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Evolutionary biology

Environmental transmission of a personality trait: foster parent exploration behaviour predicts offspring exploration behaviour in zebra finches

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Consistent behavioural differences among individuals are common in many species and can have important effects on offspring fitness. To understand such ‘personality’ variation, it is important to determine the mode of inheritance, but this has been quantified for only a few species. Here, we report results from a breeding experiment in captive zebra finches, *Taeniopygia guttata*, in which we cross-fostered offspring to disentangle the importance of genetic and non-genetic transmission of behaviour. Genetic and foster-parents’ exploratory type was measured in a novel environment pre-breeding and offspring exploratory type was assessed at adulthood. Offspring exploratory type was predicted by the exploratory behaviour of the foster but not the genetic parents, whereas offspring size was predicted by genetic but not foster-parents’ size. Other aspects of the social environment, such as rearing regime (uni- versus biparental), hatching position, brood size or an individual’s sex did not influence offspring exploration. Our results therefore indicate that non-genetic transmission of behaviour can play an important role in shaping animal personality variation.

1. Introduction

Consistent behavioural differences among individuals (‘personality’ variation) are widespread in the animal kingdom [1] and can have consequences for fitness [2]. Elucidating mechanisms underlying personality differences could be fundamental for understanding how inter-individual variation in behaviour, the raw material for evolutionary change, is maintained. Studies have revealed that around 30 per cent of the individual differences in behaviour are inherited [3,4]. However, the potential for non-genetic inheritance from parental effects (inclusive heritability: [5]) to shape offspring personality has generally been neglected [5–7]. Parental effects occur when the phenotype (or experience) of the mother and/or father influence the offspring phenotype independently of the effects of direct genetic transmission [7,8]. Parental effects on offspring behavioural phenotype, including personality, can occur early in development, for example via maternal hormones deposited into bird eggs [9,10]. Parents might also influence offspring behavioural phenotype at later stages of offspring development, for example via non-genetic transmission of behavioural traits from parents to offspring (e.g. during post-hatching parental care in birds). However, little is known about non-genetic parent–offspring transmission of behaviour during advanced pre-independence stages of offspring development (but see [11,12]). Individual differences in maternal care are behaviourally transmitted between generations in rats, *Rattus norvegicus* [11]. In contrast, Alpine swifts, *Apus melba*, resemble their genetic but not foster parents

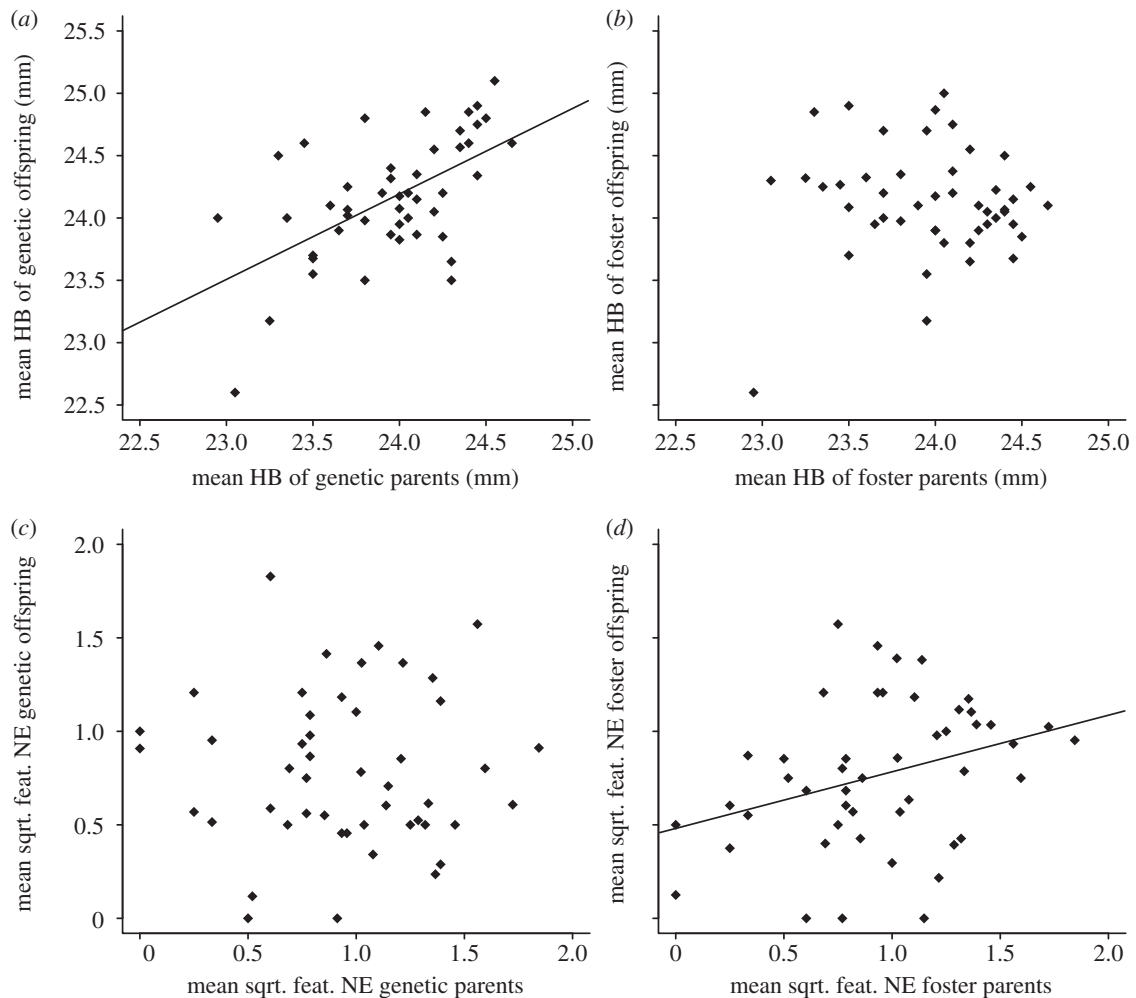


Figure 1. Mid-head–bill length (HB; *a,b*) and number of features visited in the novel environment (feat. NE; *c,d*) for parents and their genetic (*a,c*) and foster offspring (*b,d*). Sqrt, square-root transformed.

in their anti-predator behaviour [12]. Here, we aim to disentangle the genetic and early (pre-hatching) parental effects from later parental (personality) effects on offspring personality using a cross-foster breeding experiment with zebra finches. Hatchlings were cross-fostered and the relative contribution of genetic and foster-parents' exploratory type and size on the exploratory type and size of their genetic and foster offspring, respectively, assessed. Exploration is a consistent personality trait in the zebra finch that is under sexual and (potentially) viability selection [13–15] and probably influences coordination of behaviours during parental care [14]. Although repeatability can be high, the heritability of behavioural traits is on average lower than that of morphological traits [3,16]. For exploration, permanent environmental (PE) effects have been found to explain a substantial amount of among-individual variation in adult behaviour [17,18]. Here, we ask whether non-genetic transmission of parental behavioural phenotype contributes to this among-individual variation observed later in life.

2. Material and methods

Specific details are provided in the electronic supplementary material. General methods are detailed in Schuett *et al.* [14]. After measuring size (e.g. head–bill length, HB) and exploration (number of features visited in a novel environment) twice, males and females were paired up and allowed to breed. Fifty-three

clutches were cross-fostered just prior to hatching. The rearing regime was manipulated and brood sizes adjusted to maintain a consistent brood size/parent: the foster father was removed when offspring were 3 days until the offspring reached independence in some cages (uniparental regime) but not in others (biparental regime). One hundred and fifty-four (of 159) offspring survived to adulthood when they were size measured and tested twice for their exploration behaviour. The experiment was conducted in 2007 and repeated in 2008, using offspring from 2007 as the new parental generation.

Firstly we used parent–offspring regressions (PO) to investigate the inheritance of HB and exploration. Exploration was scored as the square root of the number of features visited by an individual in a novel environment test, and averaged within individuals across the two trials. Genetic (and non-genetic) transmission of size and exploration was estimated as the slope of the regression between mid-parent (and foster-parent) trait values and brood-mean values [19]. Secondly, we analysed the data using repeated measures animal models (AMs; [20]). Here, the two (four for parental generation 2008, i.e. offspring in 2007) behavioural trials per individual allowed us to estimate the repeatability of exploration before partitioning of the among-individual variance into genetic and non-genetic components. For each response variable, random effects were fitted to partition phenotypic variance into additive genetic, PE and foster clutch (foster environment) components (table 2). Heritability (h^2) was estimated as the proportion of phenotypic variance explained by additive genetic variance (VA). We assumed variance attributable to dominance and/or unmodelled early maternal effects was negligible, and estimated phenotypic

Table 1. Results from mid-parent mid-offspring regressions. Mean $\sqrt{\text{feat.}}$, mean of square-rooted number of features visited over two trials; HB, head–bill length. Significant *p*-values in italics.

trait	view	slope	s.e.	<i>R</i>	<i>F</i>	d.f.	<i>p</i>
HB	genetic	0.686	0.15	0.57	22.08	1,45	<0.0001
		0.756 ^a	0.13 ^a	0.64 ^a	31.55 ^a	1,45 ^a	<0.0001 ^a
	foster	−0.003	0.16	<0.01	<0.01	1,45	0.98
mean $\sqrt{\text{feat.}}$	genetic	−0.005	0.14	<0.01	<0.01	1,46	0.97
		0.303	0.13	0.33	5.55	1,46	0.02
	0.296 ^a	0.12 ^a	0.35 ^a	6.48 ^a	1,46 ^a	0.01 ^a	
	0.309 ^b	0.14 ^b	0.37 ^b	5.03 ^b	1,32 ^b	0.03 ^b	

^aWeighted regression, accounting for the number of chicks measured at adulthood per clutch.

^bClutches with biparental regime only.

variance as the sum of the variance components partitioned (i.e. conditional on fixed effects). For size (model 1) and exploratory behaviour (model 2a), we initially included fixed effects of year and status (i.e. adult versus juvenile at the time of trial). We then fitted additional fixed regressions of foster and genetic mid-parent phenotypes to explicitly test the hypothesized non-genetic inheritance on exploratory behaviour (model 2b). Finally, given that mid-foster parent exploration predicted offspring exploration behaviour (see below), we modelled each foster parent phenotype separately, as well as their interaction (model 2c). The significance of fixed effects was assessed using conditional Wald *F*-statistics, whereas random effects were tested using conservative (two-tailed) likelihood ratio tests. Our three generational pedigree structure contains 225 individuals with 51 mothers, 51 fathers and maximum full-sib family size of 6. We assume that the 2007 parental generation comprised unrelated individuals. Data were analysed in R [21], using the ASReml package for AM, and have been deposited in Dryad: doi:10.5061/dryad.tf767.

3. Results

Size was strongly heritable, and largely independent of foster-parents' size (PO: figure 1a,b and table 1; AM model 1: table 2; electronic supplementary material, table S1). Estimates of h^2 were similar from the two analytical approaches (HB: 0.69 ± 0.15 from PO and 0.63 ± 0.08 from AM model 1). Qualitatively, this pattern was reversed for the offspring personality trait. The number of features visited was repeatable (mixed model with individual and foster clutch as random terms: $R \pm \text{s.e.} = 0.277 \pm 0.068$, $\chi^2 = 21.71$, d.f. = 1, $p < 0.001$) but not significantly heritable (PO: table 1 and figure 1c; AM: table 2). Among-individual variation in exploration behaviour was partitioned primarily as PE effects, whereas foster clutch did not explain significant variance (AM model 2a: table 2). Nonetheless, direct testing showed that mid-foster-parent exploration behaviour positively predicted foster–offspring behaviour (PO: figure 1d and table 1; AM model 2b: table 2), and accounted for a large proportion of among-individual variance (shown by reduction of V_{PE} from model 2a to 2b: table 2). Separately modelling foster mother and father exploration scores (as well as their interaction) suggests that personality variation arises primarily as a maternal effect (AM model 2c: table 2). The effects of foster parent (and specifically foster mother) phenotype indicated by models 2b and 2c did not significantly differ between

parental care regimes (uni- versus biparental; full results not shown). Additionally, there were no main effects of hatching position, sex, parental care regime or manipulated brood size on offspring exploratory behaviour (mixed model: electronic supplementary material, table S2).

4. Discussion

Offspring size was primarily genetically inherited, while exploratory behaviour was predicted by foster but not genetic parent exploratory behaviour. These results are one of the first experimental demonstrations that consistent behavioural tendencies can be non-genetically transmitted from parents to offspring.

Our results are consistent with previous studies showing that morphological traits are moderately to highly heritable [16,22], whereas behavioural traits have low to moderate heritability and are significantly influenced by the environment ([17,22,23], but see [24]; note that we did not assess heritability *per se* but a composite of heritability and pre-hatching parental effects). Previous studies, however, often do not specifically identify the aspects of the environment that influence the individual behaviour (but see [11]). Here, we found that PE effects accounted for most of the repeatable variation in exploratory behaviour, but also demonstrated that a large proportion of this variation could be explained by the behavioural phenotype of the foster parents (mothers in particular). This finding is consistent with direct or indirect transmission of a behavioural trait via non-genetic parental effects. Other environmental factors, such as aspects of the early social environment (hatching position, foster clutch size or rearing regime), did not significantly influence the exploratory behaviour of offspring. The behavioural transmission occurred as a post-hatching parental effect. Parental effects may also occur earlier in development, for example via differential maternal allocation of hormones into eggs, or through variation in incubation behaviour. Given the available data structure, statistical partitioning of maternal effects arising from the genetic mother (e.g. egg effects) from additive variance is not likely to be robust [20]. We also note that the full sibling pedigree structure precludes separation of additive from dominance variance. Nevertheless, the estimated heritability of exploration was low regardless of these possible sources of upward bias. Personality traits in zebra finches have previously been found to heritable (e.g.

Table 2. Parameter estimates from animal model analyses of size (HB; model 1) and individual exploratory behaviour ($\sqrt{\text{features}}$; models 2a–c). Statistical inference was based on conditional F -statistics for fixed effects, and likelihood ratio tests for random effects (see text for details). Significant p -values in italics. Prop. of VP, proportion of total variance explained; status at test, age at personality test (factor with two levels: offspring (juv.) tested at ca 90 days of age, parents tested at greater than 1 year of age).

model	response variable	explanatory variable	estimate (s.e.)	prop. of VP (s.e.)	χ^2 (d.f. = 1)	F (d.f.)	p	
1	HB	random effects						
		additive genetic	0.189 (0.039)	0.625 (0.081)	31.2		<0.001	
	fixed effects	permanent environment	0.000 (–) ^d	0.000 (–)	0		1	
		foster environment	0.000 (–) ^d	0.000 (–)	0		1	
	fixed effects	mean	24.0 (0.062)			340 000 (1,92.6)	<0.001	
		year (effect of 2008) ^a	–0.121 (0.071)			2.93 (1,167.6)	0.091	
		status at test (juv.) ^b	0.177 (0.066)			7.15 (1,179.1)	0.009	
		additive genetic	0.036 (0.036)	0.067 (0.067)	1.36		0.244	
	2a	$\sqrt{\text{features}}$	random effects					
			permanent environment	0.118 (0.045)	0.221 (0.082)	7.55		0.006
fixed effects		foster environment	0.023 (0.027)	0.044 (0.051)	0.009		0.922	
		mean	0.932 (0.066)			315 (1,29.1)	<0.001	
fixed effects		year (effect of 2008) ^a	0.141 (0.075)			7.95 (1,289.3)	0.064	
		status at test (juv.) ^b	–0.224 (0.066)			10.5 (1,242.6)	0.001	
		additive genetic	0.064 (0.053)	0.123 (0.010)	2.04		0.153	
		permanent environment	0.066 (0.052)	0.127 (0.101)	1.48		0.224	
2b		$\sqrt{\text{features}}$	random effects					
			foster environment	0.000 (–) ^d	0.000 (–)	0		1
	fixed effects	mean	0.589 (0.155)			171.1 (1,20.1)	<0.001	
		year (effect of 2008) ^a	0.404 (0.122)			10.94 (1,157.6)	0.001	
	fixed effects	status at test (juv.) ^b	0.069 (0.137)			0.25 (1,134.3)	0.613	
		mid $\sqrt{\text{features}}$ foster parents ^c	0.322 (0.112)			8.19 (1,111.9)	0.005	
		mid $\sqrt{\text{features}}$ genetic parents ^c	0.149 (0.126)			1.39 (1,33.0)	0.247	

(Continued.)

Table 2. (Continued.)

model	response variable	explanatory variable	estimate (s.e.)	prop. of VP (s.e.)	χ^2 (d.f. = 1)	F (d.f.)	p
2c	$\sqrt{\text{features}}$	random effects					
		additive genetic	0.054 (0.056)	0.104 (0.106)	1.12		0.290
		permanent environment	0.077 (0.52)	0.148 (0.098)	2.24		0.135
	fixed effects	foster environment	0.010 (0.028)	0.019 (0.053)	0.154		0.694
		mean	0.732 (0.156)			170 (1,20.1)	<0.001
		year (effect of 2008) ^a	0.255 (0.114)			4.93 (1,50.2)	0.031
		status at test (juv.) ^b	-0.077 (0.133)			0.34 (1,60.7)	0.560
		mean $\sqrt{\text{features}}$ foster mother ^c	0.177 (0.081)			4.77 (1,42.4)	0.035
		mean $\sqrt{\text{features}}$ foster father ^c	0.120 (0.095)			2.46 (1,42.4)	0.221
		mean $\sqrt{\text{features}}$ foster mother ^c					
		*mean $\sqrt{\text{features}}$ foster father ^c	0.040 (0.155)			0.07 (1,47.2)	0.795

^aEffect of being tested in 2008 relative to the mean of being tested in 2007 (mean).^bEffect of being tested at an age of ca 90 days relative to the mean of being tested at an age greater than 1 year (mean).^cVariables were mean centred.^dParameter estimate bound at zero, therefore no s.e. estimated.

behaviour towards a novel object: [24]) and our sample size was quite small. We therefore interpret the lack of significant heritability for exploration with some caution. However, although we did not find significant additive genetic effects on the expression of personality in our study, we did find significant (non-genetic) PE effects, despite the small sample size (AM model 2a; table 2).

Behavioural transmission might provide adaptive benefits if the success of different exploratory types is context-dependent, and (social) environmental conditions (e.g. population density) vary predictably and stably across generations but not so long that genetically determined behaviours predominate. Our

study provides evidence that personality traits can be non-genetically inherited, via behavioural transmission, in zebra finches. Further studies are needed to assess how widespread this mode of inheritance is for personality traits across species.

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