versus exploration, and they also differed in how strongly the currently experienced reinforcement value at the feeders affected this balance. In the flexibility experiment on the other hand, individuals differed in how strongly their memory of a recently reinforced behaviour pattern continued to control their choices or action selection. By this account, it seems plausible that the contextual plasticity and the flexibility measured here are independent traits.

4. Conclusion

Appendix

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Authorship and contribution

S.W. Conceptualization, Methodology, Software, Formal Analysis, Data collection, Writing—original draft.
V.N. Conceptualization, Methodology, Software, Formal Analysis, Data curation, Writing—review and editing, Visualization, Supervision, Project Administration.
Y.W. Conceptualization, Resources, Methodology, Software (data acquisition), Writing—review and editing, Supervision.

Competing interests

The authors declare that they have no competing interests.

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