Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird

Nicolaus, M.; Brommer, J. E.; Ubels, R.; Tinbergen, J. M.; Dingemanse, N. J.

Published in:
Journal of Evolutionary Biology

DOI:
10.1111/jeb.12210

Publication date:
2013

Supporting information of the manuscript entitled:

Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird

Marion Nicolaus, Jon E. Brommer, Richard Ubels, Joost M. Tinbergen and Niels J. Dingemanse

Appendix S1: power, accuracy and precision of random regression models applied to the Lauwersmeer great tit population

Appendix S2: Clutch size-density reaction norms with homogeneous errors

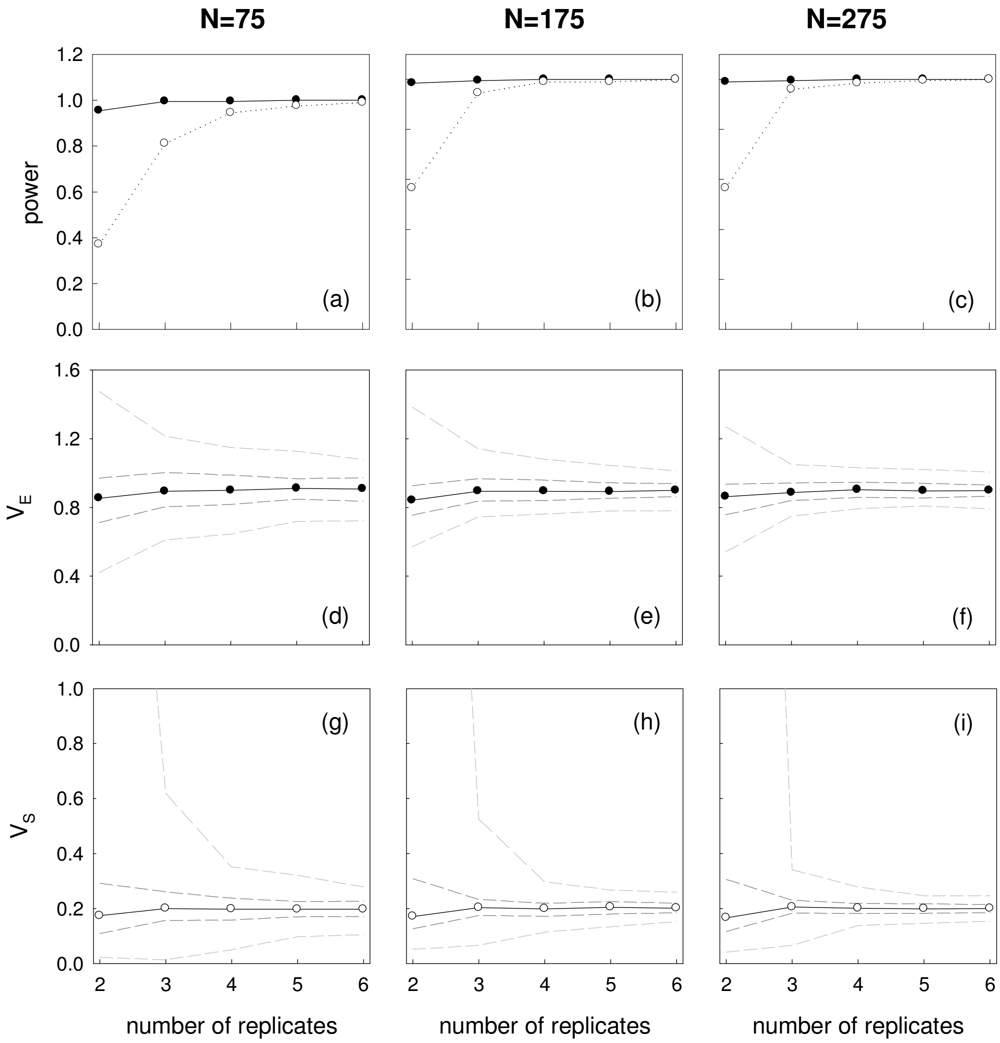
Appendix S3: Clutch size-density reaction norms with heterogeneous errors fitted for the low and high density period

Appendix S4: Conceptual representation of the reaction norms clutch size-density reaction norms in the Lauwersmeer population.

Appendix S1: power, accuracy and precision of random regression models applied to the Lauwersmeer great tit population

We used the R-package 'odprism' to simulate data sets, run random regression on these datasets and quantify model performance (van de Pol 2012). Because we were interested in quantifying among- and within-individual variance in clutch size, which represents an annually expressed trait, we simulated 200 data sets for a population sampled once a year and where individual annual survival probability was set at 0.5 (close to the adult annual survival probability in this population, Nicolaus *et al.* 2012). We simulated data sets for three population sizes (75, 175 and 275) which correspond roughly and respectively to the minimal, average and maximal annual number of females monitored in the Lauwersmeer during the study period. The number of replicates per female ranged between 2 and 6, which reflects the natural range of longevity in this population (see main text). Assuming that dead individuals are replaced (i.e. constant population size), the expected number of individuals that can be sampled depends thus on the annual survival, monitored population size and number of years monitored. Estimates of the model parameters were based on a restricted maximum likelihood (REML) approach in which estimated variance–covariance matrices was constrained to be positive-definite. Among-individual variance in elevation (V_E), in slope (V_S) and correlation among individual's elevation and slope (r_{ES}) were set respectively to 0.9, 0.2 and 0.1 which was close to the estimates found in this population (see main text).

Figure S1: (a–c) Power to detecting individual heterogeneity in elevation (black dots) and slopes (white dots) and accuracy and precision of variance in elevations (d–f) and of variance in slopes (g–i). These parameters are presented for different total sample sizes (N) and for up to 6 replicates per individual. In (d–i), dots represent the median estimates of 200 simulated data sets, while the dark and light grey dotted lines, respectively, the 25–75% and 2.5–97.5% distribution of parameter estimates.



Appendix S2: Clutch size-density reaction norms with homogeneous errors

Consistent with the random regression animal model (RRAM) fitted with heterogeneous residual errors (main manuscript), clutch size decreased linearly and significantly with annual breeding density and with lay date (Table S2). Clutch size also exhibited a quadratic relationship with female age. RRAM further revealed that *year* and *plot* explained significant parts of the variance in clutch size (models 2 and 3; Table S2). The inclusion of $ind_{0,}$ the individual-specific intercepts for the clutch size-density reaction norm ("I" or elevation), increased the fit of the model significantly (model 4; Table S2), implying that females differed significantly in their clutch size at the mean-centred density. Furthermore, the inclusion of $ind_{1,}$ the individual-specific slopes for the clutch size-density reaction norm ("I×E" or plasticity), subsequently increased the fit of the model (model 5; Table S2). This finding implies that females differed in their plastic response to annual breeding density. The significance of I×E differs from the same RRAM fitted with heterogeneous residual errors. This major difference in conclusion presented in the main manuscript highlights the fact that ignoring heterogeneity of residual variances can lead to spurious results and false interpretation of biological patterns. Adjusted repeatability (r) ± SE, values of r after controlling for the fixed effects in model 4 was 0.38 ± 0.04. Elevation and slope of the reaction norm (model 5; Table S2) were negatively and significantly correlated, implying that the between-individual differences were larger under low compared to high densities (r ± SE = -0.41 ± 0.15, likelihood ratio test with model where the correlation was constrained to zero: χ^2 = 5.96, d.f. = 1, P = 0.010). Subsequently, splitting I into its additive genetic (a_0 or "G") and environmental (pe_0 or "PE") components further improved the fit of the model (model 6; Table S2), confirming that clutch size is partly heritable in this population (narrow-sense heritability (h^2) ± SE = 0.20 ± 0.05). Finally, splitting I×E into its genetic (a_1 or "G×E") and permanent environmental (pe_1 or "PE×E") components did not result in a better fit (model 7; Table S2), implying that we could not demonstrate statistically that plasticity in clutch size had a genetic basis.

Table S2: Results from the univariate random regression animal model of clutch size as a function of annual breeding density (a) Estimates of random regression variances are given with their standard error in parentheses (as specified in equations 1 and 2 of the main text). For each model, variance terms are provided with the likelihood ratio test (LRT, χ^2 statistics with associated d.f.) between the given model and the previous model. The LRT was based on a mixture of χ^2 probability distributions with 0 and 1 d.f. (indicated by d.f. = 0.5) when testing a single variance component, and an equal mixture of chi-square probabilities with 1 and 2 d.f. (indicated by d.f. = 1.5) for tests involving one variance and one covariance. The most parsimonious model is denoted in bold. All models are fitted with *homogeneous* residual variances (b) Estimates of the fixed effects of the most parsimonious model (β) are given with their standard error in parentheses. Their significance is tested using F tests.

Table S2

(a)	*random regression variances*									*Test*			
Model	residuals	year	Plot	I(ind$_0$)	I×E(ind$_1$)	G(a$_0$)	G×E(a$_1$)	PE(pe$_0$)	PE×E(pe$_1$)	LogL	χ^2	d.f.	P
1	2.485 (0.071)	-	-	-	-	-	-	-	-	-2369.60			
2	2.302 (0.066)	0.254 (0.098)	-	-	-	-	-	-	-	-2312.27	114.66	0.5	<0.0001
3	2.152 (0.062)	0.270 (0.103)	0.238 (0.087)	-	-	-	-	-	-	-2237.89	121.12	0.5	<0.0000
4	1.199 (0.061)	0.267 (0.101)	0.216 (0.079)	0.970 (0.079)	-	-	-	-	-	-2147.81	180.16	0.5	<0.0001
5	1.182 (0.063)	0.264 (0.100)	0.210 (0.080)	0.850 (0.101)	0.171 (0.089)	-	-	-	-	-2144.58	6.46	1.5	0.025
6	**1.181 (0.063)**	**0.263 (0.100)**	**0.189 (0.073)**	**-**	**0.168 (0.086)**	**0.537 (0.127)**	**-**	**0.330 (0.140)**	**-**	**-2133.82**	**21.52**	**0.5**	**<0.0001**
7	1.182 (0.063)	0.264 (0.100)	0.190 (0.073)	-	-	0.432 (0.155)	0.156 (0.134)	0.420 (0.160)	0.025 (0.144)	-2133.24	1.16	1.5	0.42

(b)	*Fixed effects*				
	β	Wald`s F	d.f. (nom)	d.f. (denom)	P
intercept	10.320 (0.440)	673.45	1	137	<0.001
density	-0.866 (0.223)	15.11	1	25.8	<0.001
lay date	-0.044 (0.006)	57.87	1	1941.3	<0.001
age	-0.061 (0.020)	11.82	1	1436.7	<0.001
age^2	0.482 (0.142)	9.19	1	1350.5	0.003

Appendix S3: Clutch size-density reaction norms with heterogeneous errors fitted for the low and high density period

Table S3. Results from the univariate random regression animal model of clutch size as a function of annual breeding density (a) Estimates of random regression variances are given with their standard error in parentheses (as specified in equations 1 and 2 of the main manuscript). For each model, variance terms are provided with the likelihood ratio test (LRTS, χ^2 statistics with associated d.f.) between the given model and the previous model. The LRT was based on a mixture of χ^2 probability distributions with 0 and 1 d.f. (indicated by d.f. = 0.5) when testing a single variance component, and an equal mixture of chi-square probabilities with 1 and 2 d.f. (indicated by d.f. = 1.5) for tests involving one variance and one covariance. The most parsimonious model is denoted in bold. All models are fitted with *heterogeneous* residual variance estimated for the low and high density period (b) Estimates of the fixed effects of the most parsimonious model (β) are given with their standard error in parentheses. Their significance is tested using F tests.

Table S3

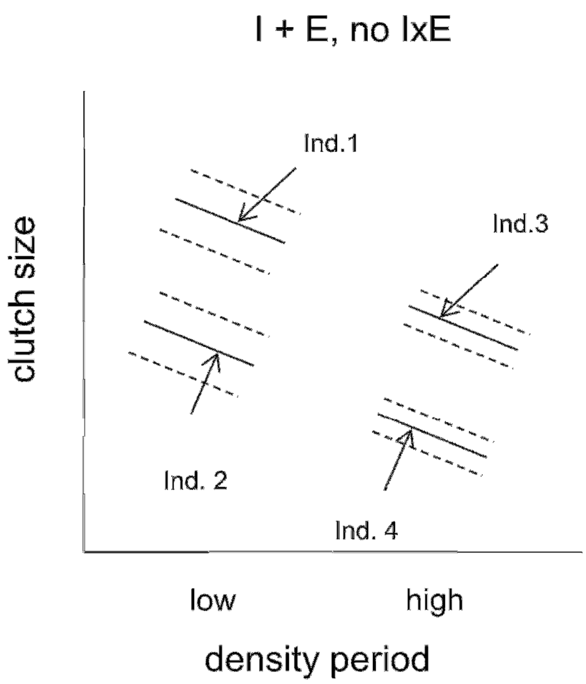
(a)	*random regression variances*								*Test*			
Model	Residuals(LOW)	Residuals(HIGH)	year	Plot	I(ind_0)	I×E(ind_1)	G(a_0)	PE(pe_0)	LogL	χ^2	d.f.	P
1	2.948 (0.131)	2.237 (0.083)	-	-	-	-	-	-	-2381.40			
2	2.764 (0.123)	2.027 (0.076)	0.252 (0.097)	-	-	-	-	-	-2297.97	166.86	0.5	<0.001
3	2.467 (0.110)	1.931 (0.073)	0.271 (0.104)	0.233 (0.086)	-	-	-	-	-2229.15	137.64	0.5	<0.001
5	1.452 (0.099)	1.021 (0.0652)	0.268 (0.102)	0.213 (0.081)	0.970 (0.078)	-	-	-	-2139.21	179.88	0.5	<0.001
6	1.450 (0.112)	0.982 (0.069)	0.267 (0.102)	0.212 (0.080)	0.843 (0.097)	0.152 (0.085)	-	-	-2137.33	3.76	1.5	0.103
7*	**1.457 (0.098)**	**1.018 (0.065)**	**0.266 (0.101)**	**0.192 (0.074)**	**-**	**-**	**0.556 (0.130)**	**0.425 (0.129)**	**-2128.20**	**22.02**	**1**	**<0.001**

(b)	*Fixed effects*				
	B	Wald`s F	d.f. (nom)	d.f. (denom)	P
intercept	9.194 (0.327)	792.16	1	287.8	<0.001
density	-0.790 (0.205)	14.86	1	25.7	<0.001
lay date	-0.0437 (0.006)	56.57	1	1951.2	<0.001
Age	-0.064 (0.020)	13.54	1	1374.6	<0.001
age^2	0.514 (0.140)	10.48	1	1280.2	0.001

*LRT performed between model 5 and model 7

Appendix S4:

Figure S4: Conceptual representation of the reaction norms clutch size-density reaction norms in the Lauwersmeer population. Our results show that the decrease in clutch size variance between the low and high density period is caused by a decrease of within-individual variance (i.e. heterogeneity of residual variance) but not by a change in between-individual variance (no I×E). We depicted here the reaction norms for four individuals (solid lines) (two in each density period). Within-individual variance is depicted by dashed lines.



References

Nicolaus M., Michler S.P.M., Ubels R., van der Velde M., Bouwman K.M., Both C. & Tinbergen J.M. 2012. Local sex ratio affects the cost of reproduction. *J. Anim. Ecol.,* **81**: 564-572.

van de Pol M. 2012. Quantifying individual variation in reaction norms: How study design affects the accuracy, precision and power of random regression models. *Methods. Ecol. Evol.*. **3**: 268-280.