

The Genetic and Environmental Structure of Reproduction-Related Variables: The Case of Fertility and Breastfeeding

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Life history theory studies the evolution of traits related to reproductive fitness. Fertility and parental investment are key life history traits which, from an evolutionary standpoint, appear strongly interrelated. The aim of this work was to analyze the genetic and environmental structure and relationship of two behaviors associated with reproductive fitness: total number of offspring and mean duration of breastfeeding. A total of 1,347 women distributed in 239 monozygotic pairs, 236 dizygotic pairs, and 393 individual twins from opposite sex pairs provided information about their reproductive history. We conducted separate univariate analyses to study the sources of variance of both variables; and a bivariate analysis, with threshold liability models. The sources of variance for number of children and breastfeeding were best explained by a model including familial and unique environmental factors, being $E = 0.54$ (CI 95%: 0.44, 0.66) and $E = 0.46$ (CI 95%: 0.34, 0.61), respectively. The phenotypic correlation between number of children and breastfeeding was low but significant ($r = 0.16$, CI 95%: 0.07, 0.25). Familial correlation between these variables did not reach significance, but unique environmental correlation did ($r_e = 0.20$, CI 95%: 0.02, 0.37). In conclusion, results do not support the existence of a clear common structure for the number of children a woman has and the time she spends breastfeeding them, at least in modern societies. The relationship found was mainly due to unique environmental factors. More research on these and related phenotypes is needed to better understand women's reproductive decisions and how natural selection acts on the life history traits.

■ **Keywords:** life history traits, fertility, breastfeeding, twin study

Individual differences in women's decisions about reproduction-related behaviors are a consequence of multiple internal and external factors that might change over time and environmental conditions. Life history theory (LHT) is a general theoretical framework that incorporates environmental and contextual influences, as well as heritable variation. This model attempts to give a conceptual explanation of the evolution of traits related to reproductive fitness, by trying to predict how natural selection shapes the way organisms adjust their resources to produce successful offspring (Rudzik, 2011). In the case of humans, natural selection should act on the final phenotypic outcome of a coordinated system of physiological, psychological, and cultural processes (Kaplan, 1996), which makes life history traits quite difficult to systematize and study.

Fertility and parental investment are key life history traits which, from an evolutionary standpoint, appear strongly interrelated. Parental investment in offspring is considered

a critical component of life history strategy and typically involves provisioning and protecting the young (MacDonald, 1999). Together with fertility, they represent one of the classical trade-offs between quantity and quality, or between maximizing fitness through increasing the number of offspring or their chance of survival. Hence, variation in fertility in human populations represents optimization of the life history trade-off between reproductive rate and parental investment (Lawson & Mace, 2011).

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It has been suggested that decisions regarding fertility and parental investment would be the product of psychological mechanisms that direct attention to the balance between investments and outcomes, and that detect diminishing return to investments (Kaplan, 1996; Kaplan & Lancaster, 2003). The behavioral consequences of those decisions would affect fertility indirectly via maternal physiology. One of the routes for this influence is through breastfeeding (Kaplan & Lancaster, 2003), which represents one of the main forms of maternal-specific investment (Volk, 2009). The relationship between fertility and breastfeeding is bidirectional and extends to physiological inter-regulation. Hormones secreted by a new fetus during the third trimester block milk production, while prolonged breastfeeding has a contraceptive effect (Kaplan, 1996; Meij et al., 2009). Hence, the length of the interbirth interval depends, in part, on the frequency and duration of breastfeeding, and lactation physiology adjusts to competition for resources between consecutive offspring. The evolution of these physiological systems is thought to be due to natural selection on birth spacing (Kaplan, 1996), but such evolution depends upon genetic variation on which selection could produce adaptations to different environmental conditions (Fabian & Flatt, 2012).

That relevance of genetic variation does not always show up through high heritabilities for life history traits. Actually, heritability is usually low for these phenotypes, which could be due to little amounts of additive genetic variance, or to the effect of large environmental variation (Fabian & Flatt, 2012; Price & Schlter, 1991). A number of studies have been published exploring the genetic and environmental variance underlying both fertility outcomes (e.g., number of children) and precursors (e.g., age at first intercourse, age at marriage, or age at first pregnancy attempt; Rodgers et al., 2007). These studies have revealed that not only fertility outcomes (such as final family size) but also motivational precursors to fertility (such as desired family size) are, to some extent, genetically determined (Kohler et al., 2006; Rodgers et al., 2001a). For instance, moderate heritability estimates for number of children have been reported in different populations (0.22 and 0.16, respectively) (Kosova et al., 2010; Miller et al., 2010). Nevertheless, heritability seems to be higher for having at least one child than for the total number of children (Rodgers et al., 2001a), and it is even higher for some precursors (i.e., getting married or age at first attempt to get pregnant) (Rodgers et al., 2001a, 2001b). However, both the magnitude of heritability and environmental influences would be expected to change over the lifetime (Rodgers et al., 2007), and over short periods of time. Social norms and relations with significant others (e.g., partner or nuclear family) are needed to adequately explain the genetic influence on fertility (Rodgers et al., 2001a).

For its part, breastfeeding is a life history trait that could be defined as a biocultural behavior (Holman & Grimes,

2003), which depends on physiological processes, but it is also strongly affected by a number of environmental factors (Colodro-Conde et al., 2011; Earle, 2002; Ekstrom et al., 2003; Swanson & Power, 2005). There is some evidence that nearly half of the variation found nowadays in breastfeeding behavior is due to genetic variability among women (Colodro-Conde et al., 2013). This is consistent with the idea that, given the high levels of infant mortality that characterize recent and evolutionary human history (Volk & Atkinson, 2008), a mother's ability to successfully breastfeed her infant was of tremendous evolutionary significance.

Taking into account the theoretical background that we have tried to summarize from the scientific literature, it appears to be assumed that there is a relationship between traits related to offspring survival and investment that shape women's decisions related to reproduction. This relationship would be modulated by physiological processes (Kaplan & Lancaster, 2003) as well as by socioeconomic characteristics that influence the relative returns to parental investment (Lawson et al., 2012). However, there is a lack of information about how these variables relate to each other, and a scarcity of studies that could present evidence regarding the shape of such an association. This study is an attempt to provide information on this issue, by determining the genetic and environmental structure and relationship of two relevant phenotypes (i.e., number of children and duration of breastfeeding) related to women's reproductive decisions in a cohort of adult female twins.

Materials and Methods

Subjects and Measures

A population-based sample of adult female twins registered on the Murcia Twin Register (MTR; Ordoñana et al., 2006, 2013) provided data for this study. The MTR reference population comprises all twin pairs who were born between 1940 and 1966 in the region. The MTR has been approved by the Murcia University Ethical Committee and it follows national regulations regarding personal data protection. All applicable institutional and governmental regulations concerning the ethical use of human volunteers were followed during this research.

The sample selected for this study comprised 1,347 female twins distributed in 239 (35.6%) monozygotic (MZ) pairs, 236 (35.1%) dizygotic (DZ) pairs, and 393 (29.3%) individual twins from opposite sex pairs. Mean age of the selected participants was 51.2 years (*SD*: 7.4; range: 41–68). Zygosity was determined by questionnaire and DNA testing.

The data analyzed in this report were collected in 2007 and 2009, by telephone and personal interview, respectively. Women were asked about different aspects of their reproductive history, including number of children and initiation and duration of breastfeeding periods for each of their children, with no distinction between full and partial breastfeeding. Data were retrospective and based on self-report.

Data from the first wave of collection were used as the reference set and data from those women who were interviewed for the first time during the second wave were incorporated to the data set. Given that participants were over 41 when they were interviewed, we assumed that the reported number of biological children should be definitive at both time points for nearly all cases. Additionally, given that breastfeeding had taken place long ago we assumed that no differences should be expected according to the moment of data collection (2007 vs. 2009) and both were treated as indistinguishable.

The two variables for this study were fertility or number of children, and mean duration of breastfeeding to each of the offspring. Data distributions were skewed for both variables, and therefore categorized: number of children had six categories and five thresholds (0, 1, 2, 3, 4, and 5 or more children); mean duration of breastfeeding to all the children was collapsed in three categories (3 months or less, 3 to 6 months, and more than 6 months). Year of birth was modeled as a covariate.

Data Analyses

Data preparation as well as descriptive and preliminary analyses were performed in SPSS v.19 (SPSS, 2010). Assumptions of the twin design were checked. Further details of the twin design, including assumptions, can be found elsewhere (Neale & Cardon, 1992; Posthuma et al., 2003).

As a first step, we determined twin-pair correlations per zygosity group for number of children and breastfeeding, each considered in isolation. We tested whether MZ twin pairs correlated more strongly than DZ twin pairs, which would suggest a genetic influence on individual differences in these two traits. Then, variance component model-fitting was conducted to partition the variation in number of children and breastfeeding into genetic, shared environmental, and non-shared environmental influences.

The next step was to conduct a bivariate analysis in order to explore the sources of covariance between fertility (i.e., the number of children) and average duration of breastfeeding of all children. In a bivariate model, the A, C, and E matrices are specified in a Cholesky decomposition. Bivariate models are concerned with estimating A, C, and E of the individual variables through MZ and DZ cross-twin within-trait correlation, as well as with partitioning the covariance between the two traits into A, C, and E by means of the cross-twin cross-trait MZ to DZ correlation ratios. Significant cross-twin within- or cross-trait covariances imply that common etiological factors between the two traits are related. Whether these common familial etiological influences are due to genetic or environmental factors is inferred by the MZ to DZ ratio of the cross-twin within- or cross-trait covariances (Neale & Cardon, 1992). The partitioning of the covariation of any two variables into the genetic, shared environmental, and unique environmental sources of covariation yields additive genetic (r_a), common envi-

ronmental (r_c), and individual-specific environmental (r_e) correlations, respectively; where, for example, r_a indicates the extent to which the same genetic factors influence both phenotypes (i.e., number of children and breastfeeding).

Threshold liability models were used on the categorized twin data, assuming that the classes reflect an imprecise measurement of an underlying normal distribution of liability, with one or more thresholds discriminating between the ordered categories (Rijsdijk & Sham, 2002). This liability may be influenced by genetic and environmental factors and is normally distributed with a mean value of 0 and a variance of 1. Observed frequencies in each category are translated in proportions under an assumed normal distribution by estimating associated thresholds (z values). Twin similarity is estimated by the polychoric correlation between the liability distributions. Full Information Maximum Likelihood estimation (FIML) on raw data was used, allowing the use of both complete and incomplete pairs in the analyses. In this method, twice the negative log-likelihood ($-2LL$) of the data for each family is calculated, and parameters are estimated so that the likelihood of the raw data is maximized. Estimates of the full models only (with 95% CIs) are presented. In order to estimate the MZ and DZ twin correlations for number of children and breastfeeding, we fitted a constrained correlational model to the twin-pair data to get one overall within-twin cross-trait correlation (equal across all the individuals regardless of their zygosity); one cross-trait cross-twin correlation within zygosity group (regardless of twin order); and two cross-twin correlations within zygosity group. These analyses were conducted with the Mx statistical package (Neale et al., 2006).

Results

Almost nine out of ten women in this sample ($n = 1,188$; 88%) had been biological mothers at least once in their lives. They had 2.55 children on average ($SD: 1.15$, range: 1–11). The mean duration of breastfeeding was 4.16 months ($SD: 4.49$, range: 0–36). Table 1 presents the correlation matrix for the duration of breastfeeding for the first five children. For more information about the distribution of the data by zygosity once they were categorized, see Table 2.

Univariate Analyses

Table 3 shows twin correlations and the estimates for variance distribution of univariate analyses: for number of children and for mean breastfeeding duration (only for women who had at least one child).

All twin correlations were significant. MZ twin correlations were greater than DZ twin correlations for number of children and mean duration of breastfeeding. The lower bound for additive genetic (A) and shared environmental (C) was zero in both variables, meaning that any distinction between the proportions of variance due to the familial factors must be made cautiously. Unique environmental

TABLE 1
Correlation Matrix for Breastfeeding Duration in the First Five Children

	1st child	2nd child	3rd child	4th child	5th child
1st child	1 (1,155)				
2nd child	.62* (836)	1 (841)			
3rd child	.54* (365)	.70* (362)	1 (369)		
4th child	.55* (135)	.72* (132)	.85* (136)	1 (136)	
5th child	.40* (49)	.57* (48)	.70* (49)	.78* (49)	1 (49)

Note: Spearman's ρ (N). * $p < .01$.

TABLE 2
Number of Children and Mean Breastfeeding Duration, Presented by Zygosity

		MZ % (n = 491)	DZ % (n = 503)	DZ OS % (n = 353)	Total % (n = 1,347)
Number of children	0	10.4	13.3	10.8	11.6
	1	12.2	7	8.2	9.2
	2	44.2	43.3	42.8	43.5
	3	21.6	22.1	21.8	21.8
	4	6.5	9.3	10.8	8.7
	≥ 5	5.1	5	4.8	5
	Ref/DK	0	0	100	2
		% (n = 440)	% (n = 436)	% (n = 312)	% (n = 1,188)
Mean breastfeeding duration (only mothers)	<3 months	53.9	51.6	49.4	51.9
	3–6 months	22.7	28.7	28.2	26.3
	>6 months	21.8	15.8	21.5	19.5
	Ref/DK	1.6	3.9	1	2.3

Note: Ref/DK = refused/did not know; MZ = monozygotic twins; DZ = dizygotic twins; DZ OS = dizygotic twins from opposite sex pairs.

TABLE 3
Polychoric Twin Correlations and Proportions of Variance Explained by Additive Genetic Influences (A), Common Environment (C), and Unique Environment (E) with 95% CI, Extracted From the Univariate Analyses

	r_{MZ} (n = 239 pairs)	r_{DZ} (n = 236 pairs)	A (%)	C (%)	E (%)
NCh	0.46 (0.34, 0.56)	0.35 (0.22, 0.46)	0.22 (0, 0.54)	0.24 (0, 0.46)	0.54 (0.44, 0.66)
BF	0.54 (0.39, 0.66)	0.32 (0.12, 0.50)	0.42 (0, 0.66)	0.11 (0, 0.49)	0.46 (0.34, 0.61)

Note: MZ = monozygotic twins; DZ = dizygotic twins; NCh = number of children; BF = mean breastfeeding duration.

effects (E) accounted for 54% of the variance in fertility (95% CI: 0.44, 0.66) and for 46% of the variance in mean breastfeeding duration (95% CI: 0.34, 0.61).

Bivariate Analyses

Due to the limitation to differentiate clearly between familial factors, conservatively we choose to present the bivariate analysis with only two sources of variance, A and E, A including both genetic and shared environmental factors (A + C).

The phenotypic correlation between number of children and mean breastfeeding duration was low but significant ($r_{ph} = 0.16$; 95% CI: 0.07, 0.25). However, the cross-twin cross-trait correlations were non-significant (see Table 4). The bivariate model was fitted to decompose the association between number of children and mean breastfeeding duration.

The extent to which these two traits share the same familial (genetic and common environmental) or unique environmental factors is given by the r_{a+c} and r_e correlations, respectively. Familial correlation between number of children and breastfeeding was non-significant. Unique envi-

ronment correlation was 0.20 (CI 95%: 0.02, 0.37). The covariance between number of children and breastfeeding duration due to unique environmental factors was 0.10 (CI 95%: 0.01, 0.18).

Discussion

This article reports the etiology of possible relationships between phenotypes related to women's reproductive decisions (i.e., childbearing and breastfeeding) to explore the extent to which they can be considered related parts of a theoretical construct associated with reproductive behavior. The main and general conclusion is that the relationship between number of children and breastfeeding duration appears to be complex and modulated by multiple factors. We found a low but significant positive phenotypic correlation between these variables. This finding is not surprising and should be interpreted cautiously, in light of the possibility that phenotypic correlations between life history traits mask the real trade-offs experienced by individuals (Hill & Kaplan, 1999). Additionally, their genetic and environmental structure appeared different in nature when analyzed

TABLE 4
Polychoric Twin Correlations, Familial (r_{a+c}) and Unique Environment (r_e) Correlations with 95% CI, and Variances and Covariances of the Familial Influences (A + C) and Unique Environment (E) Extracted from the Bivariate Analyses

	$r_{MZ} (n = 239 \text{ pairs})$			$r_{DZ} (n = 236 \text{ pairs})$			r_{a+c}			r_e			A + C			E		
	NCh	BF		NCh	BF		NCh	BF		NCh	BF		NCh	BF		NCh	BF	
NCh	0.46 (0.34, 0.56)			0.35 (0.22, 0.46)			1			1			0.49 (0.39, 0.58)			0.51 (0.42, 0.61)		
BF	0.08 (-0.03, 0.19)	0.54 (0.39, 0.66)		-0.03 (-0.16, 0.10)	0.32 (0.11, 0.49)		0.13 (-0.08, 0.33)	1		0.20 (0.02, 0.37)	1		0.07 (-0.04, 0.17)	0.54 (0.44, 0.66)		0.10 (0.01, 0.18)	0.46 (0.34, 0.59)	

Note: MZ = monozygotic twins; DZ = dizygotic twins; NCh = number of children; BF = mean breastfeeding duration.

individually. While unique environment was the most relevant source of variance for number of children and breastfeeding, additive genetic effects appear to be also important for the latter. All in all, both reproductive decisions appear to be dependent on different factors.

Regarding the sources of variance for number of children, a recent work with Swedish twins found both significant genetic and shared environment variation in number of offspring (Zietsch et al., 2013). Also, a previous review on human fertility (Rodgers et al., 2001a) concluded that differences between individuals in their genetic makeup affect their fertility outcomes and precursors. However, these authors also state that if fertility-related social norms dictate universal and consistent childbearing, variance caused by genetic influences may be hidden or suppressed; the opposite would occur if fertility norms shift to support reproductive flexibility and choice by the individual or couple; in such a case it is when genetic influences are more easily expressed and realized (Rodgers et al., 2001a). In our sample, low heritability in the number of children could be due to high environmental variance, which would be the result of social factors that affect the capacity of women/couples to take individual decisions regarding reproduction. The weight of environmental factors influencing the final offspring in this sample suggests that, in the period studied, choices might have been determined by experiences in the societal mandate. This is consistent with a recent thesis (Papadimitriou, 2008), which concluded that the factors that might better predict a woman's desire to have children were: family of origin experiences, sex role identity, individual factors (e.g., personal value of children, or personality factors), situational factors (e.g., number of previous children, or partner influences), values (e.g., valuing career/education more than having a family), social/cultural influences, family and community support (vs. isolation, or lack of support).

Moving to breastfeeding duration, the bigger intrapair correlations in MZ twins point to the presence of genetic factors playing a part in the probability of a mother choosing to start and maintain to breastfeed her offspring. A caution should be made, however, regarding the values of confidence intervals for the heritability estimates, which appear wide, probably as a result of small sample size and limited power. There is agreement among all theorists that some of the variation in life history variables is the result of genetic variation (MacDonald, 1999). Within this perspective, individual differences in parental investment patterns result partly from heritable variation, and that seems to be the case for breastfeeding. Consequently, our results support the idea that there is a moderate proportion of genetic variance underlying the breastfeeding duration that could have an adaptive value for the individual. The rest of the variance (apart from measurement error) is accounted for by unique environmental factors associated with the decisions that women take regarding breastfeeding (e.g., availability and length of maternity leave, perceived social norms,

experience/training, or perceived support; Barona-Vilar et al., 2009; Ekstrom et al., 2003; Kools et al., 2005).

Given these results, the posited relationship between fertility and breastfeeding is far from clear, at least in this sample. As stated before, the phenotypic correlations between number of children and breastfeeding duration were significant but low. The environmental correlation between them was also significant, while the correlation due to familial factors did not reach significance. Limited power of the sample to distinguish between the magnitude of the MZ and DZ cross-trait cross-twin correlations resulted in the conclusion that the only certain source of this small overlap comes from individual-specific environmental effects. Additionally, these results must be analyzed within the context of modern society, which imposes a set of environmental determinants that differ largely from those in preindustrial societies. Thus, modern women seem to adjust investment in children based on their family size and resource availability (Huber et al., 2010). Reduction of child mortality rates and changing characteristics of successful survival introduce new environmental conditions masking the hypothetical trade-off between fertility and parental investment (Kaplan & Lancaster, 2003; Lawson & Mace, 2011; Meij et al., 2009). The possibility of actively controlling the number of offspring through contraceptive technology, and the chance to substitute natural breastfeeding by milk formula, without reducing parental investment, adds even more complexity to this picture.

To summarize, according to the findings of the present study, there is not a clear picture of the genetic and environmental structure and relationship between the number of children a woman has and the time she spends breastfeeding them, at least in modern societies. Hence, although both variables are clearly related to women's reproductive choices, we found little support for any hypothetical trait (e.g., 'motherhood') encompassing both phenotypes. Nonetheless, these findings should be seen in the context of limitations due to statistical power. The sample size is likely responsible for the wide confidence intervals found for the estimations of variance distribution. A replication of results, with a bigger sample, would be needed in order to get a better insight on this issue.

In conclusion, the present study is an exploratory attempt to increase our knowledge about the relations between two relevant life history traits, a complex and intriguing association that needs better clarification and characterization in order to allow for scientific scrutiny. As such, we think it provides information that may be useful in the effort toward a better understanding of women's decisions regarding reproduction issues.

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