

Research



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Animal behaviour

Digit ratio predicts the number of lifetime recruits in female collared flycatchers

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The early environment in which an organism grows can have long-lasting impacts on both its phenotype and fitness. However, assessing this environment comprehensively is a formidable task. The relative length of the second to the fourth digit (2D:4D) is a broadly studied skeletal trait that is fixed for life during ontogeny. 2D:4D has been shown to indicate various early effects including the perinatal steroid milieu in both humans and non-human animals. However, the fitness relevance of the early effects indicated by 2D:4D remains unknown. Here, we investigated hindlimb 2D:4D and measures of lifetime performance in wild collared flycatcher (*Ficedula albicollis*) females. We found that females with higher 2D:4D had a greater number of recruiting offspring to the breeding population. This was the case despite the fact that such females did not lay more eggs or breed more frequently during their reproductive life. Our results support the suggestion that 2D:4D, known to be a retrospective marker of perinatal development, positively associates with female quality in the collared flycatcher.

1. Introduction

The relative length of the second to the fourth digit (2D:4D) is a sexually dimorphic skeletal trait in humans, with higher 2D:4D in women [1]. This sexual difference develops during a narrow window of prenatal development and remains after birth. Zheng and Cohn [2] clarified the underlying mechanism in CD-1 laboratory mice. They found that testosterone increased while oestrogen decreased the expression of genes involved in chondrocyte proliferation in specific phalanges of the fourth digit. One of these could be the gene coding for SMOC1 (secreted modular calcium-binding protein 1), which also has a role in limb development and the sexually dimorphic development of the gonads [3]. But this mechanism can only be generalized across taxa with caution considering, for example, the differences between birds and mammals in the direction of sexual dimorphism in 2D:4D (female-biased in mammals while male-biased in birds) [4], or in the identity of the responsible digit (4D in taxa with female-biased 2D:4D, while 2D in taxa with male-biased 2D:4D) [5]. Besides sex steroid levels, several other hormonal factors can affect digit ratio, such as the abundance and responsiveness of steroid hormone receptors as well as the functional attributes of steroidogenic enzymes [2,6–8]. Furthermore, beside sexual steroids, several other hormones, such as somatotropin, thyroid hormones or glucocorticoids, can affect chondrocyte proliferation [9]. Thus, it is possible that some of these

Table 1. Repeatabilities of digit parameters in female collared flycatchers. Measurements of digit lengths and digit ratio from 40 randomly selected females were used to calculate the repeatabilities of measuring and footprinting procedures. We also calculated between-year repeatabilities based on the digit parameter values from the first two breeding attempts of 37 females.

	measuring repeatability				footprinting repeatability				between-year repeatability			
	<i>R</i>	<i>F</i> _{39,40}	<i>p</i>	s.e.	<i>R</i>	<i>F</i> _{39,80}	<i>p</i>	s.e.	<i>R</i>	<i>F</i> _{36,37}	<i>p</i>	s.e.
2D	0.989	180	<0.001	0.004	0.655	6.7	<0.001	0.073	0.416	2.43	0.004	0.137
4D	0.993	279	<0.001	0.002	0.879	22.8	<0.001	0.031	0.670	5.10	<0.001	0.091
2D : 4D	0.983	119	<0.001	0.005	0.507	4.1	<0.001	0.091	0.610	4.12	<0.001	0.104

Table 2. Descriptive statistics for breeding lifespan, lifetime egg production (LEP), lifetime recruit production (LRP) and 2D : 4D of recruit and immigrant female collared flycatchers.

	recruits (<i>N</i> = 96)		immigrants (<i>N</i> = 172)		total (<i>N</i> = 268)	
	mean	s.d.	mean	s.d.	mean	s.d.
breeding lifespan	1.719	1.013	1.767	0.963	1.750	0.980
LEP	10.500	6.306	11.105	6.316	10.888	6.308
LRP	0.438	0.844	0.407	0.770	0.418	0.796
2D : 4D	0.835	0.037	0.836	0.037	0.835	0.037

above factors mask the effects of sexual steroids on the development of sexually dimorphic 2D : 4D.

Initially, the majority of digit ratio studies searched for sexual dimorphism in 2D : 4D and tried to verify the role of perinatal steroid factors in its development, both correlatively and experimentally. Afterwards, 2D : 4D was used as a putative marker of perinatal sex-hormone action. However, independent of the drivers of variation in digit ratios, it is also important to examine whether the early environmental effects coded in 2D : 4D have long-term relevance to reproductive success, thereby making digit ratio an indicator of expected fitness. In humans, 2D : 4D was found to be associated with health, disease risk, fertility, attractiveness and may indicate reproductive success as well [1]. In animal digit ratio studies, the commonly examined fitness-related traits are secondary sexual characters [10–14]. To the best of our knowledge, no animal digit ratio study has examined the relationship of 2D : 4D with reliable estimates of Darwinian fitness, such as lifetime reproductive success (LRS).

We aimed to fill this gap by using long-term breeding data and 2D : 4D measures from collared flycatchers (*Ficedula albicollis*). We analysed how 2D : 4D is associated with fitness-related life-history traits, namely breeding lifespan and two estimates of LRS, lifetime egg production (LEP) and lifetime recruit production (LRP). We focused on females only to avoid the error caused by extra-pair paternity in LRS estimation for males.

2. Material and methods

The collared flycatcher is a common breeding species in our study area, which lies in the Pilis-Visegrádi Mountains, Hungary (47°43' N, 19°01' E). Between 2004 and 2011, we collected footprints from the right foot of breeding individuals following the

method of Burley & Foster [15]. Lengths of the second and fourth toes were measured twice at different times from the three most complete footprints with outstretched toes with a digital calliper (accuracy of 0.02 mm) by the same person. We calculated repeatabilities using the method of Lessells & Boag [16]. Both measuring repeatability (between the two measurements of the same footprint) and footprinting repeatability (between the three footprints) of digit lengths were highly significant (table 1). Then, we averaged the measurements per digit before calculating 2D : 4D. There was no significant within-individual change from the first breeding event to the next one in females' digit lengths or digit ratio (paired *t*-tests: 2D: $t_{36} = 0.058$ $p = 0.954$, 4D: $t_{36} = -1.589$ $p = 0.121$, 2D : 4D: $t_{36} = 1.498$ $p = 0.143$) and the between-year repeatabilities were also significant (table 1). Therefore, in the case of multiply sampled females, we used the mean of 2D : 4D data from different footprints taken at different times.

The three life-history traits were defined as follows: breeding lifespan as the number of consecutive years in which females bred; LEP as the total number of eggs laid over the lifetime; and LRP as the number of lifetime offspring that returned to the breeding population as mature individuals.

We excluded females that were involved in field experiments that could influence their reproductive success. We also excluded females that were not captured in each season between their first and last breeding events to reveal the breeding histories of females as accurately as possible. Because a significant proportion of recruits return at 2 or 3 years of age, we needed breeding data from 3 years after the last breeding event of the females to estimate their LRP. Since the last year for which we had available breeding data was 2015, we excluded females that bred after 2012. A female not recaptured for at least 3 years after its last breeding event was considered dead. Finally, we had adequate data from 268 females, of which 96 were recruits and 172 were immigrants. Descriptive statistics of the relevant variables are given in table 2.

We built generalized linear models to explore the relationship between 2D : 4D and LRS estimates, using Poisson distribution

Table 3. Associations between 2D:4D and lifetime recruit production (LRP) as well as lifetime egg production (LEP) based on the data of 96 recruited collared flycatcher females. Generalized linear models using backward stepwise model simplification were conducted with Poisson error and log link in the case of LRP models and Gamma error and log link in the case of LEP models. Terms in the final models are marked with asterisks. Statistics for non-significant terms were calculated by re-entering them in the final model. The number of degrees of freedom was 5 in the case of year of birth and 1 in all other cases.

	LEP				LRP			
	estimate	s.e.	Wald χ^2	<i>p</i>	estimate	s.e.	Wald χ^2	<i>p</i>
breeding lifespan	0.473	0.017	819.42	<0.001*	0.594	0.107	30.91	<0.001*
year of birth			1.26	0.939			5.85	0.321
year of birth 2003	0.002	0.034	0.00	0.962	0.339	0.353	0.92	0.337
year of birth 2004	-0.034	0.033	1.04	0.308	-0.526	0.473	1.24	0.266
year of birth 2005	0.006	0.050	0.02	0.899	0.774	0.488	2.52	0.112
year of birth 2006	0.013	0.044	0.08	0.775	-0.404	0.706	0.33	0.567
year of birth 2007	0.020	0.039	0.27	0.606	0.368	0.493	0.56	0.456
tarsus length	0.000	0.003	0.01	0.908	-0.011	0.035	0.09	0.759
2D:4D	-0.018	0.458	0.00	0.969	13.148	4.728	7.73	0.005*

with log link for LRP and Gamma distribution with log link for LEP. We entered LRP or LEP as dependent variable, breeding lifespan, tarsus length and 2D:4D as continuous predictors, and status, classified as recruits (ringed as nestlings) or immigrants (ringed as breeding adults), and the year of first breeding (coding for possible cohort effects) as categorical predictors. Interaction of status with 2D:4D as well as breeding lifespan was also entered because recruits and immigrants may differ in the strength of maternal effects and their reproductive strategy.

The models that included immigrant females proved to be problematic because status and its interactions had a variance inflation factor value that far exceeded 10, suggesting a multicollinearity problem. The interpretation of these models is also complicated because we could not control for year of birth, and there may be difference in the accuracy of LRS estimations between recruits and immigrants. Therefore, we restricted the models to the 96 recruit females (born between 2003 and 2008). We first fitted simple models with only 2D:4D as predictor, and then also examined the effect of 2D:4D while controlling for other predictors such as breeding lifespan and tarsus length (continuous) and year of birth as cohort effect measure (categorical). The dispersion parameter of the LRP model (estimated as the ratio of Pearson's chi-square statistic to its degrees of freedom) was 1.33, and we took it into account in the analysis.

To test the relationship between breeding lifespan and 2D:4D we applied a generalized linear model with Poisson distribution and log link with breeding lifespan as the dependent variable and 2D:4D as continuous predictor. The dispersion parameter of this model was 0.59 and we took it into account in the analysis.

During the analyses we performed backward stepwise model simplification by sequentially removing non-significant terms. Statistics for removed variables were calculated by re-entering them in the final model. All statistical analyses were conducted in Statistica 6.1 (StatSoft, Inc.).

3. Results and discussion

We found that females with higher 2D:4D produced more recruits during their life (estimate = 9.07, s.e. = 4.17, Wald Chi-square = 4.73, $p = 0.03$, $n = 96$), even though they did not breed more often (estimate = -1.55, s.e. = 1.64, Wald

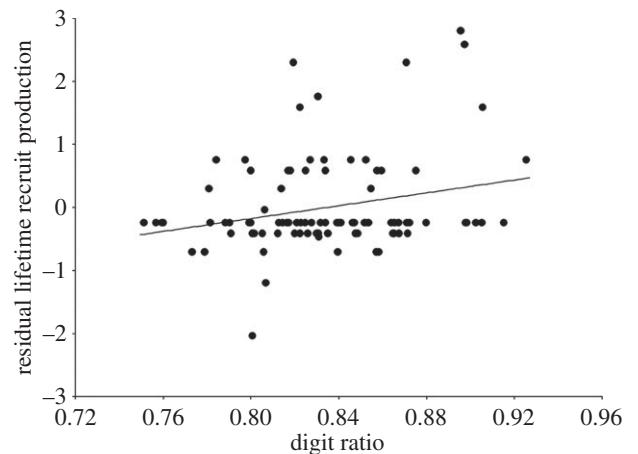


Figure 1. Correlation between the residuals of lifetime recruit production on breeding lifespan and digit ratio (2D:4D) in the 96 recruited female collared flycatchers.

Chi-square = 0.89, $p = 0.35$, $n = 96$), nor did they lay more eggs during this time (estimate = -2.09, s.e. = 1.41, Wald Chi-square = 2.20, $p = 0.14$, $n = 96$). When we took tarsus length, year of birth and breeding lifespan into consideration, similar results were obtained (table 3, figure 1). Moreover, the significant contribution of breeding lifespan to LRS [17] was also confirmed (table 3). The higher recruitment success of the offspring therefore resulted from their higher post-fledging survival, natal philopatry or breeding ability, so it may reflect higher offspring quality. This would mean that females with higher 2D:4D produce offspring of better quality; hence they have more recruits and greater genetic contribution to the next generation, that is, higher fitness. Thus, 2D:4D may indicate individual quality in females, suggesting that the genetic or early environmental determinants of 2D:4D development could also have long-term effects on LRS. These early environmental determinants could be both maternal hormonal effects [18–20] and environmental effects during embryonic or postembryonic development [10].

Focusing mainly on maternal hormonal effects, we discuss three possible, mutually non-exclusive explanations for the relationship between female 2D:4D and LRP. We previously found in a 1-year experiment that elevated yolk testosterone increased left 2D:4D of collared flycatcher fledglings [20]. Although our long-term data were based on the measurements of the right 2D:4D, if we suppose that body sides differ only in their responsiveness to testosterone but share similar developmental mechanisms, then it could be suggested that yolk testosterone improves the LRS of females in this species. To the best of our knowledge, no study has investigated the effects of yolk hormones on LRS of the returning offspring. However, experimentally increased yolk testosterone was found to negatively influence the size, production and fertility of eggs in females during the first breeding attempt in two precocial bird species [21,22], and this pattern contradicts our above suggestion.

It is also possible that other yolk androgens have simultaneous positive effects on 2D:4D and fitness-related traits. In our collared flycatcher population eggs contain seven times more androstenedione (precursor of testosterone) than testosterone, moreover, offspring from eggs with relatively higher androstenedione concentrations within a clutch had a higher recruitment rate [23]. Furthermore, Tschirren *et al.* [24] found in the same species that females that produced eggs with high yolk androstenedione and low yolk testosterone produced more recruits and lived longer. Based on these and our findings, we would expect that females from eggs with higher yolk androstenedione levels would have higher 2D:4D and recruitment success; moreover, they would deposit more androstenedione into the eggs, thereby having more recruited offspring. However, in conflict with this speculation, yolk androstenedione deposition shows little mother–daughter resemblance in collared flycatchers [25].

Another possible explanation for the positive relationship between females' 2D:4D and their offspring's recruitment success is provided by glucocorticoids. We suggest the following scheme: stressed mothers lay eggs with high corticosterone levels so their daughters have impaired growth and increased hypothalamo–pituitary–adrenal (HPA) axis responsiveness [26,27] accompanied by low 2D:4D [28]. There is potential for these more responsive females to deposit more corticosterone in their eggs [29], which will also have detrimental effects on their offspring's phenotype. Thus, both low 2D:4D females and their offspring are low quality individuals with increased glucocorticoid reactivity. The frequent or chronic activation of the HPA axis by environmental stressors has deleterious physiological

consequences, which can negatively affect adult survival and recruitment of fledglings [30] as well as female reproductive success [31]. Beside the stress-induced corticosterone deposition, the epigenetic modification of hippocampal glucocorticoid receptor gene expression may provide an alternative mechanism for the transgenerational transmission of stress responsiveness. In altricial bird species, post-natal maternal stress appears to have greater effects on adult phenotype than pre-natal maternal stress [32]. It is therefore conceivable that the quality of maternal care is associated with offspring 2D:4D [10] and affects the levels of hippocampal glucocorticoid receptor expression [33] via epigenetic alterations. If these epigenetic modifications are heritable, then this results in similar responsiveness of the HPA axis in offspring and grand-offspring, causing the relationship between offspring 2D:4D and grand-offspring recruitment success.

The contribution of the environmental component differs between the factors shown to affect 2D:4D development. Moreover, the relative significance of these various developmental factors may depend on maternal environmental conditions. However, irrespective of the exact physiological mechanisms underlying digit ratio development, researchers are interested in this trait under the assumption that the influences it reflects are relevant for the reproductive life of the individual. Our results are the first to support this by suggesting a positive association between the number of lifetime recruits and 2D:4D in female collared flycatchers.

Ethics. The study was conducted under licences from the relevant authorities (Duna-Ipoly National Park and Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management) (permits 2573/2/2004, 15951/2005, 22021/2006, 16360-2/2007 and 43355-1/2008).

Data accessibility. Data file is available at <http://dx.doi.org/10.5061/dryad.m8hb503> [34].

Authors' contributions. G.N. and J.T. conceived the ideas, designed the methodology and collected footprints; G.N. made the measurements; G.N. and G.H. analysed the data; G.N. led the writing of the manuscript. All authors collected breeding data, contributed critically to the drafts, approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. The authors declare no competing interests.

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References

- Manning JT. 2002 *Digit ratio: a pointer to fertility, behavior, and health*. New Brunswick, NJ: Rutgers University Press.
- Zheng ZG, Cohn MJ. 2011 Developmental basis of sexually dimorphic digit ratios. *Proc. Natl Acad. Sci. USA* **108**, 16 289–16 294. (doi:10.1073/pnas.1108312108)
- Lawrance-Owen AJ, Bargary G, Bosten JM, Goodbourn PT, Hogg RE, Mollon JD. 2013 Genetic association suggests that SMOC1 mediates between prenatal sex hormones and digit ratio. *Hum. Genet.* **132**, 415–421. (doi:10.1007/s00439-012-1259-y)
- Lombardo MP, Thorpe PA, Brown BM, Sian K. 2008 Digit ratio in birds. *Anat. Rec. (Hoboken)* **291**, 1611–1618. (doi:10.1002/ar.20769)
- Lofeu L, Brandt R, Kohlsdorf T. 2017 Phenotypic integration mediated by hormones: associations among digit ratios, body size and testosterone during tadpole development. *BMC Evol. Biol.* **17**, 175. (doi:10.1186/s12862-017-1021-0)
- Forstmeier W, Mueller JC, Kempenaers B. 2010 A polymorphism in the oestrogen receptor gene explains covariance between digit ratio and mating behaviour. *Proc. R. Soc. B* **277**, 3353–3361. (doi:10.1098/rspb.2010.1007)
- Vaillancourt KL, Dinsdale NL, Hurd PL. 2012 Estrogen receptor 1 promoter polymorphism and

- digit ratio in men. *Am. J. Hum. Biol.* **24**, 682–689. (doi:10.1002/ajhb.22297)
8. Ökten A, Kalyoncu M, Yariş, N. 2002 The ratio of second- and fourth-digit lengths and congenital adrenal hyperplasia due to 21-hydroxylase deficiency. *Early Hum. Dev.* **70**, 47–54. (doi:10.1016/s0378-3782(02)00073-7)
 9. Gkiatas I, Lykissas M, Kostas-Agnantis I, Korompilias A, Batistatou A, Beris A. 2015 Factors affecting bone growth. *Am. J. Orthop.* **44**, 61–67.
 10. Forstmeier W. 2005 Quantitative genetics and behavioural correlates of digit ratio in the zebra finch. *Proc. R. Soc. B* **272**, 2641–2649. (doi:10.1098/rspb.2005.3264)
 11. Navarro C, de Lope F, Møller AP. 2007 Digit ratios (2D : 4D), secondary sexual characters and cell-mediated immunity in house sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.* **61**, 1161–1168. (doi:10.1007/s00265-006-0329-3)
 12. Dreiss AN, Navarro C, de Lope F, Møller AP. 2008 Digit ratios, secondary sexual characters and condition in barn swallows *Hirundo rustica*. *Behav. Ecol.* **19**, 16–21. (doi:10.1093/beheco/arm095)
 13. Garamszegi LZ, Hegyi G, Szöllösi E, Rosivall B, Török J, Eens M, Møller AP. 2007 Phenotypic correlates of digit ratio in a wild bird: implications for the study of maternal effects. *Anim. Behav.* **74**, 641–647. (doi:10.1016/j.anbehav.2006.11.023)
 14. Ruuskanen S, Helle S, Ahola M, Adamczyk F, Möstl E, Laaksonen T. 2011 Digit ratios have poor indicator value in a wild bird population. *Behav. Ecol. Sociobiol.* **65**, 983–994. (doi:10.1007/s00265-010-1099-5)
 15. Burley NT, Foster VS. 2004 Digit ratio varies with sex, egg order and strength of mate preference in zebra finches. *Proc. R. Soc. Lond. B* **271**, 239–244. (doi:10.1098/rspb.2003.2562)
 16. Lessells CM, Boag PT. 1987 Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121. (doi:10.2307/4087240)
 17. Newton I. 1989 *Lifetime reproduction in birds*. London, UK: Academic Press.
 18. Romano M, Rubolini D, Martinelli R, Bonisoli-Alquati A, Saino N. 2005 Experimental manipulation of yolk testosterone affects digit length ratios in the ring-necked pheasant (*Phasianus colchicus*). *Horm. Behav.* **48**, 342–346. (doi:10.1016/j.yhbeh.2005.03.007)
 19. Saino N, Rubolini D, Romano M, Boncoraglio G. 2007 Increased egg estradiol concentration feminizes digit ratios of male pheasants (*Phasianus colchicus*). *Naturwissenschaften* **94**, 207–212. (doi:10.1007/s00114-006-0188-9)
 20. Nagy G, Blázi G, Hegyi G, Török J. 2016 Side-specific effect of yolk testosterone elevation on second-to-fourth digit ratio in a wild passerine. *Sci. Nat.* **103**, 1–7. (doi:10.1007/s00114-015-1328-x)
 21. Uller T, Eklof J, Andersson S. 2005 Female egg investment in relation to male sexual traits and the potential for transgenerational effects in sexual selection. *Behav. Ecol. Sociobiol.* **57**, 584–590. (doi:10.1007/s00265-004-0886-2)
 22. Rubolini D, Martinelli R, von Engelhardt N, Romano M, Groothuis TGG, Fasola M, Saino N. 2007 Consequences of prenatal androgen exposure for the reproductive performance of female pheasants (*Phasianus colchicus*). *Proc. R. Soc. B* **274**, 137–142. (doi:10.1098/rspb.2006.3696)
 23. Hegyi G, Herényi M, Szöllösi E, Rosivall B, Török J, Groothuis TGG. 2011 Yolk androstenedione, but not testosterone, predicts offspring fate and reflects parental quality. *Behav. Ecol.* **22**, 29–38. (doi:10.1093/beheco/arq165)
 24. Tschirren B, Postma E, Gustafsson L, Groothuis TGG, Doligez B. 2014 Natural selection acts in opposite ways on correlated hormonal mediators of prenatal maternal effects in a wild bird population. *Ecol. Lett.* **17**, 1310–1315. (doi:10.1111/ele.12339)
 25. Tschirren B, Sendekka J, Groothuis TG.G., Gustafsson L, Doligez B. 2009 Heritable variation in maternal yolk hormone transfer in a wild bird population. *Am. Nat.* **174**, 557–564. (doi:10.1086/605379)
 26. Hayward LS, Wingfield JC. 2004 Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. *Gen. Comp. Endocrinol.* **135**, 365–371. (doi:10.1016/j.ygcen.2003.11.002)
 27. Saino N, Romano M, Ferrari RP, Martinelli R, Møller AP. 2005 Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *J. Exp. Zool.* **303A**, 998–1006. (doi:10.1002/jez.a.224)
 28. Lilley T, Laaksonen T, Huitu O, Helle S. 2010 Maternal corticosterone but not testosterone level is associated with the ratio of second-to-fourth digit length (2D:4D) in field vole offspring (*Microtus agrestis*). *Physiol. Behav.* **99**, 433–437. (doi:10.1016/j.physbeh.2009.11.015)
 29. Hayward LS, Satterlee DG, Wingfield JC. 2005 Japanese quail selected for high plasma corticosterone response deposit high levels of corticosterone in their eggs. *Physiol. Biochem. Zool.* **78**, 1026–1031. (doi:10.1086/432854)
 30. Blas J, Bortolotti GR, Tella JL, Baos R, Marchant TA. 2007 Stress response during development predicts fitness in a wild, long lived vertebrate. *Proc. Natl Acad. Sci. USA* **104**, 8880–8884. (doi:10.1073/pnas.0700232104)
 31. Schmid B, Tam-Dafond L, Jenni-Eiermann S, Arlettaz R, Schaub M, Jenni L. 2013 Modulation of the adrenocortical response to acute stress with respect to brood value, reproductive success and survival in the Eurasian hoopoe. *Oecologia* **173**, 33–44. (doi:10.1007/s00442-013-2598-7)
 32. Henriksen R, Rettenbacher S, Groothuis TG.G. 2011 Prenatal stress in birds: pathways, effects, function and perspectives. *Neurosci. Biobehav. Rev.* **35**, 1484–1501. (doi:10.1016/j.neubiorev.2011.04.010)
 33. Banerjee SB, Arterbery AS, Fergus DJ, Adkins-Regan E. 2012 Deprivation of maternal care has long-lasting consequences for the hypothalamic–pituitary–adrenal axis of zebra finches. *Proc. R. Soc. B* **279**, 759–766. (doi:10.1098/rspb.2011.1265)
 34. Nagy G, Garamszegi LZ, Hegyi G, Herényi M, Laczi M, Rosivall B, Szöllösi E, Török J. 2019 Data from: Digit ratio predicts the number of lifetime recruits in female collared flycatchers. Dryad Digital Repository. (doi:10.5061/dryad.m8hb503)