

University of Groningen

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](https://doi.org/10.1111/jeb.12210)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Nicolaus, M., Brommer, J. E., Ubels, R., Tinbergen, J. M., & Dingemanse, N. J. (2013). Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird. *Journal of Evolutionary Biology*, 26(9), 2031-2043. <https://doi.org/10.1111/jeb.12210>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

1 Supporting information of the manuscript entitled:

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

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

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

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

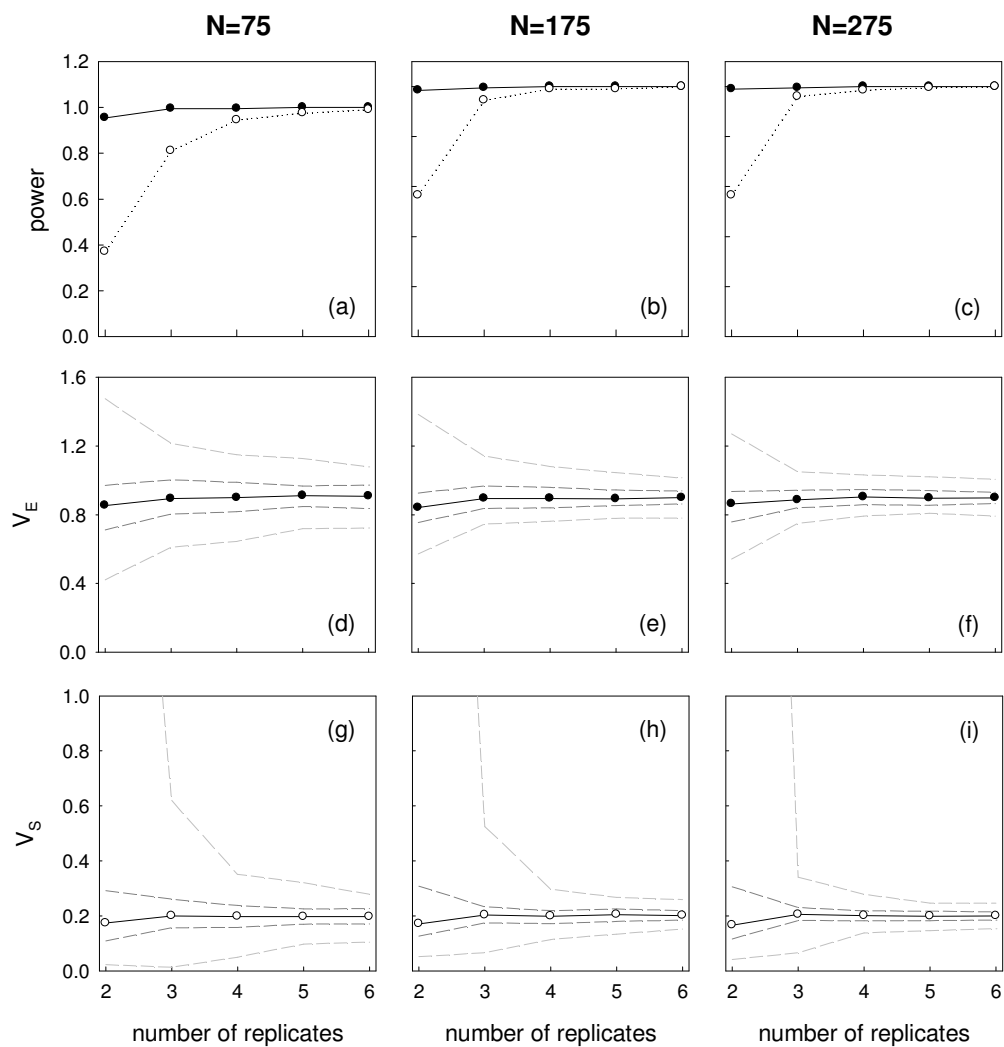
8 **Appendix S3:** Clutch size-density reaction norms with heterogeneous errors fitted for the low
9 and high density period

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

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

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

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



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

39 Consistent with the random regression animal model (RRAM) fitted with heterogeneous residual errors
40 (main manuscript), clutch size decreased linearly and significantly with annual breeding density and with
41 lay date (Table S2). Clutch size also exhibited a quadratic relationship with female age. RRAM further
42 revealed that *year* and *plot* explained significant parts of the variance in clutch size (models 2 and 3; Table
43 S2). The inclusion of *ind₀*, the individual-specific intercepts for the clutch size-density reaction norm (“I”
44 or elevation), increased the fit of the model significantly (model 4; Table S2), implying that females
45 differed significantly in their clutch size at the mean-centred density. Furthermore, the inclusion of *ind₁*,
46 the individual-specific slopes for the clutch size-density reaction norm (“I×E” or plasticity), subsequently
47 increased the fit of the model (model 5; Table S2). This finding implies that females differed in their
48 plastic response to annual breeding density. The significance of I×E differs from the same RRAM fitted
49 with heterogeneous residual errors. This major difference in conclusion presented in the main manuscript
50 highlights the fact that ignoring heterogeneity of residual variances can lead to spurious results and false
51 interpretation of biological patterns. Adjusted repeatability ($r \pm SE$, values of r after controlling for the
52 fixed effects in model 4 was 0.38 ± 0.04 . Elevation and slope of the reaction norm (model 5; Table S2)
53 were negatively and significantly correlated, implying that the between-individual differences were larger
54 under low compared to high densities ($r \pm SE = -0.41 \pm 0.15$, likelihood ratio test with model where the
55 correlation was constrained to zero: $\chi^2 = 5.96$, d.f. = 1, $P = 0.010$). Subsequently, splitting I into its
56 additive genetic (a_0 or “G”) and environmental (pe_0 or “PE”) components further improved the fit of the
57 model (model 6; Table S2), confirming that clutch size is partly heritable in this population (narrow-sense
58 heritability (h^2) $\pm SE = 0.20 \pm 0.05$). Finally, splitting I×E into its genetic (a_1 or “G×E”) and permanent
59 environmental (pe_1 or “PE×E”) components did not result in a better fit (model 7; Table S2), implying that
60 we could not demonstrate statistically that plasticity in clutch size had a genetic basis.

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

(a) <i>random regression variances</i>										<i>Test</i>			
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
				0.970									
4	1.199 (0.061)	0.267 (0.101)	0.216 (0.079)	(0.079)	-	-	-	-	-	-2147.81	180.16	0.5	<0.0001
				0.850									
5	1.182 (0.063)	0.264 (0.100)	0.210 (0.080)	(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) <i>Fixed effects</i>													
	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								

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

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

88 **Table S3**

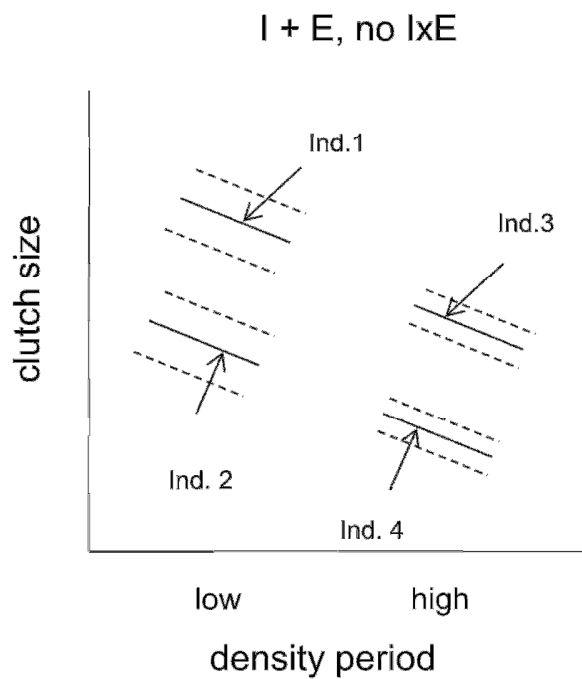
(a) <i>random regression variances</i>										<i>Test</i>		
Model	Residuals(LOW)	Residuals(HIGH)	year	Plot	I(ind ₀)	IxE(ind _i)	G(a ₀)	PE(pe ₀)	LogL	χ^2	d.f.	P
1	2.948 (0.131)	2.237 (0.083)	-	-	-	-	-	-	-2381.40			
2	2.764 (0.123)	2.027 (0.076)	0.252 (0.097)	-	-	-	-	-	-2297.97	166.86	0.5	<0.001
3	2.467 (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) <i>Fixed effects</i>					
	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

89 *LRT performed between model 5 and model 7

90 **Appendix S4:**

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



98 **References**

- 99 Nicolaus M., Michler S.P.M., Ubels R., van der Velde M., Bouwman K.M., Both C. & Tinbergen
100 J.M. 2012. Local sex ratio affects the cost of reproduction. *J. Anim. Ecol.*, **81**: 564-572.
- 101 van de Pol M. 2012. Quantifying individual variation in reaction norms: How study design
102 affects the accuracy, precision and power of random regression models. *Methods. Ecol. Evol.*
103 **3**: 268-280.