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RESEARCH ARTICLE

Inhibitory control, exploration behaviour and manipulated ecological context are associated with foraging flexibility in the great tit

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Abstract

1. Organisms are constantly under selection to respond effectively to diverse, sometimes rapid, changes in their environment, but not all individuals are equally plastic in their behaviour. Although cognitive processes and personality are expected to influence individual behavioural plasticity, the effects reported are highly inconsistent, which we hypothesise is because ecological context is usually not considered.
2. We explored how one type of behavioural plasticity, foraging flexibility, was associated with inhibitory control (assayed using a detour-reaching task) and exploration behaviour in a novel environment (a trait closely linked to the fast–slow personality axis). We investigated how these effects varied across two experimentally manipulated ecological contexts—food value and predation risk.
3. In the first phase of the experiment, we trained great tits *Parus major* to retrieve high value (preferred) food that was hidden in sand so that this became the familiar food source. In the second phase, we offered them the same familiar hidden food at the same time as a new alternative option that was visible on the surface, which was either high or low value, and under either high or low perceived predation risk. Foraging flexibility was defined as the proportion of choices made during 4-min trials that were for the new alternative food source.
4. Our assays captured consistent differences among individuals in foraging flexibility. Inhibitory control was associated with foraging flexibility—birds with high inhibitory control were more flexible when the alternative food was of high value, suggesting they inhibited the urge to select the familiar food and instead selected the new food option. Exploration behaviour also predicted flexibility—fast explorers were more flexible, supporting the information-gathering hypothesis. This

tendency was especially strong under high predation risk, suggesting risk aversion also influenced the observed flexibility because fast explorers are risk prone and the new unfamiliar food was perceived to be the risky option. Thus, both behaviours predicted flexibility, and these links were at least partly dependent on ecological conditions.

5. Our results demonstrate that an executive cognitive function (inhibitory control) and a behavioural assay of a well-known personality axis are both associated with individual variation in the plasticity of a key functional behaviour. That their effects on foraging flexibility were primarily observed as interactions with food value or predation risk treatments also suggest that the population-level consequences of some behavioural mechanisms may only be revealed across key ecological conditions.

KEYWORDS

behavioural plasticity, detour-reaching task, exploration behaviour, foraging flexibility, great tit, inhibitory control, personality, predation

1 | INTRODUCTION

Organisms are constantly under pressure to adapt to changes in their environment. Behavioural plasticity—that is, the reversible change in individual behaviour induced by environmental variation—allows individuals of many species to adapt throughout the course of their lives (Snell-Rood, 2013; Stamps, 2016). However, behavioural plasticity is influenced by a diversity of costs and mechanisms that differ among individuals, and consequently some individuals are more plastic than others (Dall & Johnstone, 2002; Dewitt et al., 1998; Snell-Rood, 2013; Stamps, 2016). Explaining why this individual variation arises is a major focus of research in evolutionary ecological studies of behaviour (Dewitt et al., 1998; Dingemanse et al., 2009; Snell-Rood, 2013; Stamps, 2016; Wolf et al., 2008). In particular, the role that cognition and personality (or behaviours associated with well-known personality axes) have in driving behavioural plasticity is receiving increasing attention (Dingemanse et al., 2009; Dubois, 2019; MacLean et al., 2014; Snell-Rood, 2013; Spierer et al., 2013; Stamps, 2016), but their role in doing so under realistic ecological scenarios is poorly understood.

Inhibitory control is an executive cognitive function that is central to decision-making and allows animals to adapt to sudden changes in the environment (Aron et al., 2004; Diamond, 2013). It is defined as the suppression of a dominant, prepotent or impulsive behaviour in favour of one that is more beneficial or appropriate (Diamond, 2013; but see also MacKillop et al., 2016 for another definition). In psychology, inhibitory control is a form of self-regulation that is often studied in the context of emotional control and addiction to food or other substances (Bari & Robbins, 2013; Luijten et al., 2014), and describes how individuals vary in their ability to ignore new stimuli that would otherwise lead to a potentially harmful change in behaviour. Very few ecological studies have linked inhibitory control to functional behaviour generally, and those that do have primarily studied inhibitory control in relation to foraging behaviour. Stevens, Hallinan, et al. (2005) examined a temporal form of inhibitory control (temporal discounting) and demonstrated that cotton-top tamarins *Saguinus oedipus* in captivity discount future high-quality rewards in favour of immediate low-quality rewards, a strategy that is likely beneficial given the temporal variability in the tamarins' natural diet, although the authors did not examine individual variation. Other studies have shown that inhibitory control predicts dietary breadth, although the direction of the effect is inconsistent and the analyses were primarily conducted at the interspecific level (meta-analysis in MacLean et al., 2014; but see van Horik et al., 2018 for a study at the individual level). One possible reason for these contrasting results is that, in realistic ecological scenarios, the dominant or prepotent behaviour is difficult to predict due to conflicts between how the brain simultaneously processes information from past and present stimuli (Anderson & Weaver, 2009). Identifying the most appropriate behaviour is also difficult because the prepotent behaviour may be affected by trade-offs with other traits and individual state (Dall et al., 2004). Even though inhibitory control influences how individuals respond to the sudden appearance of alternative stimuli, by controlling impulsive and potentially inappropriate changes in behaviour, its role in driving behavioural plasticity in a functional, ecological context when conditions change is largely unknown.

Behavioural plasticity is central to evolutionary and ecological studies of animal personality (Dingemanse et al., 2009; Herborn et al., 2014; Sih, Bell, Johnson, 2004). Animal personality refers to consistent differences between individuals in behaviour across time or context, or to correlations between different traits (Groothuis & Carere, 2005; Sih, Bell, Johnson, Ziemba, 2004). Recently, the field has also moved towards determining whether correlations between different traits arise at the between-individual rather than at the within-individual level (Dingemanse & Dochtermann, 2013; Mitchell & Houslay, 2021; Reichert et al., 2021). Considerable focus in the field has been placed on behavioural axes that are known to predict many different behaviours (Réale et al., 2007). For example, the 'fast–slow exploration' personality axis contrasts fast individuals who are more exploratory, more predation-risk prone and more routine like in their behaviour, with 'slow' individuals who are less exploratory, more predation risk-averse and more responsive to their environment (Groothuis & Carere, 2005). This axis has been widely studied in birds and shows strong similarity to the reactive–proactive axis described in small mammals (Groothuis & Carere, 2005; Réale et al., 2007). Individual variation in exploration behaviour has been linked to physiological, permanent environment and additive genetic effects, and can predict a wide range of functional behaviours (Firth et al., 2018; Koolhaas et al., 1999; Quinn et al., 2009, 2011). All of these correlations imply general constraints on behavioural plasticity, though the observed effects are often dependent on social or ecological context (Réale et al., 2007; Webster & Ward, 2011). Furthermore, specific facets of the axis (e.g. responsiveness) suggest that some individuals are more responsive to changes in their environment than others (Benus et al., 1991; Koolhaas et al., 1999; Quinn & Cresswell, 2005; Rojas-Ferrer et al., 2019; Verbeek et al., 1994). As such, ecological conditions and exploration behaviour may interact to affect behavioural plasticity.

This study investigated whether inhibitory control and exploration behaviour were associated with behavioural plasticity, and whether these effects varied depending on ecological context. We focused on flexibility, a specific form of behavioural plasticity that involves changes in learned behaviour (following Stamps, 2016), in the context of foraging. Although there is growing interest (Sih & Del Giudice, 2012), and some evidence (Dougherty & Guillette, 2018) for links between behavioural traits associated with personality and cognition in general, there is little empirical evidence that inhibitory control and our assay of personality, exploration behaviour, are linked (Stow et al., 2018). We therefore expected them to have independent effects on foraging flexibility. We examined choices made between two food options while varying two variables: (a) the value of the alternative food options (high or low value), and (b) the perceived risk of predation (high or low risk). We did this using the great tit *Parus major*, a model species for studies on individual variation in cognition (Amy et al., 2012; Cole et al., 2011; Morand-Ferron et al., 2015) and animal personality (Dingemanse et al., 2012; Marchetti & Drent, 2000; Verbeek et al., 1994). Initially, we assayed inhibitory control and exploration behaviour using a standard detour-reaching task and 'exploration behaviour of a novel environment' (henceforth, exploration behaviour) respectively. Next, we trained individuals to retrieve patchy, high-value but hidden food. We then presented birds with the hidden food and an alternative visible food source simultaneously, and quantified the number of times the birds chose the alternative visible food, instead of continuing to retrieve the hidden food. We considered that choosing, that is switching to, the alternative visible option was the flexible response, and therefore the proportion of choices for the visible option during trials after training was a concise, simple measure of foraging flexibility. Although individual variation in plasticity is increasingly analysed using a random regression, reaction norm approach (Araya-Ajoy et al., 2015; Nussey et al., 2007), this is appropriate only when the gradient is continuous and replication is high (Stamps, 2016). When the 'gradient' is discrete, individual plasticity can be described by the difference between the individual mean scores for the discrete treatments (Auld et al., 2010). Since all of our individuals behaved the same way in the training phase treatment, the proportion of choices in subsequent treatments can be viewed as a measure of flexibility. We made no assumption about which food option was optimal, since our focus was the behavioural mechanisms underlying flexibility, a measure that does not necessarily reflect a single optimal behaviour because of state dependence, behavioural trade-offs and uncertainty (Dall et al., 2004).

We had three main aims. First, we examined whether individuals differed consistently in their foraging flexibility by estimating repeatability across all four treatments. Second, we explored whether inhibitory control was associated with foraging flexibility (i.e. whether individuals tended to switch to the visible food option). We assumed that training made the hidden food the prepotent (dominant) stimulus because they had been trained to feed in this way before the trials, leading to the following prediction: individuals with high inhibitory control (as measured in the standard detour-reaching task) would show greater foraging flexibility because they would be more likely to inhibit searching for the hidden food and switch to feeding on the visible food, when the value of the latter was equal relative to the former. We expected little or no effect of inhibitory control on foraging flexibility when the visible food was of lower value relative to the hidden food. Furthermore, given the expectation that the influence of inhibitory control on flexibility is likely dependent on contexts other than food quality (Cauchoix et al., 2020; Griffin et al., 2020; Sih & Del Giudice, 2012; Stevens, Rosati, et al., 2005; Tsukayama et al., 2012), we also explored the context of predation risk. Stress can suppress an animal's tendency to choose an alternative, potentially more rewarding behaviour (Schwabe & Wolf, 2009), and theory suggests that animals should choose the most easily available food when predation risk is higher in order to reduce search time and maximise vigilance (Lima & Bednekoff, 1999; Stephens & Krebs, 1986). Thus, we expected that any association between flexibility and inhibitory control in the low predation risk treatment could be weakened or disappear entirely under the risk of predation. Specifically, we expected that all individuals would revert to the safest option—which we assumed would be to feed on the visible food, thus allowing them to be more vigilant than when searching for the hidden, patchy food.

Third, we predicted exploration behaviour would also be associated with foraging flexibility in one of two contrasting ways. In line with the information-gathering strategy hypothesis (Arvidsson & Matthysen, 2016; Rojas-Ferrer et al., 2019), we expected fast explorers would be more likely to switch to an alternative, novel, visible food source (because of the higher sampling behaviour associated with their behavioural phenotype), primarily when the alternative food source was of high value. Alternatively, according to the behavioural flexibility hypothesis (Coppens et al., 2010; Koolhaas et al., 1999; Verbeek et al., 1994), we predicted slow explorers to be more responsive to the sudden availability of a new alternative food source and to switch to the alternative visible food, primarily when it was of high value. Once again, we also explored how predation risk influenced the relationship between exploration behaviour and foraging flexibility, for the same reasons mentioned above for the analysis on inhibitory control, and with the same predictions. Together these three aims allowed us to explore whether our measure of foraging flexibility captured intrinsic differences between individuals; whether this flexibility was influenced by inhibitory control and exploration behaviour; and how these relationships depended on the context of food value and predation risk.

2 | MATERIALS AND METHODS

2.1 | Aviary housing

We caught wild great tits (22 females and 27 males) at seven field sites (three mixed deciduous and four coniferous woodland fragments from the same study population) in County Cork, Ireland and held them in an aviary on the university campus for a maximum of 2 weeks from January to March 2018. We fitted birds with a colour ring and a British Trust for Ornithology ring for identification, before placing them in individual plywood cages (62 × 50 × 60 cm, H × W × D; Figure S1) where they could hear but not see each other. Each box had independent air circulatory systems to remove any risk of disease transmission. It is not a concern for the birds to be housed individually and there was never any indication that males being adjacent to another male caused any stress. When not participating in experiments, birds were fed ad libitum sunflower seeds, peanuts and water with added vitamin drops (AviMix$^{®}$). Live mealworms *Tenebrio molitor* were provided three times a day, during experimental training and tests. Before each experiment, we deprived birds of food, but not water, for 2 hr.

2.2 | Exploration behaviour and inhibitory control assays

On the day after their arrival to the aviary, we released the birds individually into an experimental room (4.60 × 3.10 × 2.65 m, W × L × H) to run the open field ‘exploration behaviour in a novel environment’ assay (Verbeek et al., 1994). The experimental room was connected to the birds' individual cages via a sliding door that could be opened from the room and had five wooden ‘trees’ (1.53 × 0.5 m, H × W) spaced 2 m apart from one another inside (Figures S2 and S3). Trees were made of a wooden upright support and two thick branches running at right angles to each other (based on the design of Verbeek et al., 1994). One branch is at the top of the upright support and the other is further down (Figure S3). Within 2 min of entering the experimental room, the number of hops made within a tree, from one of the four branches to another, and flights between trees was totalled to give each bird an ‘exploration of a novel environment’ score, henceforth referred to as ‘exploration behaviour’ (see Dingemanse et al., 2002). This continuous measure is an indicator of the fast–slow personality axis in great tits—those with low scores represent slow explorers and those with high scores represent fast explorers. Demonstrating repeatability has become standard in animal personality studies; nevertheless, we were happy to refine this approach and assume repeatability in our sample because (a) exploration behaviour has previously been shown to be repeatable in our population (O’Shea et al., 2017), as it has in many other populations (Dingemanse et al., 2012), and indeed is true for most behaviour (Bell et al., 2009); (b) doing so minimised the number of ‘procedures’ individuals were exposed to, a key principle of animal welfare practice; and (c) our aim was not to determine whether any association between behaviours occurred at the between or within individual level in this complex experimental design, when multiple measures of all behaviours would be required.

On the following day, we assayed inhibitory control using a detour-reaching task in the individual cages, following the methods described in the study by MacLean et al. (2014). The detour-reaching task involved presenting a plastic cylinder (3.5 × 3 cm, D × L), placed perpendicularly to the direction in which the bird approached the device, 20 cm in front of a perch that was 5 cm high; thus the bird was positioned so that it faced the middle of the long edge of the cylinder before making an approach towards the cylinder (Figure S4). The assay had three phases: (a) Habituation—the birds had to acquire half a waxworm *Galleria mellonella* from the open end of an opaque cylinder three times within the same session; (b) Training—half a waxworm was placed in the centre of the cylinder and to complete training, birds had to retrieve the food without pecking at the cylinder, in four out of five consecutive attempts (Boogert et al., 2011), indicating that they had learnt the task; and (c) Test—the opaque cylinder was replaced with a transparent but otherwise identical cylinder, and birds then attempted to retrieve half a waxworm from the centre. During the test phase, a successful trial was recorded when the bird moved around to the side of the cylinder and took the waxworm from the open end without touching the front of the cylinder, as in training (Figure S5 for distribution of scores). Any contact a bird had with the cylinder before retrieving the food was scored as a fail; birds that pecked at the cylinder front could still subsequently access the reward (>90% of failed trials resulted in the bird immediately moving to the side to access the worm) but this was still recorded as a fail. Following either a successful or a failed trial, the cylinder was removed from the cage, rebaited and put back for the next trial, of which there were 10 in total. All trials were performed on the same day. A bird's final score was the proportion of trials that were successful, thus high scores indicate high inhibitory control. Note that although we generated a single measure of inhibitory control, this measure is repeatable temporally (across years) and contextually (breeding and non-breeding season) in our population (Davidson *et al*., 2021, Pre-print).

2.3 | Foraging flexibility

Before foraging flexibility was measured during four experimental treatments, birds first went through a series of stages: a food preference test, pre-training and training. The food preference test consisted of presenting birds with three mealworms and three de-husked sunflower seeds, and recording the first food eaten. Four individuals did not choose either food in 5 min, so were given the preference test again but with waxworms instead of mealworms, and all chose waxworms over seeds. Of 41 individuals who had the food preference test (the other eight that were in the aviary were not tested due to time constraints), 35 chose and ate a worm (either waxworm or mealworm) and six ate a seed as their first choice, demonstrating that the majority of the birds preferred worms to seeds. For the four birds that were given the preference test with waxworms and preferred them, they received waxworms for all of their following experimental trials and the other birds all received mealworms. For the remainder of the experiment, worms of any type were considered 'high value' and de-husked sunflower seeds were 'low value' based on the results of this preference test.

After the preference test, we gave the birds a pre-training task consisting of a 24-well tray filled with sand. We buried freshly dead mealworms underneath the sand in 10 randomly chosen wells, scattered 10 sunflower seeds (de-husked) randomly on the surface (Figure 1a) and recorded the first food chosen. We ran this task to confirm that the birds would forage on the tray, that the seeds were easier to access than the worms, and that the birds could not detect the buried worms, either visually or through smell. Of the 41 birds who received the food preference test, 39 were tested on the pre-training task (one bird was unwell and did not undertake any further behavioural tasks, the other would not participate) and of these, 38 chose a seed as their first choice, instead of searching in the sand, suggesting that the birds had to be trained to find the buried worms.

Next, we trained the birds to forage for the hidden food in sand so that they would know, when subsequently presented with a tray with sand during the main experimental trials, that their preferred food item (i.e. worms) could be found under the sand, albeit in a patchy distribution. Birds were trained in a step-wise progression. In the first step, all 24 wells were baited with hidden worms, two of which were partially visible to encourage birds to search. Birds progressed to the next step if they ate five hidden worms within 1 hr ($n = 40$). The second step was similar to the first, except only 10 wells were baited (i.e. patchy distribution), one of which was partially visible. Birds progressed if they ate three hidden worms in 1 hr. The final step was the same as the second but the worms were hidden in different wells. The birds completed training if they ate three hidden worms from this tray. Steps were repeated until birds progressed and completed the training ($n = 35$). Of the 41 individuals who received the food preference test, six did not complete training due to welfare concerns or time constraints and were excluded from the rest of the experiment. We assumed that any variation in the level of experience gained during the training (e.g. the time taken to find food) did not bias our interpretation of the results from the experimental phase, though we acknowledge this could have happened if,

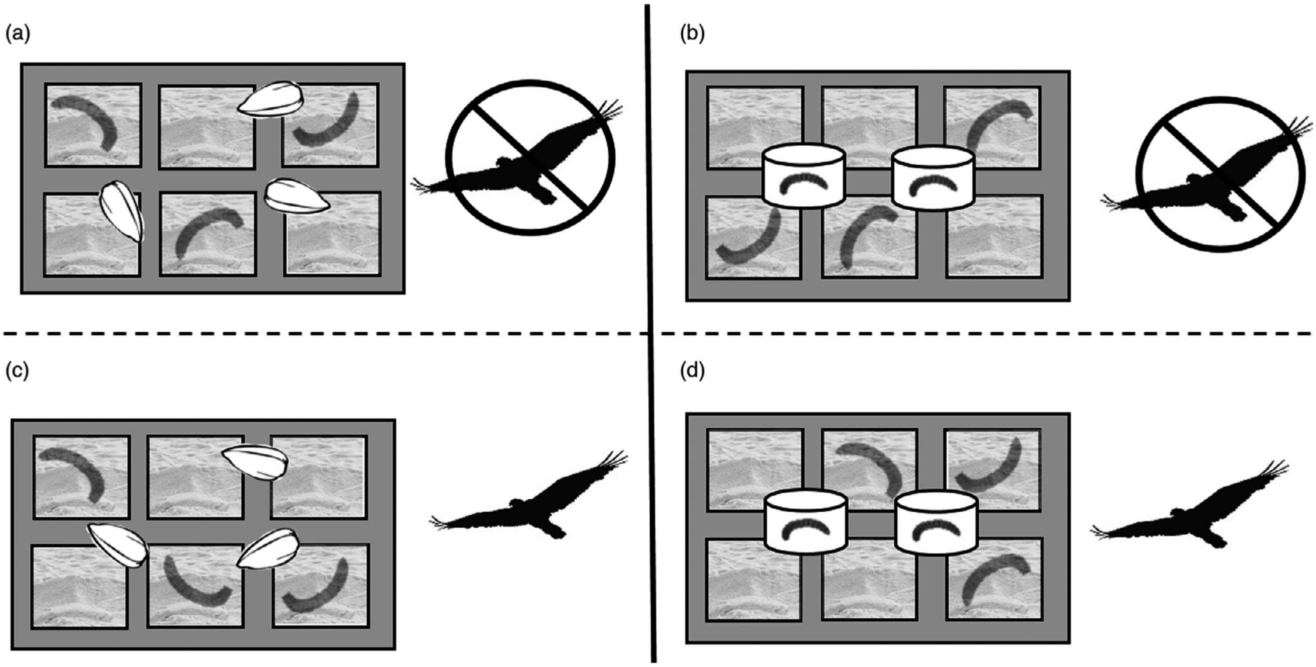

FIGURE 1 Schematic diagram showing the trays (six of 24 wells are shown here for illustrative purposes and clarity) used in the four treatments. In each treatment, we presented great tits with a tray filled with sand and buried mealworms underneath the sand in 10 of the 24 wells. The first treatment (a) had 10 sunflower seeds (de-husked) on the surface and was also presented as the pre-training task. The second (b) had two mealworms in transparent cases on the surface. The third (c) and fourth (d) treatments were as in (a) and (b) but had the addition of a simulated attack by a model sparrowhawk

for example, either inhibitory control or exploration behaviour influenced experience gained.

Birds then entered the experimental phase. All birds underwent 4-min trials in each of four experimental treatments (described below), during which birds were offered a choice between food hidden in the sand and a new visible, alternative food source on the surface. Crucially, because birds had become familiar with searching through the sand during training when there was only one foraging option, which we considered to have then become part of the birds' behavioural repertoire, switching to choosing the visible food on the surface of the tray during the treatments when there were two options was considered to be the flexible response. We determined all of the food choices made during the 4-min trials from video recordings, and scored food choices as either 'hidden' (two or more pecks in the sand in the same well) or 'visible'. Our main response variable, *foraging flexibility*, was defined as the proportion of choices where birds fed on the visible rather than the hidden food out of the total choices made during that 4-min trial. A second coder (C.A.T) watched 20% of the videos to ensure the records of food choice were not biased. Strong agreement was found between coders (intra-class correlation coefficient: ICC = 0.977, 95% confidence interval = 0.938–0.994). See Figure S6 for the distribution of the total number of choices for each of the four tasks.

The treatments were organised in a 2 × 2 factorial design (Figure 1). Birds could hear but not see each other during treatments. The first factor was the type of alternative, visible food that was available on the surface (low or high value), and the second was predation risk (low or high). In all four treatments, we placed the 24-well tray, baited with 10 dead, buried mealworms in randomly assigned wells (a single mealworm per well), on a stool (1 m high) in the centre of the experimental room. We provided one artificial conifer tree (Figure S2) and one wooden tree as in the exploration assay (Figure S3) as perches, 1 m from the stool, from which the trays could be observed. Visible food was also present on the surface of the tray for all four treatments, and was one of two types: low value (10 randomly scattered de-husked sunflower seeds; Figure 1a,c) or high value, where mealworms were encased in two transparent, sealed cases (Figure 1b,d). The visible worms were encased to ensure that there was a cost to attempting to consume the worms, thus ensuring variation, in order to probe what factors explained individual variation in flexibility when an alternative food item of apparently similar value to the hidden familiar food became available. In the wild, great tits exploit both hidden and visible food resources (Gosler, 1993), so we considered these alternative choices to be ecologically relevant for this species. This design therefore reflected a realistic trade-off between the two foods; in the case of seeds, they were easy to access but less preferred, and in the case of the encased worms, they were more preferred but inaccessible. If birds chose a seed and removed it from the tray, or touched the transparent case containing the worm with foot or beak, this was scored as a choice for the visible food. Great tits sometimes flicked over the seeds with their beaks, which we did not count as a choice.

The low predation risk treatments (in the absence of any model predator; see below) were run first (Figure 1a,b). The visible low-value and low-risk treatment was considered to be the baseline response, which we therefore ran first for all individuals; and the high-value, low-risk treatment was run second for all individuals. We expected that potentially confounding carry-over effects from low-value food to high-value food treatments were much less likely than in the opposite direction (birds initially being presented with and choosing high-value visible food leading to them by default choosing the low-value visible food subsequently). The third and fourth treatments were run in the presence of a taxidermy sparrowhawk *Accipiter nisus* to simulate an increased perception of predation risk (Figure 1c,d), and the order in which the visible food alternatives were presented during the two predator treatments was chosen randomly to account for possible carry-over effects of predator attack on food choice. Taxidermic mounts are an effective way to simulate predation risk (Carlson et al., 2017), and have been used effectively on similar experiments in great tits (Kalb et al., 2019). During the third and fourth treatment, when an individual first landed on the tray to make a food choice, we released the 'hawk' from behind a sheet via a pulley system, to 'fly' across the room and 'hide' in a cardboard box. The four treatments were presented over a minimum of 2 days, with at least 2 hr between treatments, and birds that did not first participate in a treatment were given the treatment again once.

2.4 | Statistical analysis

Data were analysed in R version 4.1.0 (R Core Team, 2021). To investigate if individuals were consistent in their foraging flexibility across treatments, and indeed whether it too might be viewed as a personality trait (as defined by Dingemanse & Dochtermann, 2013), we performed a repeatability analysis on foraging flexibility using the RPTR package (Stoffel et al., 2017). The unadjusted repeatability or 'agreement repeatability' (Nakagawa & Schielzeth, 2010; single variable of individual as a random effect) was calculated for the full dataset (*n* = 35; see below).

In the analyses for the second and third aims, we used the LME4 package (Bates et al., 2015) to create two models of foraging flexibility, with either detour-reaching score (model 1, *n* = 29) or exploration behaviour (model 2, *n* = 35) as the key explanatory variables. First we ran inhibitory control and exploration behaviour (and their interactions with the two main treatments central to the hypotheses being tested) in separate models to help limit over-parameterisation and to avoid a type II error, which would inevitably have occurred by including both main effects, not least because doing so would reduce the sample size to the minimum (29 individuals in each 2 × 2 treatment, rather than 35). Furthermore, these two measures are not generally known to be interlinked and were not correlated in our population (Davidson et al., 2021, Pre-print), so we expected them to act on flexibility independently. Nevertheless, we also explored whether their effects were truly independent by fitting a single model for both behaviours and their associated interactions, with the restricted dataset

($n = 29$ individuals tested across all four treatments), which we report along with the averaged model (see below). The response variable, foraging flexibility, was the proportion of choices for the visible food, weighted by the number of total choices (Thomas et al., 2017), and was modelled with a binomial error distribution and a logit link function, with individual ID fitted as a random effect. All models had predator treatment (yes or no), visible food type (seed or encased worm) and the interaction effect between these two included as explanatory variables. Our predictions were tested by the inclusion of detour-reaching score (a proportion out of 10, treated as continuous) in model 1, and exploration behaviour (continuous) in model 2, and their interactions with both visible food type and predation risk. To investigate the influence of confounding factors on foraging flexibility, we ran an analysis including sex, age, habitat, body condition and persistence separately to avoid over-complicating our main models, and found that none of these variables had an effect (for methodological details and results, see Supporting Information).

We used the DHARMa package (Hartig, 2021) to check model fit and to test model assumptions. We used the *dredge* function from the MuMIn package (Barton, 2020) and an information-theoretic approach in combination with model averaging (Grueber et al., 2011) to generate the models with the most support, taken from the global model. The information-theoretic approach compares all possible combinations of models simultaneously, and we calculated the amount of support for each model using Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). Models with a ΔAICc < 2 were retained as the 'top' models that included the most important explanatory variables. We report the full averaged weighted parameter estimates across all models in the top set because this method takes into account that some variables are not present in all models. We ran post hoc analyses using the EMMEANS package (Lenth, 2021). Our figures were created with the INTERACTIONS package (Long, 2019) and show the partial residuals from the binomial GLMMs. Each individual is represented with four points, one for each of the treatments (except where an individual did not complete a task), and the size of the points represents the number of total choices made during the 4-min trials.

3 | RESULTS

The repeatability analyses confirmed that individuals differed consistently from one another in their foraging flexibility, across the four treatments ($n = 35$, $R = 0.31$, $p < 0.001$, 95% CI = 0.12–0.47). Foraging flexibility depended on both the value of the visible food and the predation risk treatment (Table 1; Figure 2). Birds were more flexible when the visible food was of high value and when there was no predator. Nevertheless, some birds were flexible even when the value of the visible food was low compared to the hidden food, and even when the predator was present, demonstrating individual variation in foraging flexibility.

There was no main effect of detour-reaching score, our assay of inhibitory control, on foraging flexibility (Table 1; for weights of the top models see Table 2). However, an interaction between detour-reaching with visible food type did predict flexibility (detour-reaching score × visible food; Table 1; Figure 3; for weights of the top models see Table 2). Birds that had a high score on the detour-reaching task were more flexible than

TABLE 1 The choices made by the great tits in 4 min for detour-reaching score ($n = 29$) and exploration behaviour ($n = 35$) separately. Both models are binomial GLMMs with the proportion of visible choices (out of the total number of choices made) as the response variable. The values shown are the full average of all the top models within two AICc of the best model. A positive value for the estimate means the visible food is more likely to be selected than the hidden food. For each categorical variable, the reference level is in brackets. The relative importance (averaged weight: sum of Akaike weights) for each parameter is shown. Values in bold show a significance level of $p < 0.05$

	Estimate	*SE*	95% confidence interval	Averaged weight	*p*-value
Detour-reaching score					
Intercept	−0.28	0.74	−1.73; 1.17		0.71
Predator (no)	−2.35	0.41	−3.15; −1.55	1.0	**<0.001**
Visible food (encased worm)	−0.87	0.48	−1.81; 0.07	1.0	0.07
Detour	2.14	1.48	−0.76; 5.04	1.0	0.15
Predator × visible food	2.47	0.50	1.49; 3.45	1.0	**<0.001**
Detour × visible food	−2.54	0.96	−4.42; −0.66	1.0	**0.009**
Detour × predator	−0.17	0.60	−1.35; 1.01	0.27	0.78
Exploration					
Intercept	0.23	0.28	−0.32; 0.78		0.42
Predator (no)	−2.93	0.25	−3.42; −2.44	1.0	**<0.001**
Visible food (encased worm)	−1.71	0.25	−2.20; −1.22	1.0	**<0.001**
Exploration	0.07	0.03	0.01; 0.13	1.0	**0.03**
Predator × visible food	2.45	0.31	1.84; 3.06	1.0	**<0.001**
Exploration × visible food	−0.04	0.03	−0.10; 0.02	0.54	0.27
Exploration × predator	0.10	0.03	0.04; 0.16	1.0	**<0.001**

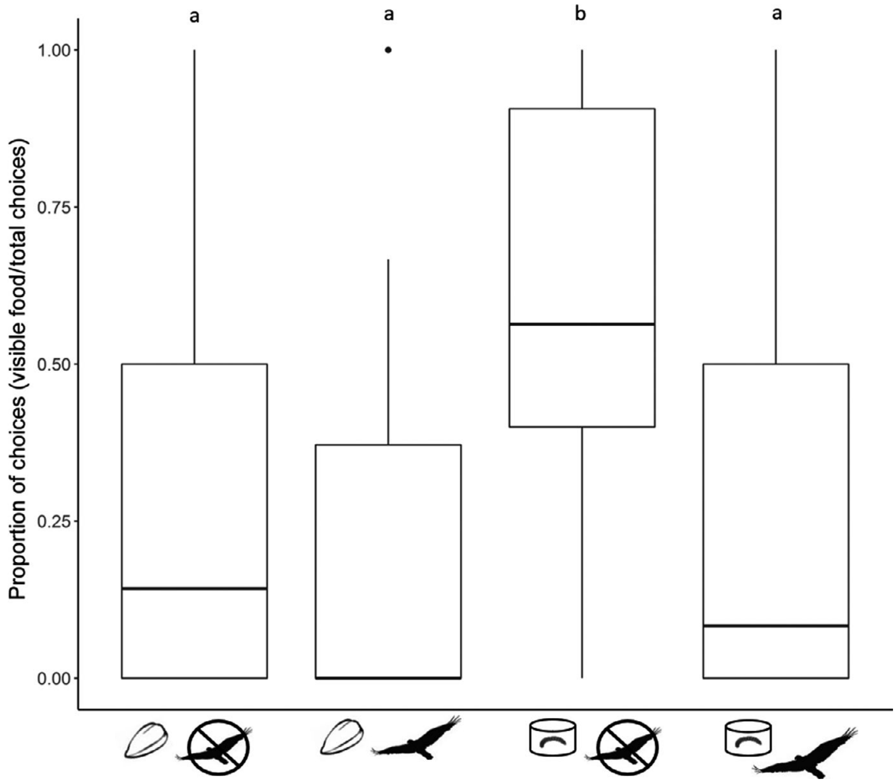

FIGURE 2 Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in 4 min) in relation to the value of the visible food (low, seed; high, encased worm) and perceived predation risk (low or high). The median, 25th and 75th quartiles are shown; the whiskers are ±1.5 × IQR. Significant differences from post hoc tests are indicated by non-matching letters

TABLE 2 The models in the top set for detour-reaching score and exploration behaviour as separate explanatory variables. The response variable was the proportion of choices for the visible food (out of all choices made) during 4 min. The table shows the variables, degrees of freedom (*df*), AICc, delta AIC and Akaike weights (ω_i) for the top set of models within two AICc of the best model

	df	AICc	Δ AIC	ω_i
Detour-reaching score				
Predator × visible food + detour × visible food	7	324.73	0.00	0.73
Predator × visible food + detour × visible food + detour × predator	8	326.70	1.96	0.27
Exploration				
Predator × visible food + exploration × visible food + exploration × predator	8	389.94	0.00	0.55
Predator × visible food + exploration × predator	7	390.38	0.44	0.45

birds that had a low score, but only when the visible food was of high value (post hoc test: Est. = 0.75, *SE* = 0.24, *z* = 3.10, *p* = 0.002; Figure 3). The effect of detour-reaching score on flexibility did not depend on predation risk (detour-reaching score × predation; Table 1).

Exploration behaviour had a positive main effect on foraging flexibility (Table 1; for weights of the top models, see Table 2). Furthermore, faster explorers were more likely to be flexible than slower explorers in the presence of a predator (exploration × predator; Table 1; Figure 4; for weights of the top models, see Table 2; post hoc test: Est. = 0.99, *SE* = 0.23, *z* = 4.34, *p* < 0.001). The relationship between exploration behaviour and flexibility was not dependent on the value of the visible food (exploration × visible food; Table 1).

When detour-reaching score and exploration behaviour were included as fixed effects, and as interactions with both of the main treatments, in the same model, the *p*-values suggested all of the same effects remained significant and similar to those reported for the single models, despite the modest sample size relative to the number of parameters estimated (see Table S1). The averaged parameters from the top four performing models, however, suggested the evidence for an independent effect of detour-reaching score (in its interaction with food value) on flexibility was weak because their averaged effects were not significant (Table S1).

4 | DISCUSSION

Foraging flexibility—defined here as the proportion of choices that were made for the new alternative food option when offered at the same time as a familiar food—was observed among some individuals in all treatments. Furthermore, individuals differed consistently from one another in their foraging flexibility. When the visible food was of high value and when there was no risk of predation, individuals showed higher foraging flexibility. Foraging flexibility was also associated with both inhibitory control and exploration behaviour,

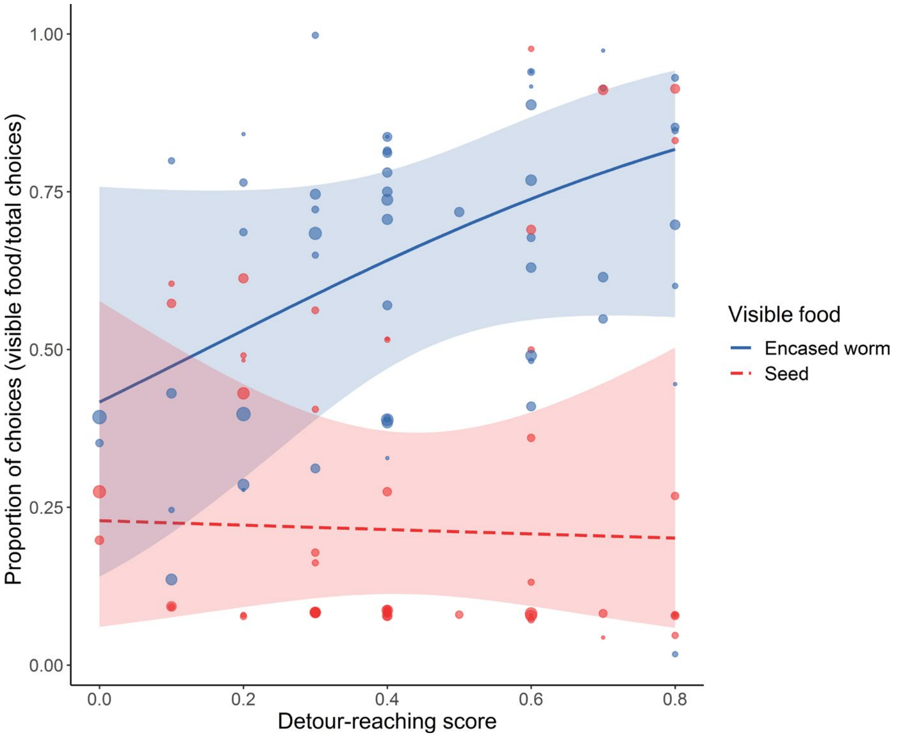

FIGURE 3 Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in 4 min) in relation to detour-reaching score (our assay of inhibitory control), for each visible food value treatment (blue for encased worm, high value; red for seeds, low value). Each individual is represented by four data points, one for each treatment (except where an individual did not complete a task), with the size of the points indicating the number of total choices made. Data are the weighted partial residuals from the binomial GLMM (controls for additional effects in the model). 95% confidence intervals are shown. Sample sizes for each treatment: without predator, seed = 27; without predator, worm = 28; predator, seed = 26; and predator, worm = 25

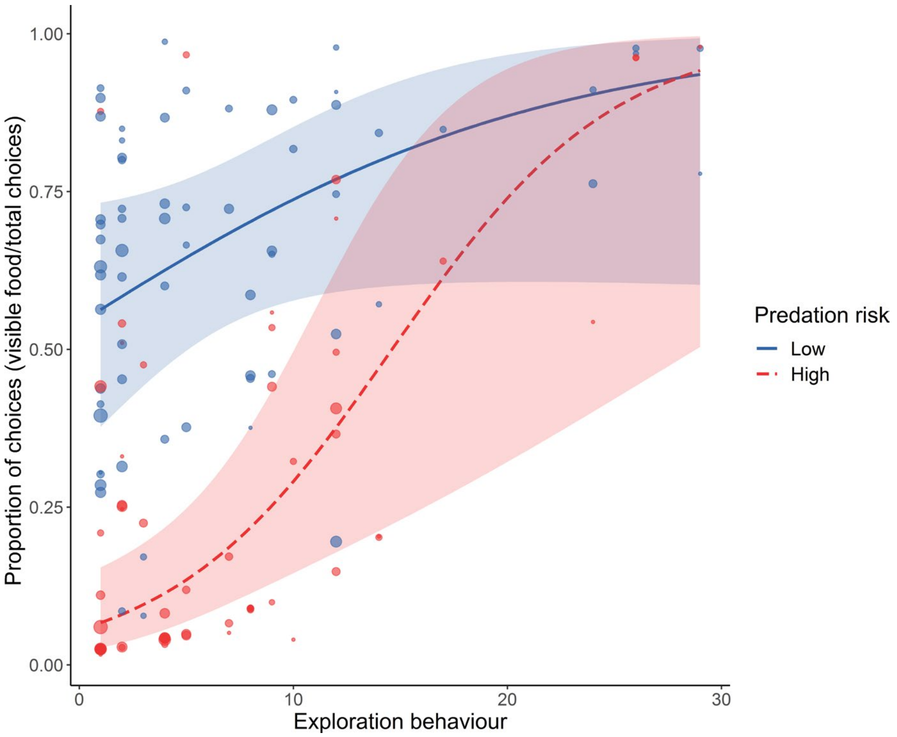

FIGURE 4 Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in 4 min) in relation to exploration behaviour, for each predator treatment (blue for low perceived predation risk; red for high perceived predation risk). Each individual is represented by four data points, one for each treatment (except where an individual did not complete a task), with the size of the points indicating the number of total choices made. Data are weighted partial residuals from the binomial GLMM (controls for additional effects in the model). 95% confidence intervals are shown. Sample sizes for each treatment: without predator, seed = 33; without predator, worm = 34; predator, seed = 32; and predator, worm = 30

though the effect of the former was weaker and dependent on food value, and the effect of the latter was especially strong when predation risk was high. Thus, individual differences in foraging flexibility were associated with individual differences in a cognitive trait (i.e. inhibitory control) as well as in a behavioural trait that is frequently used to assay the fast–slow personality axis, and these associations were moderated differentially by the ecological context.

4.1 | Food value and predation risk

When the visible food was of lower value (non-preferred) and predation risk low, birds showed limited flexibility, primarily continuing to feed on the familiar, hidden and preferred food. This is as expected because birds had a high preference for mealworms over seeds, and assuming the birds were behaving optimally (Lima & Dill, 1990;

MacArthur & Pianka, 1966; Milinski & Heller, 1978), it also suggests that the costs of having to find the hidden food were outweighed by its higher value relative to the low-value visible food. Birds were more likely to show the flexible response when the visible food source was of high value. That they continued to do so even though they could not ultimately acquire the encased high-value worm may reflect the great tit's well-known innovativeness when faced with novel food sources (Aplin et al., 2015; Serrano-Davies et al., 2017). Acquiring information about novel food likely serves as a way of generating new food sources and reducing future uncertainty (Mathot et al., 2012; Tebbich & Teschke, 2014), but these results suggest they primarily only do so when the risk of predation is low.

When predation risk increased, we expected birds to be more flexible by feeding on the visible food, because searching for hidden food would have reduced their vigilance and ability to detect an approaching predator. However, the opposite was the case: fewer birds chose the visible food when predation risk was high. One likely explanation for this finding is that great tits may have felt safer feeding on the familiar food, despite it taking more time to locate than the visible surface food, potentially compromising their vigilance. Whether animals are likely to disregard high-value foods depends on risk, certainty and reward value (Green & Myerson, 1996; Holbrook & Schmitt, 1988; Mazur, 1988). In our study, the encased worm, though of relative high value, was likely too costly to choose when there was heightened risk because it was unfamiliar and difficult to obtain. In the case of the low-value seeds, any benefit of selecting this visible option was presumably outweighed by the cost of abandoning the preferred hidden food, even when under predation risk. An alternative explanation is that stress compromises the ability to assess changes in food value, as reported from a study on humans (Schwabe & Wolf, 2009). As such, when great tits were in the presence of a perceived predator, perhaps they could not accurately assess the relative value of the foods and so fell back on their trained behaviour of searching in the sand for the hidden worms. Whatever the explanation, the effects of predation and food type in our study highlight that manipulating ecologically relevant factors leads to differential patterns of individual foraging flexibility.

4.2 | Inhibitory control

We found support for the hypothesis that inhibitory control, assayed using the detour-reaching task, is associated with flexibility when foraging. The association was only observed when the visible food was of high value. Individuals with high inhibitory control were more likely to switch to the visible food, but only when both options were of similarly high value. Birds with poor inhibitory control were less likely to override their trained behaviour and did not attempt to feed on the visible food regardless of its value; that is, they were less flexible in their observed behaviour. We also predicted that this link could be dependent on predation risk because individual differences and habitual behaviour can be more pronounced under stress (Schwabe & Wolf, 2009; Suomi, 2004), or because severe predation risk could override any effects of inhibitory control on behaviour (Quinn & Cresswell, 2005). We found no evidence for this, suggesting that the effect of this executive cognitive function on foraging flexibility is not influenced by an immediate extrinsic stressor like predation risk, although whether this is true for effects of inhibitory control on functional behaviour generally, and whether this extends to other kinds of stressors, remains to be explored. Our modest sample size and complex models meant that the model average when inhibitory control, exploration behaviour and their interactions with both of the main treatments were combined, provided weak support for an independent effect of inhibitory control (Table S1). This is likely due to limited power, however, so taken together our results suggest that inhibitory control can predict foraging flexibility, and that in natural systems this effect is most likely to be revealed when food availability changes.

One possible alternative explanation for birds with high inhibitory control being more flexible is that inhibitory control covaried with neophobia, which then drove the effect. This seems unlikely in our sample where inhibitory control does not correlate with exploration behaviour (Davidson et al., 2021, Pre-print), which itself is a predictor of neophobia (Carere et al., 2010; see below under *Personality*). At the same time we cannot rule out an underlying causal effect of neophobia entirely because there is some suggestion of a link between inhibitory control and other personality traits (Regolin et al., 1994; Gomes et al., 2020; Lucon-Xiccato et al., 2020 but see Stow et al., 2018). Another possible explanation for the observed link between flexibility and inhibitory control is that the similarity between the transparent materials used in the inhibitory control and foraging tasks led to a carry-over effect. Again this is unlikely because the devices were otherwise very different (open-ended cylinder with access to food and circular case without access), and all birds had similar experience with transparent objects before undertaking the food choice tasks.

Few studies have examined the ecological significance of inhibitory control. At the interspecific level, high inhibitory control in primates is associated with species that have pronounced fission–fusion dynamics (Amici et al., 2008, 2013) or wide dietary breath (MacLean et al., 2014). At the intraspecific level, links between inhibitory control and behaviour are well-established in humans (Bari & Robbins, 2013), but very few studies in non-human animals exist. Body condition was positively related to inhibitory control in New Zealand robins *Petroica longipes*, and although the author interpreted this to be because low glucose levels in the blood of birds in poor condition might have impaired cognitive performance (Shaw, 2017), causality could equally have been in the opposite direction: those with good inhibitory control could have been better foragers. In common pheasants *Phasianus colchicus*, dietary diversity was negatively associated with inhibitory control (van Horik et al., 2018), although the mechanisms underpinning such a link are difficult to interpret. Thus, the results presented here represent rare evidence for a link between inhibitory control and ecologically relevant behaviour, and the only example of a link with individual behavioural plasticity, not just foraging flexibility, when ecological conditions change.

4.3 | Personality

Empirical studies predict that exploration behaviour correlates with flexibility, with some suggesting that fast explorers are more flexible (information-gathering hypothesis; Frost et al., 2007; Mathot et al., 2012; Rojas-Ferrer et al., 2019), and others suggesting the opposite (behavioural flexibility hypothesis; Coppens et al., 2010; Verbeek et al., 1994; Wolf et al., 2008). We found a significant positive main effect of exploration behaviour—fast explorers were more likely to prioritise the visible food and were therefore more flexible than the slow explorers—providing support for the information-gathering hypothesis. Differences in neophobia could also play a concurrent role here if the encased worm was perceived as a novel object—faster explorers also tend to be more neophilic (van Oers et al., 2004). However, although we did not predict this a priori, given that the positive association between flexibility and exploration behaviour was especially pronounced under the high predation risk treatment (Figure 4), and that feeding on the familiar hidden food was perceived by birds to be the safest option (as discussed above), the stronger positive association in the high predation risk treatment is also likely explained in part by a differential response to predation risk, since exploration behaviour also correlates positively with risk proneness (Koolhaas et al., 1999; Quinn et al., 2009, 2011). Thus, the potential ways that individual variation in behavioural flexibility might be influenced by the fast–slow exploration personality axis—and presumably by other axes and behavioural syndromes generally—are numerous and context dependent, but in our experiment are likely explained by a combination of how individuals collect information and manage risk.

Formally, it is widely considered that for a trait to reflect ‘personality’, it should also be repeatable (Araya-Ajoy et al., 2015; Dingemanse & Dochtermann, 2013). Previously, we demonstrated that exploration behaviour is repeatable in our study population (O’Shea et al., 2017), and along with a number of reasons specified in the methods, it was appropriate to assume that exploration was also repeatable in this sample of our population. We acknowledge that support for the hypothesis that foraging flexibility was associated with ‘personality’ depends on this assumption. A natural extension to our analysis would be to establish whether the correlation between exploration behaviour and foraging flexibility, or indeed between inhibitory control and flexibility, occurred at the between- or within-individual level, the former of which would point to the correlations arising because of intrinsic differences among individuals and the latter to plasticity (Dingemanse & Dochtermann, 2013). The logistical challenge of estimating phenotypic covariance in our system—generating large sample sizes and repeated measures over lengthy periods of time in captivity (see also Edwards et al., 2013)—precluded us from taking this approach, though an increasing number of studies are now doing so in other systems, even within a reaction norm framework (e.g. Baškiera & Gvoždík, 2019; Hertel et al., 2020; Mitchell & Biro, 2017; Westneat et al., 2013).

Individual variation in behavioural plasticity is an important mechanism facilitating adaptation to ecological or environmental change. Our results show substantial and repeatable individual variation in foraging flexibility, a specific form of behavioural plasticity, and suggest that cognition and personality play context-dependent, independent roles simultaneously. They also suggest that the population-level consequences of behavioural variation may only be revealed in the presence of specific ecological conditions, such as when individuals are under predation risk, or when food types available vary over space and time.

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COMPETING INTERESTS

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

J.R.C., I.G.K., G.L.D. and J.L.Q. designed the study; J.R.C. and G.L.D. collected the data with help from I.G.K.; J.R.C. analysed the data with help from M.S.R. and C.A.T.; J.R.C., J.L.Q., M.S.R. and G.L.D. wrote the manuscript with input from I.G.K. and C.A.T. All authors approved the final manuscript and agreed to be held accountable for the contents.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.mw6m905xh (Coomes et al., 2021).

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