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PLEASE CITE AS:

Mededović, J. (2020). Human life histories as dynamic networks: using Network Analysis to conceptualize and analyze life history data. *Evolutionary Psychological Science*, advance online publication. <https://doi.org/10.1007/s40806-020-00252-y>

Human life histories as dynamic networks: using Network Analysis to conceptualize and analyze life history data

Abstract: The examination of multiple life history indicators is essential to evolutionary sciences. However, the statistical analysis of life history parameters' covariation is not apparently clear, due to the statistical limitations of “classic” procedures like Factor Analysis and conceptual problems in interpreting covariation between life-history indicators as latent factors. Here we propose that Network Analysis represents a promising framework for the exploration of life history parameters. First, we briefly describe the basic metric of Network Analysis: nodes, edges, proximities, clustering, centrality indices and small-world estimations. Next, we show the implementation of Network Analysis using the empirical set of life history variables as an example (N=460). We showed that Network Analysis provided: 1) optimal level of information - higher than factor analysis and lower than correlation analysis; 2) findings which are in accordance with the existing life history data; 3) the estimation of age at first birth as a central node in the network; 4) dynamic view of life history events which can represent a solid basis for causal life history models. In sum, Network Analysis shows high potential both for

conceptualizing life history pathways as dynamic networks and for statistical analysis of the covariation between the life history indicators.

Keywords: Life history theory; Network Analysis; factor analysis; human behavioral ecology

Introduction

Life history theory

Fitness is the central target for natural selection, and thus, one of the main features which drive biological evolution. It is defined broadly as the probability of transferring individual genes from one generation to the next (Hunt & Hodgson, 2010). Fitness comprises several components, reproductive success in the first place, but survival/longevity, mating, parenting, as well. If fitness components positively correlated between themselves, the maximization of the fitness function would be relatively straightforward: elevating any of the components would increase others as well. However, this is not the case: fitness components constrain each other - investing in one component prevents organisms from investing in others. These constraints generate evolutionary trade-offs: individuals with higher reproductive success tend to have a shorter lifespan (Jasienska, Bribiescas, Furberg, Helle, & Núñez-de la Mora, 2017), a higher number of offspring diminishes investment per individual child (Gillespie, Russell, & Lummaa, 2008), investing in parenting diminishes effort in finding new mates (Međedović, 2019), delaying reproduction enables somatic investment and resource acquisition but depletes overall fertility (Liu & Lummaa, 2011), and so forth.

Pathways of fitness maximization are heavily dependent on local ecologies. The ecological theory of evolutionary trade-offs and fitness maximization is called life history theory. Two general patterns of fitness maximization have been described (Del Giudice, Gangestad, Kaplan, 2015): in harsh environments with low population density selection favors greater somatic investment in the earlier stages of ontogeny, faster development, earlier start of reproductive activity, earlier reproduction and a higher number of offspring followed by lower parental investment. This pattern of life history indicators has been labeled as the fast life history pathway while the opposite trajectory is depicted as a slow life history. Existing findings are mostly in line with the described relations between harsher ecologies and fast life history pathway - findings show that higher mortality rates (Griskevicius, Delton, Robertson, & Tybur, 2011), lower socioeconomic status (Sheppard, Pearce, & Sear, 2016), violent intergroup conflicts (Mededović, 2019a), the absence of a father (Webster, Graber, Gesselman, Crosier, & Schember, 2014), lack of maternal sensitivity (Dunkel, Mathes, Kesselring, Decker, & Kelts, 2015), and troubled family relations (Chisholm, Quinlivan, Petersen, & Coall, 2005) are associated with fast life history dynamics. However, there are also studies that failed to find some of the theoretically expected associations: e.g. the absence of the relations between the age at first menarche and reproductive success (Hochberg, Gawlik, & Walker, 2011) or the lack of association between family socioeconomic status and pubertal timing (Xu, Norton, & Rahman, 2018). This is a consequence of the immense complexity of human populations and a large variability between the populations as well. Also, the distinction between inter-species and inter-individual level of analysis must be noted. Majority of work in evolutionary biology was performed in capturing differences in life history dynamics between the species; in contrast, evolutionary human sciences are focused on differences between individuals in life history trajectories, paying special attention

to the developmental life history pathways (Nettle & Frankenhuis, in press). However, recent theoretical work pointed out that these two levels of analysis may not be analogous (Stearns & Rodrigues, in press; Zietsch & Sidari, in press). The present manuscript is focused in the latter level of analysis - covariation of life history indicators between individuals.

Analysis of the life history data

Multiple life history indicators must be analyzed simultaneously in order to capture the patterns of fitness maximization. However, it is not clear what analytic techniques should be used in order to achieve this. Correlation analysis is certainly indispensable in this process and represents a starting point in exploration. Nevertheless, correlation analysis has two obvious limitations in this context. Firstly, it can produce only bivariate relations between the variables which could mask more complex associations. Secondly, if the number of variables is high, the correlation matrix will be large with inevitable levels of trivial (noise) information - consequently, this would make the interpretation of the findings more difficult. Multivariate analysis is thus necessary in order to analyze more complex relations between the variables in a more parsimonious manner. However, multivariate analyses, like factor analysis which is one of the most commonly used procedures to analyze the set of variables in a multivariate fashion, have their limitations as well. The first problem of factor analysis is the opposite compared to correlation analysis: collapsing the covariance between the indicators on their latent factors may over-reduce the information about the variables' relations. The second problem is a conceptual one - it is quite hard to conceive the covariation between life history indicators as some latent factors. Life history pathways are dynamic processes emerging in different stages of the

ontogeny; thus, they demand a more dynamic framework in order to properly conceptualize the relations between life history markers.

In fact, the debate regarding the life history conceptualization and measurement already exists in evolutionary social sciences. Until recently, the prevailing opinion was that slow and fast life histories are the opposite pole of a singular latent dimension (Figueredo, Vásquez, Brumbach, & Schneider, 2007; Giosan, 2006). Because of this assumption, inter-individual differences in life history trajectory could be assessed via single measure, where higher scores may reflect slower life history pathway (e.g. Figueredo et al., 2017). However, this view was criticized on various grounds. Researchers questioned the factor modeling procedures that were used to obtain singular life history latent dimension (Gruyter's, & Fleuren, 2018; Copping, Campbell, & Muncer, 2014; Copping, Campbell, Muncer, & Richardson, 2017; Richardson, Sanning, Lai, Copping, Hardesty, & Kruger, 2017; for a reply to critiques see Figueredo, Cabeza de Baca, Black, Garcia, Fernandes, Wolf, & Woodley, 2015). Other pointed out that the indicators used in these studies do not capture biodemographic life history outcomes such are maturation timing, age of first reproduction, number of children, and others; hence, they may have validity problems (Međedović, in press; Sear, 2020). Furthermore, when life history indicators closer to biological events related to reproduction are assessed, several factors are extracted; for example, in a recent research (Međedović, 2018) three factors were obtained when analyzing life histories in young adults: short-term mating, residual reproductive value (loaded by higher expected longevity, higher number of desired children and lower planned age of first reproduction), and health. This debate may be understood as a part of a broader discussion regarding the conceptualization and measurement of human life history, compared to life history studies in other animals (Del Giudice, 2019; Zietsch & Sidari, in press).

One of the scales which assumes unidimensionality of life history indicators, Arizona Life History Battery (Figueredo et al., 2007; Figueredo et al., 2017) is a good example of our previous assertion that it is hard to conceive a latent factor as a cause of the empirical life history variables' covariation (in factor analysis models, latent variables are seen as the causes of the variation in their observable indicators: Bollen & Lennox, 1991). This scale consists of the following life history markers: 1) Insight, Planning, and Control; 2) Romantic Partner Attachment; 3) General altruism; 4) Religiosity; 5) Parental Relationship Quality; 6) Family Contact and Support, and 7) Friends Contact and Support. The Authors of the scale claim that all of these indicators are the manifestations of a singular life history latent dimension with slow and fast life history at its opposite poles. But *what is* this singular dimension? We cannot think of a single concept which can cause covariation between all these variables. The authors may claim that the cause of covariation is natural selection itself (e.g. Figueredo, de Baca, & Woodley, 2013), but selection is a process acting on a population level, not some latent variable. Hence, we believe that the view on the life history indicators as states and events interacting with each other as a part of a dynamic network is a viable alternative to the standard latent variable conception on life history. Thus, we propose another way to conceptualize human life histories and to analyze life history data - the Network Analysis.

Basic metrics of the Network Analysis

It is not our goal to provide a full overview of Network Analysis - detailed reviews and tutorials on this topic already exist (e.g. Costantini, Epskamp, Borsboom, Perugini, Möttus, Waldorp, & Cramer, 2015; Epskamp, Borsboom, & Fried, 2018; Hevey, 2018). Our aim is to

describe the fundamental concepts and metrics of the Network Analysis in order to show its suitability for the life history data. Network models are graphical models where analyzed entities (in our case the life history indicators) are represented as *nodes*. The relations between them are shown as the *edges*. If the edges are thicker, the relations between the variables are higher in magnitude. Frequently the edges are colored differently in order to show the sign of the relations - red edges represent negative, while blue edges represent positive relations. The relations in question may be based on different statistics but the most frequent estimates are correlations or partial correlations between the variables - these coefficients represent the *weights* of the edges. The distances between the variables in the graph are also relevant since the variables with a higher number of interconnections are set to be closer in space and vice versa. An example of a network model can be seen in Figure 1. It is also important to note that the model presented in Figure 1 is *undirected*: the relations between the variables are not represented by arrows. This means that the causality in the relations has not been assumed: edges are interpreted simply as associations between the measures.

- Figure 1 about here -

In order to provide the optimal level of information, the estimation of the relations between variables often applies some form of penalization of the edges with low magnitude coefficients. This is similar to the frequent practice in factor analysis, where researchers do not show coefficients below .30 in order to facilitate interpretation. The optimization of the network edges is mostly done using the LASSO operator (least absolute shrinkage and selection operator: Friedman, Hastie, & Tibshirani, 2008). The goal of the LASSO estimator is to remove spurious

connections and to highlight the most important edges in the data; this results in a more parsimonious model which decreases the probability of Type 1 error. It has been shown that the LASSO method operates well in the estimation of networks based on partial correlations (Fan, Feng, & Wu, 2009).

When the network is estimated from the data, the next step in the analysis is to evaluate the importance of every node in the network. This is usually done by analyzing the various indicators of node centrality (Borgatti, 2005; Landherr, Friedl, & Heidemann, 2010; Rodrigues, 2019). The most common centrality indices are: 1) degree - number of connections of the target node with other nodes in the network; 2) strength - number of connections of the target node adjusted for the average weight of the target node (usually calculated as a product of these two parameters); 3) closeness - estimation of the position of the target node in the network based on direct and indirect connections with other nodes; 4) betweenness - the position of the target node in the shortest paths between other nodes in the network (the importance of a certain node to serve as a bridge between other nodes); 5) clustering - the centrality of the target node in a cluster of nodes (if a node has a high clustering coefficient its removal from the network decreases the ability of surrounding nodes to affect each other).

The similar logic of clustering can be applied not only to specific nodes but to the whole network. If the network comprises nodes which all have similar number of edges than the clustering coefficient of such a network is low. However, networks may be composed of the nodes which are clustered in groups: a set of nodes can have a high level of interconnections within the cluster, but a smaller number of relations with the other nodes or clusters. The latter networks are labeled as "small worlds" networks (Watts & Strogatz, 1998).

Thus, the smallworldness coefficient represents a basic indicator of the network's total topography.

The application of the Network Analysis in human behavioral ecology

We believe that Network Analysis is especially suitable for the exploration of life history pathways. It can provide the conception of life history trajectories as a dynamic set of biologically relevant events and traits emerging throughout organisms' ontogeny. Furthermore, statistical properties of Network Analysis, especially the centrality measures, may be fruitful in detecting the key life history markers - the ones which represent crucial events in life history pathways. Interestingly, Network Analysis has been used in animal behavioral ecology before; however, its' application in this field was somewhat different. Network Analysis has been applied in the exploration of social networks in animals, thus, the nodes in these networks are individuals, not variables (Croft, James, & Krause, 2008; Krause & Ruxton, 2010). By analyzing the interaction between individuals, the researchers can gain insight into group dynamics and its consequences, including fitness outcomes. This approach is especially fruitful when the analyzed groups do not comprise too many individuals, groups of monkeys for example (e.g. Sade, 1972). However, it has lower application potentials in the context when the population or sample size is very high (several hundreds or thousands of individuals) which is the frequent case in human behavioral ecology (however, note that this application of Network Analysis is suitable for human behavioral ecology research which rely on ethnographic approach: evolutionary anthropologists could examine social interaction in small scale societies to estimate its fitness-related consequences). As far as we are aware, Network Analysis was never applied to the

exploration of life history indicators' relations (when the nodes in the network are life history events), nor in human nor in animal behavioral ecology. However, we are not the first to propose the application of Network Analysis in this research field: other authors have recognized the potentials of Network Analysis to elevate our understanding of human life histories as well (Gruijters, & Fleuren, 2018; Richardson et al., 2017).

In the following part of the manuscript, we will present an empirical example of the Network Analysis in human life history research. First, we will calculate bivariate relations between examined life history measures and explore their latent space by using Factor Analysis. Afterward, we will present the Network model estimated on the same data. We will finish with the discussion of the findings, comparing some features of the Factor Analysis and Network Analysis and by providing recommendations for future research.

An empirical example: analyzing the relations between life history indicators

Sample and procedure

The study sample consisted of 460 individuals (54% females). The participants were the parents of psychology students at a college in Belgrade, Serbia. Students carried the questionnaires to their parents to fill them in as a part of a psychology course they were taking. Participation in the research was voluntary, both for the students and their parents (students received additional points if they volunteered to participate in the research). The questionnaires were put in envelopes and sealed by study participants after they filled them in, in order to increase anonymity. The participants in this sample were not related - we used observations from

only one parent per student (randomly assigned). Parents have been chosen as the participants in order to measure multiple life history indicators like number of children and grandchildren, parental investment and others (see Measures section). The mean age of participants was 52.18 years: participants' age suggests that they were at the end of their reproductive phase during the time of data collection. Participants were more highly educated than average: 47.4% of participants had finished college, 30.4% finished high school, while the rest had finished only elementary school.

Measures

It should be noted that there is a current debate on how to measure human life histories (Međedović, in press; Sear, 2020). Our view is that core set of life history measures should operationalize reproductive ecology of modern humans: desired and observed number of children, age of first and last reproduction, and others reproductively-related outcomes. Of course, environmental conditions should be assessed as well together with the indicators of mating and parenting behavior. In the present research we widened this set of measures by including the variables related to health/longevity, namely self-protection and disease avoidance. Life histories should be operationalized via broad set of indicators in order to capture wider and more detailed picture of life history trajectories; however, every indicator should be closely related to major evolutionary trade-offs in order to corroborate the validity of indicators.

Hence, we collected data about 14 life history indicators roughly divided into five groups:

Harsh environment was operationalized using two scales. *Family dysfunction* was measured using the Weak Socialization scale from the AMORAL inventory (Knežević, 2003). It

measures various dysfunctional processes in the family during a participants' childhood, operationalized by five items. It includes indicators of parental maltreatment (e.g. "My parents beat me frequently when I was a child") as well as neglect ("My parents did not care much about what I did when I was a child"). Childhood *Poverty* (Međedović, 2019b) was explored as well. It is a four-item scale (item examples: "My family never had enough money", "Growing up, there was always a threat that my parents would be out of work").

We used the Fundamental social motives questionnaire (Neel, Kenrick, White, & Neuberg, 2016) to measure self protection motives, care for own kin and mating effort. *Self protection* was measured by two scales: The *Self protection* scale (six items; item example: "I am motivated to protect myself from dangerous others") and *Disease avoidance* (six items; item example: "I avoid places and people that might carry diseases").

Two scales have been used for the assessment of kin care as well. *Kin care-family* assesses the general care and investment in family members (6 items; item example: "Being close to my family members is extremely important to me"). *Kin care-children* measures the relations with own biological children (6 items; item example: "I often think about how I could stop bad things from happening to my children"). The latter scale may be used as a proxy measure for parental investment (Međedović, 2019).

Similarly to previous concepts, mating effort had two indicators: *Mate seeking* (6 items; item example: "I spend a lot of time thinking about ways to meet possible dating partners") and *Mate retention* (6 items; item example: "It is important to me that my partner is emotionally loyal to me"). Both AMORAL and Fundamental social motives inventories are the self-report questionnaires with a standard Likert-type scale ranging from 1 to 5: 1 stands for "I disagree completely" while 5 stands for "I agree completely".

Finally, we measured several indicators related to sexual behavior, partner relations and reproduction: 1) *Age at first sex* (participants were asked to write how old they were when they had their first sexual intercourse); 2) *Age at first reproduction* (the age when they had their first child); 3) *Desired 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?"); 4) *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 we asked them to write the longest relationship with any of them); 5) *Number of children*, and 6) *Number of grandchildren* they have.

Results

Descriptive statistics and correlations between the examined variables

First, we calculated the descriptive statistics for the analyzed measures, the reliabilities (Cronbach's coefficients of internal consistency) for the multi-item measures, and the correlations (Pearson's coefficients of linear correlation) between the analyzed variables. These statistics are shown in Table 1. Since large number of analyzed variables showed deviation from the normal distribution (which is expected, especially for the count data, but for measures of environmental harshness, mating, and parental investment as well - see Međedović, 2019), we normalized the variables using the Blom's algorithm (Blom, 1958) before further analyses.

- Table 1 about here -

Latent space of the life history indicators

Psychometric studies in life history usually identify a single latent dimension capturing the variation of life history indicators (Figueredo et al., 2007; Figueredo et al., 2017). Hence, we first tried to fit a model with a single latent factor explaining the variation of observed life history measures. We used exploratory maximum likelihood analysis to obtain a single-factor solution from the data. This solution had relatively low fit: CFA: $\chi^2(77)=310.48$; $p<.001$; NFI=.40; GFI=.93; RMSEA=.08. The reason for this is the fact that many empirical life history indicators had low loadings on a single latent factor which can be seen in Table 1. Loadings above .30 were shown by Kin Care-Family and Children, Mate retention (positive loadings), Mate seeking, and Family dysfunctions (negative loadings).

Since a single-factor model failed to adequately describe data we explored the solution with several factors. We conducted parallel analysis to estimate the number of factors which should be retained. This algorithm estimated that four latent factors explain significantly more variance of original indicators than their random counterparts (the percentage of explained variance was 8.4% for the fifth empirically extracted factor while it was 9.8% for the randomly generated factor). The fit indices for this model were relatively high: $\chi^2(41)=80.16$; $p<.001$; CFI=.90; GFI=.99; RMSEA=.05. Empirically extracted factors were then rotated in the promax position in order to estimate the correlations between them. The pattern matrix of extracted factors is shown in Table 2.

- Table 2 about here -

The first extracted component is quite complex: it is comprised of indicators of parental investment, care for family members in general, beneficial environmental conditions, and the tendency for prolonging the relationship with the romantic partner. The second factor was loaded by the duration of the longest partner relationship, a higher number of grandchildren, and delayed onset of sexual behavior. The third factor was most highly loaded with indicators of self protection. Finally, the fourth factor was constituted by a lower age of first reproduction followed by higher desired and observed number of children. There is a pattern of low positive correlations between the extracted components.

Network model of life history indicators

We used the *qgraph* R package (Epskamp, Cramer, Waldorp, Schmittmann, & Borsboom, 2012) to build the network model from the present data. The network was built on the partial correlations between the variables; adaptive LASSO optimization (Zou, 2006) was implemented in order to provide a parsimonious model. Simulation studies showed that adaptive LASSO is especially good in reducing the chance of false positive results in the estimation of network edges (Krämer, Schäfer, & Boulesteix, 2009). Adaptive LASSO can be implemented via the *parcor* R package (Krämer et al., 2009). The network model of life history indicators with LASSO optimization is shown in Figure 2.

- Figure 2 about here -

We can see that the variables are roughly grouped in an expected manner. The highest associations emerged between Family dysfunctions and Poverty; Care for family and Children; Self Protection and Disease avoidance and the negative correlation between Age at first reproduction and the Number of children. However, there are interesting deviations from expected patterns as well. Age at first sex was not highly associated with other indicators of mating – it was positively related to Self protection and Age at first reproduction. The Number of grandchildren was not related to Number of children when all other variables are controlled in the analysis, however, it was still positively associated to the Relationship duration and it had a low negative association to the Age at first birth. The network clearly shows that Childhood poverty is not related to any other nodes in the network except via dysfunctions in family relations

The stability of the network can be estimated by calculating confidence intervals for the edges' weights. This is usually done by bootstrapping (Epskamp et al., 2018). This procedure allows to estimate the accuracy of the weights (lower the confidence interval is - the estimation is more accurate) and to compare weights between themselves (if the confidence intervals between two weights do not overlap, we may conclude that the weights coefficients differ significantly). The estimation of the confidence intervals for the edges is performed in *bootnet* R package (Epskamp et al., 2018). The graphical representation of the confidence intervals for edges weights is shown in Figure 3. We can see that the intervals which do not overlap with zero are quite wide which means that the estimation of edges weights should be interpreted with caution since they may differ from the obtained values.

- Figure 3 about here –

Next, we calculated three centrality measures for the network nodes: strength, closeness, and betweenness. The values of these measures for every node are shown in Figure 4. The analysis distinguished three nodes as the most central in the network: 1) Age at first reproduction has the highest strength and closeness; 2) Relationship duration has the highest betweenness, with two other indicators also high; 3) Kin care - family has all three indicators relatively high compared to the other nodes.

- Figure 4 about here –

Finally, we explored the overall topography of the network by estimating the degree to which the network corresponds to the small-world clustering structure. The smallworldness index we obtained was 0.87 which indicates that the network does not contain clear and distinctive clusters (the smallworldness index > 3 would indicate that the network is structured in clusters, while values between 1 and 3 would indicate they are considered as borderline: Humphries & Gurney, 2008).

Discussion

The main results of network analysis

The goal of the present manuscript is not to provide novel findings of human life history associations. However, it is important to analyze the present results in the context of existing life history data in order to examine the structure of obtained network. The present data showed

negative relations between Family dysfunctions, the onset of sexual behavior, mate retention and general care for biological relatives. These data are in accordance with a number of studies that detected associations between harsh environment and fast life history indicators (e.g. Dunkel, Mathes, Kesselring, Decker, & Kelts, 2015; Kogan, Cho, Simons, Allen, Beach, Simons, & Gibbons, 2015; Mell, Safra, Algan, Baumard, & Chevallier, 2018; Međedović, 2019a). Interestingly, in our data, the crucial indicator of environmental harshness was disrupted family relations while economic poverty did not have direct associations with other life history markers, except via dysfunctional family relations.

Age at first reproduction, long-term romantic relations and the desired number of children were the most important predictors of the participants' number of children. The negative link between age at first birth and reproductive success is quite robust and it has been reported in numerous studies (e.g. Sanjak, Sidorenko, Robinson, Thornton, & Visscher, 2018; Sheppard, Pearce, & Sear, 2016; Tropf, Stulp, Barban, Visscher, Yang, Snieder, & Mills, 2015). Similarly, previous studies showed significant positive associations between planned or intended fertility and observed reproductive success (Miller, Bard, Pasta, & Rodgers, 2010; Miller, Rodgers, & Pasta, 2010). This relation reflects the fact that contemporary humans can intentionally plan their reproduction and control their fertility, probably by using modern birth control and contraceptive technology. However, this association is far from perfect (as shown by other studies as well, see for example Morgan & Rackin, 2010) which means that there are many other factors which influence observed fertility.

Age at first reproduction and relationship duration have been shown to be the most important traits for understanding the variance in the number of grandchildren; self-protection motivation is the third node in the network which is connected to the number of grand-offspring.

This finding is in line with theoretical notions that long-term mating may be especially beneficial for fitness since it enables biparental care for offspring (Stewart-Williams & Thomas, 2013). Self-protection may be viewed as a specific type of somatic investment aimed at elevating longevity/survival as a fitness component. Thus, it may elevate the number of grandchildren by enabling grandparental investment, which is detected in both traditional and industrial societies (Coall & Hertwig, 2010). Note that the long-term mating was connected to parental investment as well (measured by the Kin care - children scale) which is in line with the previous hypothesis.

Age at first reproduction was negatively related to general kin care, self-protection, number of children and grandchildren, and positively to age at first sexual intercourse and relationship duration. This is why it is not surprising that it has been distinguished as the most central node in the whole network: it had the highest values on strength and closeness centrality indicators. Researchers in human behavioral ecology have already assumed that age at first reproduction represents one of the central life history traits (Liu & Lumma, 2011) - it is involved in many evolutionary tradeoffs including the fertility-longevity tradeoff (Hayward, Nenko, & Lummaa, 2015). The most central nodes beside age at first birth were care for biological relatives and relationship duration. The central role of the former suggests that close family ties and intense interaction between family members are important in regulating various life history outcomes. Relationship duration turns out to have high centrality since it is connected to several fitness-related outcomes like the onset of sexual behavior, age at first birth and the number of both children and grandchildren.

The small-world analysis showed that the basic topography of the network is closer to more evenly distributed connections in the network than to a highly clustered one. This result probably emerged because many nodes are estimated to be non-different from zero. This finding

is in line with the previously obtained bivariate associations between the biodemographic life history indicators which reveal correlations of small magnitude with many nonsignificant associations in matrices (e.g. Međedović, 2018; 2019a; Kogan et al., 2015; Mell et al., 2018; see Table 1 as well). It can be expected that the connections between the life history indicators should be low and in many case non-existent for at least two reasons: 1) in low fertility populations the tradeoffs are relatively low in magnitude - this is why the tradeoffs can be more easily detected in natural fertility populations where mean reproductive output is high (Gagnon, Smith, Tremblay, Vézina, Paré, & Desjardins, 2009; Meij et al., 2009); 2) our participants mostly come from a higher socio-economic background - on the contrary, evolutionary tradeoffs are larger in magnitude in harsh environmental conditions (Gillespie et al., 2008). This is why we believe that the estimated topography of the network reflects the real state of affairs, at least in post-industrial, low fertility populations belonging to WEIRD countries.

The estimation of the nodes' stability produced wide confidence intervals which warn us that true values of the nodes may differ from the estimated ones. This finding poses a question of the networks' replicability: some authors stated that empirically estimated networks have low replicability (Forbes, Wright, Markon, & Krueger, 2017). However, others replied that if proper methodology and formal statistical tests are conducted to test replicability, the networks turn to be quite stable (Borsboom, Fried, Epskamp, Waldorp, van Borkulo, van der Maas, & Cramer, 2017) with high correlations between network structures and centrality estimates (Fried et al., 2018). On the other hand, when assessing life history networks, we must ask if we should expect high replicability in the first place. Associations between the life history indicators should be highly variable among populations as a result of many known and unknown ecological and biological parameters. If these associations are variable, the network structure will be variable as

well. In fact, these variations in network nodes and centrality indices may be quite important for our understanding of life history evolution in the first place: we should not expect high stability of the results between the populations but invest efforts in explaining the differences between the networks, i.e. finding causes which lead to different associations between the nodes or their centrality in different populations.

Interpreting networks: comparing the network edges and zero-order correlations

Network edges are estimated via partial correlations between the variables. Hence, it is useful to compare the network model with zero-order correlations, similarly to other multivariate analyses like multiple regression or structural equation modeling. In order to provide an example of such analysis we focused only to a part of network: relations between the measures of reproductive ecology (Desired number of children, Age at first reproduction, Number of children, Number of grandchildren) and kin investment (Kin Care Children and Kin Care Family). Correlation matrix showed similar relationships between these measures: both Kin Care measures correlate positively with Desired number of children and negatively to Age of first reproduction. However, only the relations between Kin Care Family, Desired number of children, and Age of first reproduction were replicated in network model - associations regarding Kin Care Children were not represented as the network edges. This suggest that despite the theoretical importance of care for children (as an indicator of parental investment), care for family in general (which partly captures wider psychosocial processes of kin care) is more fundamental life history trait, at least for individuals approaching post-reproductive stage. Note that this conclusion is confirmed by the

centrality analysis as well. Hence, we may view care for children as a part of general kin care - a finding which in functional sense may point us to the concept of inclusive fitness.

Network and factor analysis: similarities and distinctions

Both Network and factor analysis estimate the relations between the variables in a multivariate fashion. This is certainly a more appropriate way of data analysis since true associations between the variables may be obscured in a bivariate analysis. Furthermore, these two analytical techniques produced some similar findings as well. For example, both analyses showed that the unidimensional solution for the latent structure of life history indicators is not the optimal one – the solution consisted of only one factor had poor fit which was caused by the fact that majority of variables had low loadings on this factor. In fact, the associations between the measures are low and sparse (as it can be seen in the correlation matrix) which resulted in a four-dimensional solution in EFA (it is important to acknowledge low loadings of many variables on their latent factors - in some cases the highest loadings of variables on any factor were lower than .30) and low smallworldness index in Network Analysis. Note that the percentages of observable indicators' variance that are explained by factors suggest that unidimensional solution is inappropriate as well: explained variance by all four factors is high and it decreases gradually with every subsequent extracted factor; in contrast, the presence of a general factor would be reflected in a disproportionally high percentage of explained variance which is attributable to the first extracted factor, compared to others. Some of the detected associations are quite similar as well: both analyses showed inverse associations between mate retention, Kin care – family, and environmental harshness, highlighted the associations between desired and observed number of

children and age of first reproduction and so forth. So, if we do analyze the latent space of life history data, the findings of the current study are in line with the multidimensional solutions of life history indicators' latent space (Međedović, 2018; Richardson et al., 2017) and against the unidimensional views of human life history (Figueredo et al., 2007; Figueredo et al., 2017; Giosan, 2006).

There are some important differences between the two analyses as well. First of all, there are discrepancies in the results: factor analysis showed that the age at first sex loaded on the same factor together with relationship duration and the number of grandchildren; however, age at first sex was not directly related to the number of grandchildren in the Network Analysis, only indirectly via relationship duration. Similarly, economic poverty was not directly related with any other life history outcome except via dysfunctional family relations – a finding which was masked in factor analysis results. Secondly, it is apparent that Network Analysis provides a higher amount of information regarding the connections between the variables. Factor analysis cannot tell us anything about the relations between specific variables which belong to different latent entities – it can only provide the correlations between the factors themselves. Finally, some of the extracted factors are rather hard to interpret. For example, the first extracted factors gather the markers of environmental harshness, mating effort and the indicators of fitness itself like parental investment (care for children). It stretches from childhood environment to mating-parenting tradeoff. It is unlikely that we can describe these relations via a single latent variable – it is much more appropriate to depict them as a dynamic process emerging in different stages of ontogeny.

The difference can be observed in the analysis of the most “important” indicators in life history trajectories as well. We can compare the results of two analysis by examining the

measures which have the highest loadings on a single-factor solution and centrality indices from the network analysis. The highest positive loadings in the unidimensional solution have Mate retention, Kin Care-Family and Children; the highest negative loadings have Mate seeking and Family dysfunctions. Note that this result is conceptually plausible – it is quite probable that these are the most important life history features for individuals approaching post-reproductive age. However, this factor may be the artefact of measurement method as well – all the variables with highest loadings on the single factor are measured by the multi-item self-report scales. So, the shared variance between them may partly be based on the shared measurement method. On the other hand, the centrality analysis identified the age of first reproduction, the duration of longest relationship and Kin Care Family as the central nodes in network. We already highlighted the crucial status which age of first reproduction has in life histories (Liu & Lumma, 2011); recent research revealed the associations between longest partner relationships (as the measure of long-term mating) and reproductive fitness as well (Međedović, 2019b). The differences between the results of two analyses should not be surprising – they are based on different metrics. Centrality analysis finds the nodes which are crucial for holding the network together – they are the ones which, if removed, the network structure is affected the most. The results also suggest that the centrality indices are less affected by measurement method, because of three identified nodes one is measured by a multi-item self-report scale while the other two are exact biodemographic data. Hence, factor and network analysis provide different results in identifying the crucial indicators of human life histories and this can affect the conclusions the researchers make in analyzing life history dynamics.

Network and factor analysis: is the debate over?

It seems that Network Analysis provides both conceptual and statistical advantages compared to factor analysis (we believe that this could be generalized to other “classic” multivariate analyses such as cluster or correspondence analysis). However, the usage of factors may still be appropriate in a slightly different context. For example, if a researcher wants to study the variation in reproductive fitness, she/he may use latent variables extracted from empirical indicators of reproduction. Usually, researchers analyze only reproductive success as a proxy measure for fitness; however reproductive fitness certainly would be better estimated by extracting the common variation of several indicators related to reproduction, e.g. number of children and grandchildren, and age at first birth. If the researcher does not want to make assumptions about the latent sources of the reproductive fitness indicators’ variance, component analysis may help to better operationalize reproductive fitness and to use more robust and comprehensive variables in the analysis. But in fact, factor analysis is appropriate in this case as well. It is quite easy to conceive the unobserved latent cause of the covariation between these phenotypic measures – their shared genetic underpinnings. There is a perfect genetic correlation between number of children and grandchildren (Zietsch, Kuja-Halkola, Walum, & Verweij, 2014). Furthermore, there is a genetic correlation between age of first reproduction and number of children (Sanjak et al., 2018; Tropf et al., 2015) as well. Hence, the covariation between these three phenotypic traits may partially be a consequence of the pleiotropic effects of the same set of genes; hence, the usage of factor analysis in this context is conceptually appropriate. However, if the relations between life history indicators are the primary goal of the research, we believe that Network Analysis is a more suitable analytical framework.

More generally, latent variables and network approaches should not be seen as mutually exclusive but complementary. These two modeling approaches have different focuses (e.g. the former focuses on the variance which is shared across the whole set of analyzed variables while the latter highlights the unique variance shared by a pair of variables) and different shortcomings (e.g. the former strongly relies on local independence assumption and generally makes exploratory analysis more complicated while the latter excludes the existence of latent entities). Hence, they could be integrated into the unifying modeling procedure which has a potential to overcome these shortcomings. Two approaches have been proposed so far as the result of latent modeling and Network Analysis integration: 1) *latent network modeling*, where a network between latent rather than observable variables is estimated, and 2) *residual network modeling*, where a network between residuals of the latent variables has been estimated (Epskamp, Rhemtulla, & Borsboom, 2017). This approach can be implemented to life history data as well. If we assume that life history indicators are manifestations of latent underlying causes (e.g. genes or physiological processes), latent network modeling allows us to keep latent variables in the analysis and consider them as network nodes. Our impression is that modeling only observable variation of the life history data is more beneficial due to a large number of low or non-existent associations between them, but future empirical research will show if latent network modeling is more suitable for the analysis in this field, compared to standard Network Analysis.

Networks with and without LASSO optimization

LASSO is indeed useful tool in analyzing networks with large number of nodes: it provides parsimonious view on their relations, i.e. detects non-spurious edges which carry the

essential information about the network. However, researchers should inspect both the networks with and without LASSO optimization. This is due to a fact that LASSO procedure may remove an edge which does exist in empirical data (Epskamp, Kruis, & Marsman, 2017); hence, it may lead to Type 2 error. An example in present network is the edge between two indicators of reproductive success - number of children and number of grandchildren: there is a positive zero-order correlation between these two measures (although it has quite low magnitude; this is a consequence of the fact that low number of our participants has grandchildren), but it is removed in the LASSO optimized network. However, the link between these variables certainly exists - one cannot have grandchildren if does not have children in the first place! Hence, although not spurious, this association was eliminated in the LASSO network which clearly warns us against relying only on optimized multivariate analysis: bivariate correlations, non-optimized and optimized networks should be analyzed simultaneously in order to obtain the most precise information.

What else can you do with networks?

We showed only the basic application of Network Analysis, aiming to introduce this technique to human behavioral ecologists. By examining relevant literature other applications of this method can be easily conceived. For example, researchers may focus on a specific variable with an unknown or ambiguous position in a human life history framework (e.g. height or body mass, personality traits like explorative tendency, impulsiveness, etcetera.) and empirically analyze its position in the network: the connections with other nodes, centrality indices and the network structure if the variable is removed from the network. Secondly, researchers may

compare networks in a context where there should be predictable differences in life history trajectories. For example, the networks composed of the same nodes may be compared in males and females or between individuals belonging to different populations differing in harshness, complexity or fertility regimes. Finally, there are other features of Network Analysis which were not described here like community detection (a function similar to factor analysis) or removal of the covariates in the network framework itself (Dalege, Borsboom, van Harreveld, & van der Maas, 2017).

Towards the directional network models of human life history

The network model we built using the present data was undirected: the edges did not represent causal relations but only associations without assumed causality. However, it is apparent that life history data can involve causal assumptions about the edges of the network. The causal relations can be based at the Granger causality at least (Granger, 1969) - some of the life history events precede others in ontogeny. Despite the appeal of directed networks of human life history pathways, it must be noted that directed networks suffer from at least two pitfalls compared to undirected ones. The first one is a statistical limitation: the networks with and without causal edges will have the same fit to the data (Epskamp et al., 2018), however, causal models have more assumptions and thus break the principle of parsimony. Secondly, causal models always suffer from the fact that there are non-measured variables which may be responsible for the relations between the observed variables, even the causal ones. In the case of life history, the most important confounding variables are the genetic variants which contribute to the phenotypic expressions and the ontogenetic triggering of life history events (Kirk, Blomberg,

Duffy, Heath, Owens, & Martin, 2001). However there have been improvements which may help to solve this problem - the data of life history traits' genetic underpinnings are accumulating rapidly (Barban et al., 2016; Fernández-Rhodes et al., 2018), including the causal influence between the life history outcomes (Day et al., 2016). A simple causal path may start with genetic data, individual characteristics in early ontogeny (e.g. body mass at birth), and environmental conditions in childhood. These conditions may be explored as causal determinants of life history events in adolescence like pubertal timing, the onset of sexual behavior, and mating patterns. Finally, both sets of measures can be further modeled as the sources of causal influence on the traits related to reproduction, parental investment, and longevity. Thus, despite additional problems in building causal life history networks, this should be the goal to aspire to in the Network Analysis of life history traits.

Concluding remarks

Life history theory represents one of the central conceptual frameworks in evolutionary sciences. It has been frequently implemented in evolutionary social sciences during the past several decades; however, there is ongoing debate on the applicability of life history to explain inter-individual differences (Del Giudice, 2019; Zietsch & Sidari, in press), the latent structure of life history indicators and its measurement (Međedović, in press; Sear, 2020). We believe that Network Analysis is a fruitful analytical framework which can contribute to these debates and consequently facilitate further advances in life history theory and evolutionary human sciences in general.

Conflict of interest statement:

Author states that there is no conflict of interest.

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Table 1

Descriptive statistics, reliabilities and the correlations between the examined measures

	M(SD)	α	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. Family dysfunctions	1.98(0.85)	.77													
2. Poverty	2.45(0.82)	.64	.32**												
3. Self protection	2.90(0.83)	.82	.07	.10*											
4. Disease avoidance	2.83(0.87)	.83	-.05	.09	.42**										
5. Mate seeking	1.91 (0.87)	.74	.12**	.12*	.07	.13**									
6. Mate retention	4.40 (0.58)	.64	-.25**	-.04	.10*	.06	-.25**								
7. Relationship duration	23.64(9.56)		-.02	.06	-.06	-.03	-.25**	.06							
8. Age at first sex	18.91(2.95)		-.10*	-.04	.11*	.04	-.11*	.06	.18**						
9. Desired number of children	2.59(1.21)		.05	.09	.10*	.04	-.04	.06	.01	-.01					
10. Age at first reproduction	27.29(4.79)		-.05	-.01	-.12*	.08	.09	-.07	.11*	.09	-.06				
11. Number of children	2.21(2.65)		.03	-.01	.06	.01	-.06	.03	.12**	.02	.35**	-.30**			
12. Number of grandchildren	0.21(0.61)		.01	-.02	-.10*	-.04	-.07	.03	.25**	.03	-.01	-.07	.09*		
13. Kin Care-Family	4.62(0.57)	.76	-.21**	-.05	.05	.04	-.19**	.26**	.13**	.08	.13**	-.17**	.10*	.00	
14. Kin Care -Children	4.52(0.51)	.64	-.14**	-.06	.20**	.17**	-.12*	.17**	.10*	.14**	.10*	-.10*	.07	.02	.44**

Notes: * - $p < .05$; ** - $p < .01$

Table 2

Extracted latent factors of life history indicators

	Single factor solution	Four factor solution			
		1. Beneficial environment/Kin care	2. Long term reproductive success	3. Self protection	4. Short term reproductive success
Random % of explained variance		17.7	13.9	12.0	11.3
Empirical % of explained variance		14.4	13.1	12.0	10.9
Desired number of children	.17	.01	.01	.10	.19
Self protection	.17	-.07	-.06	.67	.11
Disease avoidance	.13	.02	-.05	.65	-.14
Mate seeking	-.32	-.31	-.20	.18	-.11
Mate retention	.41	.42	-.01	.06	.04
Kin Care-Family	.67	.52	.05	.04	.22
Kin Care-Children	.59	.43	.02	.25	.14
Number of children	.18	-.06	.14	-.02	.44
Number of grandchildren	.06	-.03	.26	-.11	.10
Age at first reproduction	-.19	.03	.10	.09	-.66
Age at first sex	.19	.17	.15	.13	-.11
Relationship duration	.23	-.03	.98	.01	-.05
Family dysfunctions	-.33	-.58	.08	.07	.23
Poverty	-.12	-.37	.11	.19	.13
1.		1			
2.		.20**	1		
3.		.14**	.04	1	
4.		.24**	.04	.18**	1

Notes: the results of parallel analysis are shown in the first two rows; correlations between the components are shown in the last four rows; ** - $p < .01$.

Figure 1
Hypothetical Network model consisted of five variables
Notes. Numbers may represent correlations or partial correlations between the variables.

Figure 2
Network model of life history indicators with LASSO optimization

Notes: green line represent positive correlations; red lines represent negative correlations; thickness of the lines correspond to the magnitude of the correlations; SPROT - Self protection; RELD - Relationship duration; POV - Poverty; NGRAN - Number of grandchildren; NCHIL - Number of children; MSEEK - Mate seeking; MRET - Mate retention; KCF - Kin care family; KCC - Kin care children; FDYS - Family dysfunctions; DISAV - Disease avoidance; DESCH - Desired number of children; AFS - Age at first sex; AFR - Age at first reproduction

Figure 3

Bootstrapped confidence intervals for the network edge weights

Notes: The red line indicates sample values; the black line indicate bootstrapping means; confidence intervals are shown as gray lines; the edge weights are shown on the y axis but the labels are removed to avoid cluttering.

Figure 4

Centrality indices for the network nodes

Notes: z scores of centrality indices are shown on x axis; SPROT - Self protection; RELD - Relationship duration; POV - Poverty; NGRAN - Number of grandchildren; NCHIL - Number of children; MSEEK - Mate seeking; MRET - Mate retention; KCF - Kin care family; KCC - Kin care children; FDYS - Family dysfunctions; DISAV - Disease avoidance; DESCH - Desired number of children; AFS - Age at first sex; AFR - Age at first reproduction