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RESEARCH ARTICLE

Examining the link between religiousness and fitness in a behavioural ecological framework

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Abstract

In recent years there have been attempts to explain religiousness from an evolutionary viewpoint. However, empirical data on this topic are still lacking. In the present study, the behavioural ecological theoretical framework was used to explore the relations between religiousness, harsh environment, fitness (reproductive success and parental investment) and fitness-related outcomes (age at first birth, desired number of children and the romantic relationship duration). The data were collected from 461 individuals from a community sample who were near the end of their reproductive phase (54% females, $M_{age} = 51.75$; SD = 6.56). Positive links between religiousness, harsh environment, fitness and fitness-related outcomes were expected, with the exception of age at first birth, for which a negative association was hypothesized. Hence, the main assumption of the study was that religiousness has some attributes of fast life-history phenotypes – that it emerges from a harsh environment and enables earlier reproduction. The study findings partially confirmed these hypotheses. Religiousness was positively related to environmental harshness but only on a zero-order level. Religious individuals had higher reproductive success (this association was especially pronounced in males) but religiousness did not show associations with parental investment. Religiousness was positively associated with desired number of children and negatively associated with age at first birth, although the latter association was only marginally significant in the multivariate analyses. Finally, path analysis showed that desired number of children and age at first birth completely mediated the relation between religiousness and reproductive success. The data confirmed the biologically adaptive function of religiousness in contemporary populations and found the mediating processes that facilitate fitness in religious individuals. Furthermore, the findings initiate a more complex view of religiousness in a life-history context which could be fruitful for future research: a proposal labelled as 'ontogeny-dependent life-history theory of religiousness'.

Keywords: Religiousness; Life-history theory; Human behavioural ecology

Introduction

> After the Scopes Trial in 1925 and the subsequent establishment of evolutionary theory in state schools in the United States, there was a broad conviction among educated Westerners that the defeat of anti-evolutionist fundamentalism and probably all religion was a matter of time. But to the great surprise of many, religious activity including Creationism and Intelligent Design today enjoy a worldwide resurgence. The reason is simple: evolutionary theorists brought up far more scientific arguments – but committed believers in supernatural agents brought up far more children. (Blume, 2009)

In the past fifteen years there has been an increasing effort to explain the evolution of religiousness (for review see Kirkpatrick, 2015). Although advances in this goal have been made, a crucial

question has remained unanswered: is religiousness an evolutionary adaptation or a byproduct? Various authors believe that religiousness is a byproduct of evolution (Bourrat, 2015). Byproduct or spandrels do not have an adaptive function, which means that they did not enhance survival and reproduction in ancestral populations. Scholars think that religiousness can emerge as a byproduct of several psychological mechanisms: hyperactive cognitive heuristics for the detection of agency (Boyer, 2001; Atran & Norenzayan, 2004), as an extension of the attachment processes to supernatural beings (Kirkpatrick, 2005; Granqvist & Kirkpatrick, 2013) or as a side-effect of evolved social cognition, which enables humans to infer the motives, emotions, goals and intentions of others (Bering, 2011). On the other hand, a vast number of researchers think that religiousness is an adaptation: a characteristic that elevated human fitness. Several authors assume that religiousness promotes in-group co-operation based on honest signals of devotion to religious rituals and norms (Alcorta & Sosis, 2005; Bulbulia, 2012). The evolution of religiousness is certainly a problem of great complexity since social and cultural factors contribute to its potential biological adaptiveness (Rowthorn, 2011).

It is highly arguable whether the evolution of religion in ancestral populations is an empirical question at all; with the current methodology the answer to this question cannot be provided. This is why behavioural ecology focuses on examining the current adaptiveness of a behavioural trait. This is done by exploring the relations between a trait and evolutionary fitness, usually operationalized as reproductive success. Religiousness is a behavioural trait with substantial heritability; studies show that 27% to 65% of phenotypic religious expression can be explained by genetic contributions (reviewed in Kandler & Riemann, 2013). Hence, if individuals with higher religiosity have elevated reproductive success, then natural selection could actively propagate alleles that contribute to the phenotypic expression of religious affiliation. In this case it could be reasonably assumed that religiousness does have an adaptive function in contemporary humans. And indeed, empirical data usually confirm the positive link between religiousness and number of children (Sanderson, 2008; Blume, 2009; Fieder & Huber, 2016). It is important to note that religious affiliation may not be biologically adaptive by enhancing only individual fitness, but inclusive fitness as well. Inclusive fitness is a concept that emphasizes propagation of the shared genes between an individual and her/his kin; natural selection can positively act on a trait that contributes to kin survival and reproduction as well (Hamilton, 1964). According to recent theoretical predictions, religiousness could boost inclusive fitness by emphasizing mutualism in family, kin altruism and social bonding (Crespi & Summers, 2014).

It is also important to reveal the specific ways the trait contributes to fitness, i.e. to explore the mediators in the religiousness–fitness link. Religions are generally pro-life orientated: major world religions often explicitly advocate a higher number of children and are often opposed to birth control (Sanderson, 2008). This could be important in contemporary humans since they are characterized by conscious and intentional planning of reproduction. Hence, religious individuals could have a pronounced desire to have a larger number of offspring (Hayford & Morgan, 2008). Attending religious services has been shown to be negatively associated with the time of first birth; religious individuals tend to reproduce earlier in their lifetime (Pearce & Davis, 2016). Having in mind that age at first birth is negatively related to completed fertility (Tropf *et al.*, 2015; Sanjak *et al.*, 2018), this could be another pathway religious individuals use to achieve higher fitness. Finally, religiousness may have a more indirect way to increase fitness – by enabling longer relationships between romantic partners. Previous studies have found that religiousness has a positive effect on commitment to marriage and marital satisfaction, and a negative effect on divorce rates (Mahoney *et al.*, 2002). Hence, it elevates the duration and quality of marital relationships, which may result in a higher number of offspring.

Life-history theory represents an evolutionary framework aimed at explaining the trade-offs in reproductive strategies (Del Giudice *et al.*, 2016). The theory identifies two major reproductive

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trajectories with both costs and benefits regarding fitness. The fast life-history pathway is based on early reproduction, followed by a large number of offspring and low parental investment; the slow or K pathway is related to a later age of reproduction and smaller number of offspring with high parental effort. Religions tend to regulate many aspects of sexual, mating and partner behaviour (Baumard & Chevallier, 2015); these findings motivated some scholars to assume that religiousness was a life-history trait. Since religiousness is associated with lower sexual permissiveness, restricted sexuality and monogamy, several researchers have assumed that religiousness is a part of slow life-history trajectory (Gladden *et al*., 2009; Baumard & Chevallier, 2015; Schmitt & Fuller, 2015).

However, the role of religiousness in individual life-history strategies could be more complex. The dynamics of life histories are largely dependent upon the environment. Detrimental, scarce and unpredictable environments facilitate a fast life-history strategy, while rich, supportative and predictable enviroments enable the development of a slow life-history strategy (Del Giudice *et al*., 2016). Religiousness could also promote a fast life-history strategy, especially in unfavourable environmental conditions (Reynolds & Tanner, 1995). Furthermore, religious sentiment may be related to earlier reproduction, which is a key marker of a fast life-history pathway: religious affiliation is related to earlier age at first birth (Pearce & Davis, 2016) and higher rates of teenage pregnancies (Strayhorn & Strayhorn, 2009). Hence, the assumption is that the life-history dynamics of religiousness are complex and involve both fast and slow life-history characteristics.

If religiousness contributes to fitness then its underlying gene alleles may be subject to positive directional selection. Consequently, this would mean that religiousness might be biologically adaptive in contemporary humans. Behavioural ecological research usually investigates behavioural dispositions shared by humans and other animals such as personality (Gurven *et al*., 2014) or cognitive traits (Međedović, 2017). However, it has been frequently argued that culturally shaped, complex social–psychological traits (values, lifestyles, attitudes, social norms), which are distinctive to humans, are important for their current fitness (Bouchard, 2009). The present study aimed to advance existing knowledge on religiousness' role in fitness optimization. It leaned on previous research that analysed the relations between religiousness and fitness-related and life-history traits. However, it expanded on previous studies in several ways: 1) both reproductive success and parental investment as a more complete operationalization of fitness were measured (participants were selected to be at the end of the reproductive phase because fitness can be most validly estimated in this stage of the ontogeny); 2) several fitness-related outcomes (desired number of children, age at first reproduction and duration of partner relationship) were postulated as mediators in the link between religiousness and fitness; 3) the role of a harsh environment in these links were examined as well. Contingent on the research goals, the following hypotheses were developed. It was expected that: 1) religiousness would be positively related to harsh environment, fitness, desired number of children and relationship longevity (as an indicator of long-term mating); 2) religiousness would be negatively related to age at first birth; 3) the link between religiousness and fitness would be partially mediated by the desired number of children, age at first reproduction and the duration of partner relationship. Note that if religiousness is found to be positively associated to harsh environment and negatively to age at first birth, this would indicate that religiousness has some characteristics of the fast life-history pathway.

Methods

Sample

The study sample consisted of 461 individuals (54% females). The participants were the parents of psychology students at the Singidunum University of Belgrade, Serbia. Students asked their parents to fill in a questionnaire as part of a psychology course. Participation in the research was voluntary for both students and parents (students received additional 'points' if they

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volunteered to participate in the research). The questionnaires were put in envelopes and sealed by the study participants after they had been filled in, to ensure anonymity. The participants were not related; observations from only one parent per student (randomly assigned) were used. The mean age of participants was 51.75 years (SD = 6.56). Participants' ages suggested that they were at the end of their reproductive lives at the time of data collection. If a limit for the end of the reproductive phase is set to 50 years in females and 55 years in males, it can be stated that 47% of females and 32.7% of males in the study sample were in the post-reproductive stage. Participants were more highly educated than average: 47.4% had completed faculty (4 or 5 years of college education), 30.4% had completed high school, while the rest had completed only elementary school.

Measures

Religiousness was measured using the abbreviated version of the Religiosity scale, which is part of the Arizona Life History Battery (Figueredo, 2007). Five items on this scale that have been shown to have high reliability ($\alpha = 0.85$) were administered.

Harsh environment was operationalized using two scales. *Family dysfunction* was measured using the Weak Socialization scale from the AMORAL inventory (Knežević, 2003). This scale measures various dysfunctional processes in the family during the participant's childhood, operationalized by five items. *Childhood Poverty* was explored as well, using a four-item scale. Since these two measures correlated positively in the study sample ($r = 0.33$; $p < 0.001$), the total average score on all items was calculated and labelled as *Harsh environment* ($\alpha = 0.76$ for the whole scale). These scales were self-report inventories with a standard Likert-type scale ranging from 1 to 5, where 1 stands for 'I disagree completely' and 5 stands for 'I agree completely'. Higher scores represent a harsher environment.

Two measures were used to explore participants' fitness. *Reproduction Success* was used as a major indicator of evolutionary fitness (participants were asked how many biological children they had). In addition, *Parental Investment* was measured using the Kin Care-Children scale ($\alpha = 0.64$), which is part of the Fundamental Social Motives Inventory (Neel *et al.*, 2016). Furthermore, three additional indicators assumed to mediate the relation between religiousness and fitness were measured: 1) *Age at first birth* (participants were asked how old they were when they had their first child); 2) *Planned number of children* (participants were asked the following question: 'When you started to think about having children, how many children in total did you want to have?'); 3) *The duration of the relationship* with their reproductive partner (participants were asked how long they were in a relationship with the partner they had children with; if participants had children with multiple partners they were asked to write the longest relationship with any of them). Items of the self-report inventories for assessing Religiousness, Harsh environment and Parental investment are shown in Table 1.

Data analysis

First, the distributions of the reproductive success for the whole sample and separately for the two sexes were determined. Then, descriptive statistics for all measures, scale reliabilities and the two types of correlation on the whole sample were presented: zero-order correlations and partial correlations where participants' sex and age were taken into account. Sex differences in analysed variables were determined, together with the correlations between all variables for males and females separately. Finally, path analysis was conducted to further examine the relations between the variables and to explore the postulated mediation role of age at first birth, desired number of children and relationship duration in the link between religiousness and fitness. Reproductive success and Parental investment as fitness components were set as

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Table 1. Items of the self-report scales for measuring Religiousness, Harsh environment and Parental investment

Variable	Items
Religiousness (taken from Figueredo, 2007):	1. I'm a very religious person
	2. I'm a very spiritual person
	3. It is or will be important for me to send my children to religious or spiritual services or instruction
	4. I prefer to be with other people who belong to the same religion as me
	5. I frequently attend religious or spiritual services
Kin Care-Children (Neel *et al.*, 2016):	1. I help take care of my children
	2. I like to spend time with my children
	3. Taking care of my children is not a high priority for me right now (reverse coded)
	4. I often think about how I could stop bad things from happening to my children
	5. I rarely think about protecting my children (reverse coded)
	6. Providing for my children is important to me
Weak socialization (taken from Knežević, 2003)	1. Quarrels and fights were frequent in the house where I grew up
	2. My parents beat me frequently when I was a child
	3. While I was a child, they almost never complimented me, even when I did something good
	4. When I was a child, nobody paid much attention to what I was doing
	5. When I was a child, I was afraid my parents could have a divorce
Childhood poverty	1. My family never had enough money
	2. As I grew up, there was a constant threat that my parents were out of work
	3. We have always been able to afford everything we wanted in our family (reverse coded)
	4. While I was growing up I had to do various jobs to provide myself with extra money

The last two scales were combined into the 'Harsh environment' measure.

criteria measures. Age at first birth, Relationship duration and Desired number of children were set as mediators, while Religiousness and Harsh environment were set as endogenous variables. All measures were modelled as the observable variables. It is important to highlight that age and sex were modelled in the path analysis as well, but these variables were not shown in the model in order to save space. All of the parameters were modelled except the correlation between sex and age and that between the two fitness components (since neither zero-order nor partial correlations suggested that there was a connection between these measures). Several goodness-of-fit indices were calculated in order to evaluate the ability of the model to adequately describe empirical data (Hu & Bentler, 1999): χ^2 as the most common parameter for evaluation of the discrepancy between the model and empirical data; Normed Fit Index (NFI); Comparative Fit Index (CFI); and the Root Mean Square Error of Approximation (RMSEA). The model with a high fit to the data should have a low χ^2 and RMSEA (below 0.060) and high CFI and GFI (above 0.90).

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Table 2. Distribution of reproductive success across the sexes

	Reproductive success (number of children)				
	1	2	3	4	5
Whole sample	21%	54.2%	19.1%	4.8%	0.9%
Males	23.9%	54.9%	16.4%	2.8%	1.9%
Females	18.5%	53.6%	21.4%	6.5%	0%

Table 3. Descriptive statistics and correlations between the examined variables

	M	SD	K–S *z*	1	2	3	4	5	6	7
1. Religiousness	2.65	0.99	1.54*		−0.09†	0.02	0.15**	0.12*	0.04	0.02
2. Age at first birth	27.29	4.79	2.05**	−0.17**		−0.17**	−0.06	−0.33**	−0.11*	−0.01
3. Relationship duration	22.25	10.71	4.34**	−0.05	−0.11*		0.03	0.17**	0.11*	−0.01
4. Desired number of children	2.59	1.21	3.38**	0.16**	−0.07	0.02		0.24**	0.12**	0.02
5. Reproductive success	2.11	0.82	6.53**	0.13**	−0.31**	0.14**	0.25**		0.07	−0.02
6. Parental investment	4.52	0.51	3.74**	0.05	−0.10*	0.09	0.13**	0.07		−0.17**
7. Harsh environment	2.19	0.68	1.99**	0.11*	−0.05	0.01	0.06	0.02	−0.12**	

K–S *z*: Kolmogorov–Smirnov statistic; Pearson's bivariate correlations are shown below the diagonal; partial correlations (controlled for the variance of sex and age) are shown above the diagonal.
†$p < 0.10$; *$p < 0.05$; **$p < 0.01$.

Results

The distribution of reproductive success by sex

The study sample was somewhat specific due to a fact that all participants were parents. Hence, the distribution of Reproductive success for the whole sample and for males and females separately is shown first (Table 2). It can be seen that Reproductive success was very similar for the two sexes, with a median of 2 children for both males and females. It should be noted that the distribution of Reproductive success was significantly different for both the normal ($Z = 6.50$; $p < 0.001$) and Poisson distributions ($Z = 3.62$; $p < 0.001$) on the whole sample.

Descriptive statistics and bivariate relation with study variables

The descriptive statistics were described and normality tests for all analysed variables calculated. All of the Kolmogorov–Smirnov statistics were statistically significant, which suggests that variables deviated significantly from a normal distribution. Thus measures were normalized using Blom's algorithm (Blom, 1958) and the normalized variables were used in further analyses. Pearson's coefficients of linear correlation between the analysed measures were calculated. Furthermore, partial correlations between the measures were obtained as well, with the variance of participants' sex and age controlled for. These results are shown in Table 3 (zero-order correlations are shown below the diagonal, while the partial correlations are shown above the diagonal).

Both zero-order and partial correlations produced similar results, which suggests that participant's sex and age accounted only for a small amount of the covariance between the explored measures. Religiousness correlated negatively with Age at first birth and positively with Desired number of children and Reproductive success (although, this association was significant only in the subsample of male participants). Age at first birth was negatively associated with

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Table 4. Sex differences and correlations between the examined variables by sex

	Males *M* (SD)	Females *M* (SD)	*t*	1	2	3	4	5	6	7
1. Religiousness	2.47 (1.00)	2.80 (0.95)	−3.62**		−0.14*	−0.02	0.14*	0.08	0.03	0.03
2. Age at first birth	28.24 (4.91)	26.46 (4.49)	4.06**	−0.15*		0.11†	−0.01	−0.31**	−0.14*	0.14*
3. Relationship duration	23.67 (9.74)	23.62 (8.83)	0.06	−0.07	0.11		0.07	0.13*	0.09	0.00
4. Desired number of children	2.64 (1.11)	2.52 (1.05)	1.19	0.16*	−0.12†	−0.03		0.25*	0.14*	0.06
5. Reproductive success	2.26 (1.78)	2.17 (0.85)	0.37	0.17*	−0.28**	0.15*	0.24**		0.11†	−0.08
6. Parental investment	4.48 (0.54)	4.56 (0.48)	−1.59	0.04	−0.04	0.10	0.11	0.02		−0.20*
7. Harsh environment	1.85 (0.40)	2.49 (0.73)	−11.90**	0.05	−0.12†	0.05	−0.04	0.08	−0.14*	

M (SD): means and standard deviations. Correlations for males are shown below the diagonal; correlations for females are shown above the diagonal.
†$p < 0.10$; *$p < 0.05$; **$p < 0.01$.

Relationship duration, Reproductive success and Parental investment. Individuals who had longer partner relationships had a higher number of children as well; desired number of children was positively related to both fertility and investment in children. Finally, individuals who grew up in a harsher environment showed less Parental investment. The only difference between the two types of obtained correlations emerged in the link between Religiousness and Harsh environment: the zero-order association turned out to be positive and significant while partial correlation was non-significant. All of the detected effect sizes were small to moderate.

Mean levels of examined measures, together with the associations between them, may have been affected by sex differences. Thus a *t*-test was done to examine sex differences; furthermore, the correlations in the subsamples of males and females were obtained. These results are shown in Table 4. Three significant differences between the sexes were detected: females reported harsher environmental conditions in childhood and higher mean levels of religiousness; females also had earlier mean age when they had their first child compared with males. There was one important sex difference in regard to the associations between Religiousness and the other examined variables: the association between Religiousness and Reproductive success was positive and significant in males; the sign of the correlation was positive in females as well, but it did not reach statistical significance.

Modelling the relations between the environment, religiousness and fitness-related outcomes

Finally, the path analysis that incorporated relations between Harsh environment, Religiousness and Reproductive fitness, including the role of potential mediators, was tested. Fit indices of this model were as follows: $\chi^2_{(2)} = 5.35$, $p = 0.069$; NFI = 0.990; CFI = 0.994; RMSEA = 0.060. It can be concluded that the model describes empirical data very well, which can be expected since the fit indices for the models comprised only of observed variables are usually high. The model was more successful in explaining the variance of Reproductive success (18% of explained variance) than Parental investment (7% of explained variance). The model is shown in Figure 1. In order to facilitate the analysis of the associations between the variables, only statistically significant parameters

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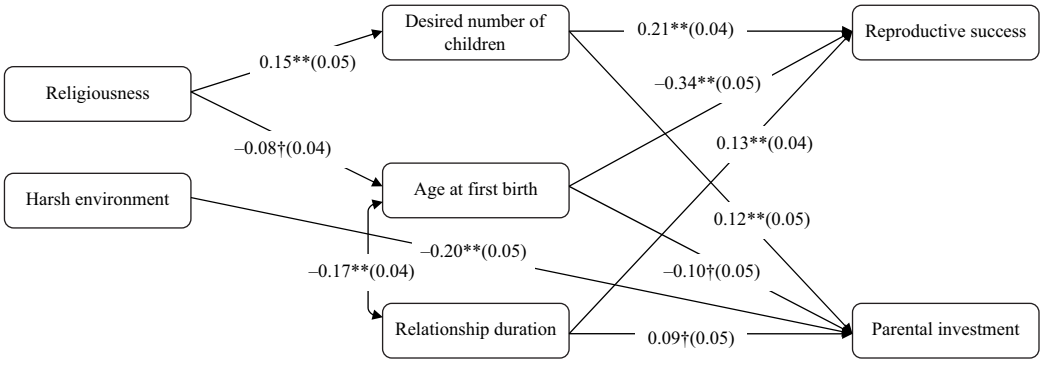

Figure 1. Path analysis of the relations between environment, religiousness and fitness outcomes. Only statistically significant coefficients (including marginal significance) are shown; one-sided arrows represent hypothetical causal pathways; the two-sided arrow represents the correlation between the variables; standardized path coefficients are provided (except for one correlation); standard errors are shown in parentheses. †$p < 0.10$; *$p < 0.05$; **$p < 0.01$.

are shown (including marginally significant ones). It can be seen that the path coefficients mostly confirmed the partial correlations between the variables, which could be expected. However, there was an exception that is important for the goals of the present study: the path between Religiousness and Reproductive success was not significant in the model. This suggests that the link between religious affiliation and fertility was completely mediated by the planned number of children and (to a lower extent) Age at first birth.

Discussion

The behavioural ecological framework enables the analysis of the evolution of any behavioural trait if the trait in question is genetically transmitted across generations. This can even be applied to complex, socially and culturally influenced traits such as religiousness. However, the trait can be targeted by natural selection only if it is related to evolutionary fitness. Furthermore, one of the fundamental assumptions of behavioural ecology is that individuals adapt to their local environments. The present research sought to explore the relations between religiousness and fitness, the potential mediators of this relation and the environmental conditions that could be involved in it. The study hypothesis was that religiousness is biologically adaptive (i.e. it is positively associated with fitness and other fitness-related outcomes, all except age of first reproduction where negative association was assumed) and that it emerges from harsh environmental conditions. These hypotheses were only partially confirmed. However, the study data provide a broader and more comprehensive view of religiousness in a behavioural ecological context, confirming its adaptiveness in a biological sense. Furthermore, it reveals some of the mechanisms that religious individuals use to achieve higher reproductive success. Finally, the results are implicative for the future life-history theory of religiousness.

The associations between fitness and fitness-related measures

From the viewpoint of behavioural ecology, it is very important to analyse the relations between measures connected with fitness. First of all, reproductive success and parental investment were found to be uncorrelated in the present research. This is not unusual – in fact, a negative correlation could be expected since number of children should be negatively related to parental investment in each of them; this is a major evolutionary trade-off called the 'quantity–quality trade-off' (Lawson & Mace, 2009). The absence of a negative correlation probably stems from the fact that the research was conducted in a low-fertility population, while the magnitude of this trade-off is higher in populations with elevated mean reproductive success (Ross *et al.*, 2016).

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Age at first birth was found to be negatively related to both fitness indicators. This finding confirms earlier findings of a negative directional selection on the timing of first reproduction: individuals who have their first child earlier in their lifetime have higher overall fitness (Tropf *et al*., 2015; Sanjak *et al*., 2018). The desired number of children was positively related to both fitness measures as well. At first glance, this may sound like a trivial finding, but actually it is very important since it shows unique features of contemporary human evolution: fertility in humans is based on, but far from completely determined by, intentional motivation and planning (Johnson-Hanks, 2008). Furthermore, it is at least partially subject to conscious control via contraception and other birth control measures. Finally, the duration of the partner relationship is positively related to reproductive success and negatively related to age at first birth: the longer individuals are in a romantic relationship, the earlier they become parents and they have more children. It is important to note that these links were unchanged when participants' age was controlled in the analysis. Thus, long-term mating is apparently evolutionarily adaptive. This is in line with the theories that assume that long-term mating is a dominant mating pattern in humans since human offspring need elevated care and investment from both parents (Stewart-Williams & Thomas, 2013). In sum, the obtained data regarding the relations between fitness-related outcomes are quite congruent with previous findings and life-histories of contemporary humans.

Behavioural ecology of religiousness

Religious individuals have been shown to desire a higher number of children at the beginning of their reproductive phase, and they have their offspring earlier in their lifetime (although this link was rather weak in the present research) and have higher total fertility in general (this association was pronounced particularly in males, but it did not reach statistical significance in a subsample of females). However, they did not show elevated parental investment. A positive relation between religiousness and parental investment was assumed since religiousness is related to a closeness towards family members and family values in general (Jensen & Jensen, 1993). The absence of this link may suggest that religious individuals are oriented towards offspring quantity but not necessarily offspring quality as a way of optimizing fitness.

A positive link between religiousness and reproductive success has been empirically obtained in previous research (Sanderson, 2008; Blume, 2009; Fieder & Huber, 2016). The present study also found a positive link between religiousness and the desired number of children. These data are in line with a previous finding that shows positive attitudes of religious individuals towards childbearing (Hayford & Morgan, 2008). Furthermore, major religions often advocate a higher family size (Sanderson, 2008). Previous research has also obtained evidence that religious individuals tend to have their first child earlier in their lifetime (Pearce & Davis, 2016). This was confirmed in the present study, although the link was relatively weak (i.e. only marginally significant in multivariate analyses). Finally, religiousness may enable high fitness in a somewhat indirect way: by facilitating longer romantic relationships via commitment to marriage, marital satisfaction and lower risk of divorce (Mahoney *et al*., 2002). However, this link was not detected in the present data and this was the only fitness-related outcome that was not associated with religiousness. It is important to note that desired number of children and age of first birth completely mediated the link between religiousness and reproductive success. This was not expected due to a fact that there could be other mediators of this link; however, this result only highlights the role these two variables have in elevating the fitness of religious individuals.

In sum, the data obtained in the present research are in line with previous results suggesting that religiousness is probably under positive directional selection on fertility. Thus, selection acts positively on the genetic basis of religious attitudes. Note that this does not necessarily mean that higher phenotypic levels of religiousness in the upcoming generations should be necessarily expected. Many complex cultural and environmental factors act on the phenotypic development of religious attitudes and some of them may be opposed to selection. This is why the frequency of

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religious commitment has in fact been found to fall in Western populations (Zuckerman, 2015). The complexity of the biological and environmental factors that shape religiousness prevents the prediction of its phenotypic levels in future populations.

Towards a future life-history theory of religiousness

Previous findings of negative associations between religiousness, sexual permissiveness and restricted sexuality together with positive associations with serial monogamy suggest that religiousness is part of a slow life-history trajectory (Gladden *et al*., 2009; Baumard & Chevallier, 2015; Schmitt & Fuller, 2015). However, this view may be oversimplified. If religiousness emerges from a harsh environment and enables earlier reproduction this would mean that it has the characteristics of the fast life-history trait as well. These associations were obtained in the present research although they were fragile. The positive link between harsh environment and religiousness was heavily dependent on the participants' sex and age. The negative link between religiousness and age at first birth was low in magnitude and marginally significant. However, these associations have been found in previous studies as well, and with more convincing effect sizes (Delamontagne, 2010; Pearce, 2010; Solt *et al*., 2011; Pearce & Davis, 2016). It should be noted that elevated offspring quantity, which is clearly associated with religiousness, is the most important indicator of a fast life-history pathway in the first place. All these data suggest that religiousness indeed has some attributes of a fast life-history trajectory.

The present study was cross-sectional by design, which prevented making conclusions about the causal relations between the measures. However, perhaps *a hypothesis* of religiousness's involvement in life-history trajectories can be made. The existing data suggest that the life-history characteristics of religiousness are contingent on the stages of ontogeny. In earlier stages of development religiousness delays mating activity (expressed, for example, in negative associations between religiousness and the onset of sexual behaviour: Jones *et al*., 2005), which means that it has slow life-history attributes. However, in the reproductive stage itself, it is associated with earlier marriage and reproduction, thus acting as a fast life-history phenotype. When family is constituted, religiousness again turns to the slow life-history trait by decreasing sexual permissiveness and promoting monogamy. Hence, the life-history characteristics of religiousness are different during the ontogeny. This proposition may be labelled as an 'ontogeny-dependent life-history theory of religiousness'. This hypothesis may be tested in future studies using a longitudinal approach.

Limitations and future directions

Some of limitations of the study have already been mentioned. The cross-sectional design of the study did not allow the causal influences between variables to be inferred. This was especially important for the present topic as it would be very important to know when the religious sentiment was developed in ontogeny. Only then can the hypothesis of the different life-history characteristics of religiousness throughout the ontogeny be tested. Another limitation was the sample structure. The study sample was not representative, and probably consisted of more educated individuals with a relatively higher socioeconomic status (this may be the reason why the link between harsh environment and religiousness was relatively weak; environmental harshness was relatively low in the present sample). The sample structure required caution when generalizing the study results to the whole population. Finally, some of the study variables could have been operationalized using a more objective measurement, particularly for harsh environment and parental investment measures. Using self-reported measures made data collection easier, but such measures have issues that may limit their validity (e.g. recollection of the environmental characteristics in childhood).

Suggestions for future research are numerous as the behavioural ecological research of religiousness is still in its infancy. Additional moderators of the religiousness–fitness link can be tested: for example, lack of motivation to use contraception and opposition to abortion, which

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could also lead to higher reproductive success (Bahr & Marcos, 2003). Since previous research has shown that religiousness can elevate not only individual fitness, but inclusive fitness as well (Crespi & Summers, 2014), some form of inclusive fitness (e.g. kin altruism) should be set as a criterion variable in future research. Previous studies have also shown that there is relatively high assortative mating on religiousness (Watson *et al*., 2004): this could lead to multiplicative fitness benefits in religious couples. The present findings suggest that future research, not only for religiousness but also for similar attitudinal dispositions (e.g. traditionalism, conservatism etc.), looks very promising. This would provide a new possibility for behavioural ecology to explore complex human behavioural dispositions and to establish new links between cultural characteristics and fitness-related outcomes in contemporary humans. Having in mind that cultural factors do have an important role in the biological evolution of humans, this could provide new insights into the patterns and consequences of natural selection in human populations.

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References

Alcorta CS and Sosis R (2005) Ritual, emotion, and sacred symbols: the evolution of religion as an adaptive complex. *Human Nature* **16**, 323–359.

Atran S and Norenzayan A (2004) Religion's evolutionary landscape: counterintuition, commitment, compassion, communion. *Behavioural and Brain Sciences* **27**, 713–730.

Bahr SJ and Marcos AC (2003) Cross-cultural attitudes toward abortion: Greeks versus Americans. *Journal of Family Issues* **24**, 402–424.

Baumard N and Chevallier C (2015) The nature and dynamics of world religions: a life-history approach. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151593.

Bering JM (2011) *The Belief Instinct: The Psychology of Souls, Destiny, and The Meaning of Life*. Norton, New York.

Blom G (1958) *Statistical Estimates and Transformed Beta-Variables*. John Wiley and Sons, New York.

Blume M (2009) The reproductive benefits of religious affiliation. In Voland E and Schiefenhovel W (eds) *The Biological Evolution of Religious Mind and Behavior*. Springer, New York, pp. 117–126.

Bouchard TJ Jr (2009) Authoritarianism, religiousness, and conservatism: I 'obedience to authority' the explanation for their clustering, universality and evolution? In Voland E and Schiefenhöven W (eds) *The Biological Evolution of Religious Mind and Behaviour*. Springer, New York, pp. 165–180.

Bourrat P (2015) Origins and evolution of religion from a Darwinian point of view: synthesis of different theories. In Heams T, Huneman P, Lecointre G and Silberstein M (eds) *Handbook of Evolutionary Thinking in the Sciences*. Springer, the Netherlands, pp. 761–780.

Boyer P (2001) *Religion Explained: The Evolutionary Origins of Religious Thought*. Basic Books, New York.

Bulbulia J (2012) Spreading order: religion, cooperative niche construction, and risky coordination problems. *Biology and Philosophy* **27**, 1–27.

Crespi B and Summers K (2014) Inclusive fitness theory for the evolution of religion. *Animal Behaviour* **92**, 313–323.

Delamontagne RG (2010) High religiosity and societal dysfunction in the United States during the first decade of the twenty-first century. *Evolutionary Psychology* **8**, 617–657.

Del Giudice M, Gangestad SW and Kaplan HS (2016) Life history theory and evolutionary psychology. In Buss DM (ed.) *The Handbook of Evolutionary Psychology: Foundations*. John Wiley, Hoboken, NJ, USA, pp. 88–114.

Fieder M and Huber S (2016) The association between religious homogamy and reproduction. *Proceedings of the Royal Society of London B: Biological Sciences* **283**, 20160294.

Figueredo AJ (2007) *The Arizona Life History Battery*. URL: https://arizona.app.box.com/s/1prthk79i0zersjeqylgbrwwyfprju4y (accessed 3rd November 2019).

Gladden PR, Welch J, Figueredo AJ and Jacobs WJ (2009) Moral intuitions and religiosity as spuriously correlated life history traits. *Journal of Evolutionary Psychology* **7**, 167–184.

Granqvist P and Kirkpatrick LA (2013) Religion, spirituality, and attachment. In Pargament KI et al. (eds.) *APA Handbook for the Psychology of Religion and Spirituality*, Vol. **1**. American Psychological Association, Washington, DC, pp. 129–155.

Gurven M von Rueden C Stieglitz J Kaplan H and Rodriguez DE (2014) The evolutionary fitness of personality traits in a small-scale subsistence society. *Evolution and Human Behavior* **35**, 17–25.

Hamilton WD (1964) The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* **7**, 17–52.

Hayford SR and Morgan SP (2008) Religiosity and fertility in the United States: the role of fertility intentions. *Social Forces* **86**, 1163–1188.

Hu L and Bentler PM (1999) Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. *Structural Equation Modeling* **6**, 1–55.

Jensen L and Jensen J (1993) Family values, religiosity, and gender. *Psychological Reports* **73**, 429–430.

Johnson-Hanks J (2008) Demographic transitions and modernity. *Annual Review of Anthropology* **37**, 301–315.

Jones RK Darroch JE and Singh S (2005) Religious differentials in the sexual and reproductive behaviors of young women in the United States. *Journal of Adolescent Health* **36**, 279–288.

Kandler C and Riemann R (2013) Genetic and environmental sources of individual religiousness: the roles of individual personality traits and perceived environmental religiousness. *Behavior Genetics* **43**, 297–313.

Kirkpatrick LA (2005) *Attachment, Evolution, and the Psychology of Religion*. Guilford Press, New York.

Kirkpatrick LA (2015) Religiosity. In Zigler-Hill V, Welling LLM and Shackelford TK (eds) *Evolutionary Perspectives on Social Psychology*. Springer International Publishing, London, pp. 69–79.

Knežević G (2003) *Koreni amoralnosti [The Roots of Amorality]*. Institut za kriminološka i sociološka istraživanja, Institut za psihologiju, Beograd.

Lawson DW and Mace R (2009) Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care. *Evolution and Human Behavior* **30**, 170–183.

Međedović J (2017) Intelligence and fitness: the mediating role of educational level. *Evolutionary Psychology* **15**, 1–6.

Mahoney A, Pargament KI and Tarakeshwar N (2002) Religion in the home in the 1980s and 1990s: a meta-analytic review and conceptual analysis of links between religion, marriage, and parenting. *Journal of Family Psychology* **15**, 559–596.

Neel R, Kenrick DT, White AE and Neuberg SL (2016) Individual differences in fundamental social motives. *Journal of Personality and Social Psychology* **110**, 887–907.

Pearce LD (2010) Religion's impact on the timing of first births in the U.S. In Hummer R and Ellison C (eds) *Religion, Families, and Health in the United States: New Directions in Population-Based Research*. Rutgers University Press, New Brunswick, NJ, pp. 19–39.

Pearce LD and Davis SN (2016) How early life religious exposure relates to the timing of first birth. *Journal of Marriage and Family* **78**, 1422–1438.

Reynolds V and Tanner R (1995) *The Social Ecology of Religion*. Oxford University Press, New York.

Ross CT, Mulder MB, Winterhalder B, Uehara R, Headland J and Headland T (2016) Evidence for quantity–quality trade-offs, sex-specific parental investment, and variance compensation in colonized Agta foragers undergoing demographic transition. *Evolution and Human Behavior* **37**, 350–365.

Rowthorn R (2011) Religion, fertility and genes: a dual inheritance model. *Proceedings of the Royal Society of London B: Biological Sciences* **278**, 2519–2527.

Sanderson SK (2008) Adaptation, evolution, and religion. *Religion* **38**, 141–156.

Sanjak JS, Sidorenko J, Robinson MR, Thornton KR and Visscher PM (2018) Evidence of directional and stabilizing selection in contemporary humans. *Proceedings of the National Academy of Sciences of the USA* **115**, 151–156.

Schmitt DP and Fuller RC (2015) On the varieties of sexual experience: cross-cultural links between religiosity and human mating strategies. *Psychology of Religion and Spirituality* **7**, 314–326.

Solt F, Habel P and Grant JT (2011) Economic inequality, relative power, and religiosity. *Social Science Quarterly* **92**, 447–465.

Stewart-Williams S and Thomas AG (2013) The ape that thought it was a peacock: does evolutionary psychology exaggerate human sex differences? *Psychological Inquiry* **24**, 137–168.

Strayhorn JM and Strayhorn JC (2009) Religiosity and teen birth rate in the United States. *Reproductive Health* **6**, 14.

Tropf FC, Stulp G, Barban N, Visscher PM, Yang J, Snieder H and Mills M (2015) Human fertility, molecular genetics, and natural selection in modern societies. *PLoS One* **10**, e0126821.

Watson D, Klohnen EC, Casillas A, Nus Simms E, Haig J and Berry DS (2004) Match makers and deal breakers: analyses of assortative mating in newlywed couples. *Journal of Personality* **72**, 1029–1068.

Zuckerman P (2015) *Faith No More: Why People Reject Religion*. Oxford University Press, Oxford.

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