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Experimental evidence for adaptive personalities in a wild passerine bird

Nicolaus, Marion; Tinbergen, Joost M.; Bouwman, Karen M.; Michler, Stephanie P. M.; Ubels, Richard; Both, Christiaan; Kempenaers, Bart; Dingemanse, Niels J.

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Electronic Supplementary Materials of the manuscript entitled “Experimental evidence for adaptive personalities in a wild passerine bird”.

M. Nicolaus, J. M. Tinbergen, K. M. Bouwman, S. P. M. Michler, R. Ubels, C. Both, B. Kempenaers and N. J. Dingemanse

Electronic Supplementary Materials S1: Treatment-specific adult survival probabilities.

The local survival probability of parental birds was altered by manipulating their brood sizes within breeding plots, and fledging sex ratio between breeding plots, resulting in 9 treatment groups per year. The full model was run for three cohorts of manipulated parents (2005, 2006 and 2007, $n = 1012$ individuals, each individual being present only once in the analysis; see [1]). The analysis revealed strong and robust effects of brood size and fledging sex ratio manipulation effects on adult local survival probability (for full details see [1]). Here we make use of the variation in adult survival induced by our manipulations to test adaptive personality theory. Because we only retained parents that were tested for their personality before and after manipulation, we restricted our data set to parents manipulated in 2006 and 2007. Survival estimates (95%CI) derived from the GLMM previously validated and published [1], and sample size ($n =$ number of individuals) are presented per treatment group for the years 2006 and 2007 (see details in the main manuscript and in [1]).

plot sex ratio treatments ¹	Female			Control			Male		
brood size treatments	Small	Intermediate	Large	Small	Intermediate	Large	Small	Intermediate	Large
2006									
survival estimate	0.30	0.35	0.40	0.27	0.30	0.26	0.45	0.25	0.25
(95%CI)	(0.29, 0.31)	(0.34, 0.37)	(0.39, 0.42)	(0.26, 0.28)	(0.29, 0.31)	(0.25, 0.27)	(0.44, 0.47)	(0.24, 0.26)	(0.24, 0.26)
n	31	16	31	55	31	58	24	11	29
2007									
survival estimate	0.32	0.37	0.42	0.28	0.32	0.28	0.47	0.26	0.27
(95%CI)	(0.31, 0.33)	(0.36, 0.38)	(0.41, 0.43)	(0.27, 0.29)	(0.30, 0.33)	(0.27, 0.29)	(0.46, 0.48)	(0.25, 0.27)	(0.26, 0.28)
n	65	35	46	54	30	48	54	25	44

¹each plot sex ratio treatment had 4 replicates per year

Electronic Supplementary Materials S2a: Sources of variation in post-manipulation risky behaviour

We present here a General Linear Mixed Effects Model (GLMM) with the same fixed and random effect structure as detailed in Table 1 of the main manuscript, but with square-root transformed post-manipulation exploration score as the response variable instead of the change in square-root transformed exploration score (after minus before the manipulation). For each fixed effect we give the estimates of modes of the posterior distributions and their 95% confidence interval following the same procedure as described in the main manuscript. This alternative modeling approach confirms all findings presented in the main text both qualitatively and quantitatively.

Fixed effect	Estimate	Confidence interval
Intercept	4.159	(3.916, 4.331)
expected future survival	-1.941	(-3.290, -1.071)
pre-manipulation score	0.542	(0.522, 0.555)
inter-test interval	0.504	(0.483, 0.543)

Electronic Supplementary Materials S2b: No significant differences in pre-manipulation exploration score among the treatment groups. We present here a General Linear Mixed Effects Model (GLMM) with square-root transformed pre-manipulation exploration score as the response variable and with Date (Julian date centered around population mean; continuous variable), Treatment group (factor) and Year (factor) as the fixed effects. Random intercepts were included for Cohort. The absence of significant effect of Treatment group on pre-manipulation exploration score implies that the application of treatments was not biased with respect to exploration type (n=146 individuals).

Fixed effects	β	SE (β)	χ^2	d.f.	P
Intercept	3.033	0.290	109.67	1	<0.001
Day	0.501	0.210	5.68	1	0.017
Year	-0.029	0.202	0.02	1	0.887
Treatment group			10.67	8	0.221

Random effect estimate (\pm SE): $\sigma^2_{\text{cohort}} = 1.035 \pm 0.121$

Electronic Supplementary Materials S3: Quantitative genetics analyses

We used restricted maximum-likelihood ('REML') models with a pedigree based on social mating to estimate variance components of exploration score. Such 'animal models' allow for the decomposition of the phenotypic variance into random and fixed effect variance components by comparing phenotypes of known relatives using pedigree information, and facilitate quantitative genetic analyses of unbalanced datasets [2]. Repeated measurements of the same individuals were included in the model, using a fixed effect structure detailed below. We included 1790 assays of 1243 individuals and ran the animal models for a pedigree that includes 25156 individuals over 14 generations (1993 - 2009).

We adopted statistical modeling and inference approaches advocated in [3] and [4] (Table S3). Our initial model (model 1) included the fixed effects detailed below. As a second step (model 2), we included random intercepts for "Individual", thereby partitioning the phenotypic variance not explained by fixed effects (V_P) into individual (V_I) and residual (V_R) variance components, i.e. $V_P=V_I+V_R$. As a third step (model 3), we decomposed V_I into its additive genetic (V_A) and permanent environment (V_{PE}) components, the latter component representing variation that is conserved (i.e. "permanent") across an individual's records but is not due to additive genetic effects, i.e. $V_P=V_A+V_{PE}+V_R$. This third model was constructed by including "Individual linked to the pedigree" as an additional random effect, with pedigree data allowing the relatedness matrix among individuals to be specified [5]. As a fourth step (model 4), "Individual linked to the pedigree" was included as the only random effect to specifically test for the significance of permanent environment effects.

The statistical significance of all random effects was derived from likelihood ratio tests (LRTs). The test statistic is twice the difference in log-likelihood between hierarchical models,

and is distributed as χ^2 with the degrees of freedom equal to the difference in the number of variance parameters estimated [6]. Specifically, (i) the significance of the individual variance (hence repeatability (r) = V_I/V_P) was based on the comparison of model 1 versus 2; (ii) the significance of the additive genetic variance (hence narrow-sense heritability (h^2) = V_A/V_P) was based on the comparison of model 2 versus 3; (iii) the significance of the permanent environment variance was based on a comparison of model 3 versus model 4.

Fixed effects included in all models were variables known to affect exploration score within individuals in West-European populations of great tits [7-8]: log-transformed “Time of year” (the days from July 1st or “Julian date”), log-transformed “Inter-test interval” (in days) between subsequent tests of the same individual, and test “Sequence” number (first tests coded as 0; subsequent tests coded as 1). We further included “Year” (2005-2008). The significance of the fixed effects was derived using numerator and denominator degrees of freedom estimated from the algebraic algorithm in ASReml 3.0 [9].

Table S3: Variance components of exploration score

We present here estimates of fixed and random effects with their associated standard errors in brackets. (a) Hierarchical models varying in random effect structure detailed in the supplementary information S2 with their associated Log-Likelihood (LogL). Model 1 does not include any random effects; Model 2 decomposes the phenotypic variance not explained by fixed effects (V_P) into individual (V_I) and residual variance components (V_R); Model 3 splits V_I into its additive genetic (V_A) and permanent environment (V_{PE}) components; Model 4 splits (V_P) into additive genetic (V_A) and residual variance components (V_R). Ratios r , pe^2 and h^2 are the proportion of V_P explained by V_I , V_{PE} and V_A , respectively. Footnotes 1-3 give significances for variance components of interest based on Likelihood Ratio Tests (LRTs).

(b) Fixed effect estimates for Log-transformed “Time of year” (Julian date), Log-transformed “Inter-test interval” between subsequent tests of the same individual, test “Sequence” (first tests coded as 0; subsequent tests coded as 1) and “Year” with associated F-tests, degrees of freedom (d.f.), and value of P derived from the full model (model 3).

(a)								
Model	V_I	V_{PE}	V_A	V_R	r	pe²	h²	LogL
1	-	-	-	1.32 (0.04)	-	-	-	-1159.01
2	0.61 (0.05) ¹	-	-	0.70 (0.04)	0.46(0.03)	-	-	-1081.90
3	-	0.47 (0.07) ³	0.14 (0.06) ²	0.70 (0.04)	-	0.36(0.05)	0.10(0.05)	-1078.90
4	-	-	0.53 (0.06)	0.85 (0.04)	-	-	-	-1100.84

(b)	β	Wald's F	d.f.	P
Constant	-0.65 (0.47)	0.84	1, 1782	0.359
Time of year	0.70 (0.09)	60.19	1, 1782	<0.001
Inter-test Interval	-0.10 (0.05)	4.32	1, 1782	0.039
Sequence ¹	1.44 (0.25)	33.88	1, 1782	<0.001
Year ²	-	18.56	4, 1782	<0.001

Footnotes table (a):

¹LRT: model 1 versus 2: $\chi^2=154.22$, $P<0.001$;

²LRT: model 2 versus 3: $\chi^2=116.34$, $P<0.001$;

³LRT: model 3 versus 4: $\chi^2=6.00$, $P=0.014$

Foot notes table (b):

¹First test is the reference category;

²2005 is the reference category. Yearly estimates (\pm SE): 2006: 0.04(0.08), 2007: 0.52(0.09), 2008: 0.24(0.11) and 2009: 0.62(0.10)

References

- 1 Nicolaus, M., Michler, S. P. M., Ubels, R., van der Velde, M., Bouwman, K. M., Both, C., and Tinbergen, J. M. 2012 Local sex ratio affects the cost of reproduction. *J. Anim. Ecol.*, 81, 564-572. (doi: 10.1111/j.1365-2656.2011.01933.x)
- 2 Lynch, M. and Walsh, B. 1998 *Genetics and analysis of quantitative traits*. Sunderland, MA.: Sinauer.
- 3 Nussey, D. H., Wilson, A. J., and Brommer, J. E. 2007 The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* 20, 831-844. (doi: 10.1111/j.1420-9101.2007.01300.x)
- 4 Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., and Nussey, D. H. 2010b An Ecologist's guide to the animal model. *J. Anim. Ecol.* 79, 13-26. (doi: 10.1111/j. 1365-2656.2009. 01639. x)
- 5 Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. B* 359, 873-890. (doi: 10.1098/rstb.2003.1437)
- 6 Shaw R.G. (1991). The Comparison of quantitative genetic parameters between populations. *Evol.* 45: 143-151.
- 7 Dingemanse, N. J., Bouwman, K. M., van de Pol, M., Van Overveld, T., Patrick, S. C., Matthysen, E., and Quinn, J. L. 2012 Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *J. Anim. Ecol.* 81, 116-126. (doi: 10.1111/j.1365-2656.2011.01877.x)

8 Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., and Sheldon, B. C. 2009 Heterogeneous selection on a heritable temperament trait in a variable environment. *J. Anim. Ecol.* 78, 1203-1215. (doi: 10.1111/j.1365-2656.2009.01585.x)

9 Gilmour, A. R., Gogel, B. J., Cullis, B. R., and Thompson, R. 2009 *ASReml User Guide Release 3.0*. Hemel Hempstead, HP1 1ES, UK: VSN International Ltd.

ESM4: Data supporting the manuscript

year_SR_BS	RRV_yr	sqrt Nloc before	sqrt Nloc after	diff sqrt Nloc	n_interval
1	0.01	2.65	3.61	0.96	-0.3569
1	0.01	4.12	4.58	0.46	0.0826
1	0.01	2.65	3.61	0.96	-0.2891
2	0.061	1.41	5.1	3.68	0.0645
2	0.061	2.65	2.24	-0.41	0.0393
2	0.061	4.36	6.16	1.81	-1.0241
2	0.061	2.65	3.87	1.23	0.754
3	0.12	3.87	4.24	0.37	0.754
3	0.12	5.29	3.74	-1.55	-0.2101
3	0.12	5.1	4.36	-0.74	0.0393
3	0.12	1.73	1.73	0	-0.9649
3	0.12	3.46	4.8	1.33	0.0826
3	0.12	3.87	4	0.13	-0.9605
3	0.12	4.12	3.87	-0.25	-0.2731
3	0.12	5	4.58	-0.42	0.754
4	-0.022	1.41	4	2.59	-0.0294
4	-0.022	3.16	4.12	0.96	-0.2318
4	-0.022	2.83	4.24	1.41	-0.2804
4	-0.022	1.73	2.83	1.1	0.0939
5	0	3.32	6	2.68	0.0333
5	0	4	4.8	0.8	0.0333
5	0	3.46	3.16	-0.3	0.0427
5	0	2	6.86	4.86	-0.2318
6	-0.035	3.16	5.2	2.03	-0.2318
6	-0.035	2.83	3.74	0.91	-0.6221
6	-0.035	1	4	3	-0.0294
6	-0.035	3.16	4.12	0.96	0.8353
6	-0.035	2.24	3.61	1.37	-0.2804
6	-0.035	1.73	3.74	2.01	-0.2848
6	-0.035	2.45	2.65	0.2	-0.3885
6	-0.035	1.73	2.65	0.91	0.7922
7	0.157	1.41	1.73	0.32	-0.0698
7	0.157	2	3.32	1.32	-0.3267
7	0.157	1.41	3.61	2.19	-0.2251
7	0.157	3.16	1.41	-1.75	-0.0564
8	-0.047	5.83	6.93	1.1	-0.3904
8	-0.047	4.12	4.69	0.57	-0.116
8	-0.047	4.12	5.29	1.17	-0.3943
8	-0.047	4.12	4.69	0.57	-0.2251
8	-0.047	2	3	1	-0.0848

8	-0.047	2	2.24	0.24	-0.1443
9	-0.043	2.45	2.45	0	-1.1559
9	-0.043	2.45	5.39	2.94	-0.9395
9	-0.043	5	4.47	-0.53	-0.116
9	-0.043	2.83	3	0.17	-1.2947
10	0.01	3.87	4.24	0.37	0.0014
10	0.01	2.83	4	1.17	-0.1296
10	0.01	3.32	4	0.68	-0.3149
10	0.01	2.65	3.87	1.23	0.0014
10	0.01	3.46	5.66	2.19	1.0401
10	0.01	1.41	5.1	3.68	0.7937
10	0.01	2.65	1.73	-0.91	0.1161
10	0.01	4.58	4.9	0.32	-0.1785
10	0.01	4.36	5.1	0.74	0.7937
10	0.01	2.45	8.19	5.74	-0.3064
10	0.01	3.61	4.47	0.87	0.0014
10	0.01	3.87	4.24	0.37	-0.3149
10	0.01	3	4.69	1.69	-0.3207
10	0.01	1.41	3.87	2.46	-0.1785
10	0.01	2.24	2.45	0.21	0.6346
10	0.01	2.24	2	-0.24	-0.1785
11	0.062	1.41	2.45	1.04	-0.2148
11	0.062	2.83	3.46	0.64	-0.3122
11	0.062	1.73	3.46	1.73	0.8633
11	0.062	3.32	4.69	1.37	-0.3149
11	0.062	3.74	4.69	0.95	0.1179
11	0.062	2.24	2.45	0.21	-0.3122
11	0.062	2	4.69	2.69	-0.2096
12	0.122	4	6.56	2.56	-0.1296
12	0.122	1.73	2.45	0.72	0.0014
12	0.122	3.87	4.9	1.03	-0.2096
12	0.122	2.83	2.45	-0.38	-0.1785
12	0.122	2.24	4.47	2.24	0.7865
13	-0.023	2.45	3.74	1.29	-0.3531
13	-0.023	3.46	4.24	0.78	-0.4181
13	-0.023	2.83	4.69	1.86	-0.3824
13	-0.023	3.74	5	1.26	-0.1363
13	-0.023	2.65	4.12	1.48	-0.3283
13	-0.023	1.73	2.83	1.1	-0.3531
13	-0.023	3.74	7.35	3.61	0.4952
13	-0.023	3	3.32	0.32	-0.4003
13	-0.023	3	3.46	0.46	-0.0829
13	-0.023	4.58	5.39	0.8	0.3163
13	-0.023	2.24	4.47	2.24	0.8703

13	-0.023	2	4.9	2.9	-0.4377
13	-0.023	5.57	5.83	0.26	-0.4441
13	-0.023	1.41	4.12	2.71	0.7275
13	-0.023	1	4.12	3.12	0.4574
13	-0.023	1	3.16	2.16	0.3199
14	0	2.65	4	1.35	-0.3531
14	0	2	2.24	0.24	-0.0898
14	0	2.83	5.39	2.56	0.93
14	0	3.32	3.87	0.56	-0.0898
14	0	4.24	6.4	2.16	-0.3283
14	0	1.41	2.24	0.82	-0.322
14	0	2.65	4.58	1.94	-0.4067
14	0	4.12	4.8	0.67	0.1057
14	0	3	3	0	-0.3531
14	0	1.73	3.46	1.73	-0.4556
14	0	3.46	3.61	0.14	-0.3283
14	0	1	3.32	2.32	0.8815
15	-0.036	2.24	3.32	1.08	-0.322
15	-0.036	1.41	3.16	1.75	-0.3757
15	-0.036	3	4.24	1.24	-0.0713
15	-0.036	3	3.61	0.61	-0.0898
15	-0.036	4.24	4.12	-0.12	-0.322
15	-0.036	2.24	2.24	0	-0.322
15	-0.036	1.41	3.61	2.19	0.4952
15	-0.036	2.24	5.29	3.06	0.93
15	-0.036	3	5.29	2.29	0.93
15	-0.036	2.83	4.9	2.07	0.7667
15	-0.036	2.83	3.16	0.33	0.4888
15	-0.036	3.16	3.16	0	-0.0829
16	0.159	2.45	4.9	2.45	0.8703
16	0.159	2.65	4.36	1.71	0.8703
16	0.159	2.24	4.36	2.12	-0.3715
16	0.159	2.24	5.1	2.86	0.7971
16	0.159	4.24	4	-0.24	0.5199
16	0.159	3.87	5.2	1.32	-0.2179
16	0.159	3	3.46	0.46	0.1173
16	0.159	5.66	4.47	-1.18	-0.4767
16	0.159	3.16	3.74	0.58	0.7004
16	0.159	2.24	4.36	2.12	0.7971
16	0.159	1.73	4	2.27	-0.1733
16	0.159	2.83	2.65	-0.18	-0.1762
16	0.159	1.73	3.87	2.14	0.7004
16	0.159	4.12	3.61	-0.52	-0.3715
16	0.159	2.24	1.73	-0.5	0.3658

16	0.159	5.57	6.4	0.84	-0.3715
17	-0.048	2.65	4	1.35	0.7056
17	-0.048	2.83	3.74	0.91	-0.1287
17	-0.048	1	4.9	3.9	0.7436
17	-0.048	1.41	4.36	2.94	0.7407
17	-0.048	3.61	4.9	1.29	-0.4256
17	-0.048	1.41	3.46	2.05	0.1539
17	-0.048	3.32	4.47	1.16	-0.1221
17	-0.048	1.41	4.12	2.71	-0.1221
18	-0.044	1.41	3.16	1.75	-0.3715
18	-0.044	2.65	2.83	0.18	0.1539
18	-0.044	2.65	4.12	1.48	-0.2179
18	-0.044	3.46	5	1.54	-0.2078
18	-0.044	2.65	2.83	0.18	-0.5242
18	-0.044	3.16	4.12	0.96	0.7066
18	-0.044	2.65	5.66	3.01	0.6709
18	-0.044	4.24	6.32	2.08	-0.2179
18	-0.044	2.45	4.12	1.67	0.295
