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The Position of Body Mass in a Network of Human Life History Indicators

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Abstract

Body mass is widely recognized as a morphological trait which is important for fitness optimization both in humans and other animals. Here, we propose that body mass is a part of fast life history trajectory – the fitness optimization pattern which emerges from harsh environment with a function to maximize reproductive output. To test this prediction, we measured body mass index (BMI) and a set of life history indicators in a large sample of reproductive individuals (N = 1,504; 32% males; $M_{\text{age}} = 27.20$; SD = 9.2). The data were collected via an online survey. Bivariate correlations showed that BMI was positively related to reproductive success, childhood poverty, and short-term mating success; furthermore, it was negatively associated to physical health, age of the first menarche, and economic reasons against reproduction. The Network Analysis confirmed that BMI is positively related to short-term mating success and reproductive success, and negatively to physical health and economic reasons against reproduction. Furthermore, centrality metrics showed that BMI has relatively low centrality indices, and thus represents a peripheral node in the network. The present data confirm that body mass is a morphological trait which participates in the fast life history trajectory of fitness optimization. A body mass which is slightly higher than population mean (but below obesity levels) probably represents an adaptive response to depriving economic conditions in childhood and contributes to the maximization of reproductive fitness. Finally, we highlight that the relations between body mass and life history may differ between and within species.

Keywords: body mass, life history theory, harsh environment, fitness, Network analysis, human behavioural ecology

Introduction

The Role of Body Mass in Fitness Optimization

Fitness is a complex trait which drives natural selection. The complexity of evolutionary fitness is expressed in the fact that it represents a multi-faceted trait, composed of characteristics which are not positively associated, e.g., reproductive success and longevity (Jasienska et al., 2017). Every trait that is heritable and related

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to fitness may be targeted by natural selection. One of the morphological traits widely considered to participate in fitness optimization is body mass. It is a trait with significant heritability (Elks et al., 2012) and the genetic variants underlying body mass show the signals which indicate they have been affected by natural selection (Yang et al., 2015). Genetic data are confirmed with phenotypic observations as well: body mass is positively associated with reproductive success as a core component of evolutionary fitness (Ellis & Haman, 2004; Schooling et al., 2011), although there are studies which find null (Hochberg et al., 2011) or negative associations (Kirchengast & Winkler, 1995).

Previously mentioned studies found linear associations between body mass and fitness; however, the link between body mass and fitness may be more complex if the broader range of body mass variation is analysed. Studies which included underweight and overweight participants found nonlinear associations between body mass and fitness: underweight and obese individuals have a lower number of offspring compared to individuals with average body mass (Jokela et al., 2007, 2008). Similarly, the extreme values of body mass are detrimental to physical health (Staub et al., 2018) and consequently can elevate mortality rates (Flegal et al., 2005). These results suggest that body mass may be under stabilizing selection, which favourizes the mean levels of a phenotypic trait.

Behavioural Ecology of Body Mass: Evidence for a Fast Life History?

In order to understand the adaptive function of a trait, it is not enough to analyse only the most direct fitness components. A whole suite of ecological conditions, mating, and reproduction events need to be explored in order to understand the role of a particular trait in fitness optimization. These patterns of associations between environmental characteristics, growth rates, mating, reproduction, and parental investment are labelled as life histories (Roff, 2002). Generally, harsh ecological conditions facilitate earlier age of maturation, earlier reproduction, and more offspring with diminished parental investment: this pattern is labelled as the fast life history trajectory (Del Giudice et al., 2015), while the opposite one is known as slow. Life history theory is a broad conceptual framework which is invaluable in analysing evolution of correlated traits.

The existing data on positive associations between body mass and fertility suggest that elevated body mass may increase reproductive output. Since heightened fertility is a core indicator of fast life history dynamics, it is plausible to assume that body mass could be a part of fast life history trajectory. And indeed, the existing data seem to corroborate this assumption. Higher body mass has been found in individuals who originated from harsh environmental conditions like poorer neighbourhoods (Wang et al., 2007) or families characterized by dysfunctional interpersonal relations (Međedović & Bulut, 2019). Individuals with higher body size (note that body size and body mass are similar measures but are not the same: body size includes height

and posture besides body mass) have more accelerated maturation which leads to earlier pubertal timing (Hochberg et al., 2011; Sheppard et al., 2016; Xu et al., 2018). This pattern of body mass's life history is expressed in sexual behaviour as well: body mass is associated with the early onset of sexual activity (Kogan et al., 2015) and positively related to the mating effort, especially the number of sexual partners (Frederick & Jenkins, 2015; Međedović & Bulut, 2019). However, the association between body mass and mating may be more complex, as is the relation between body mass and fertility. Existing data show non-linear, quadratic relations between body mass and the number of partners, as an indicator of short-term mating (Frederick & Jenkins, 2015) and the likelihood of having ever lived with a partner as a potential marker of long-term mating (Jokela et al., 2007). These findings suggest that individuals with average body mass have the highest mating success, similarly to reproductive success. Finally, body mass is negatively related to the age of first reproduction, meaning that individuals with higher body mass have their first child earlier in their lifetime (Mell et al., 2018).

Goals of the Present Research: Using Network Approach to Analyse the Role of Body Mass in Life History Dynamics

Life history theory is one of the most important conceptual frameworks in evolutionary sciences. It provides detailed insights into adaptive characteristics of the trait by analysing multiple fitness-related outcomes which emerge at different stages of ontogeny and placing them in an ecological context. By examining the relations between body mass and life history indicators, the existing data suggest that elevated body mass is a morphological trait which is closely associated with fast life history trajectory. Still, studies which analyse body mass in the life history framework are quite rare (but see Maner et al., 2017; Međedović & Bulut, 2019; Mell et al., 2018), and researchers sometimes explicitly state that the role of body mass in human life history is not clear due to inconsistent results (Xu et al., 2018). We believe that applying life history theory to body mass would have beneficial consequences for a broader and more in-depth understanding of both adaptive and maladaptive features of elevated body mass.

The main goal of the present research is to analyse the relations between body mass and various life history indicators. A broad hypothesis that elevated body mass is an indicator of fast life history trajectory is empirically evaluated. We used Network approach to examine the role of body mass in the life history dynamics (for useful examples of the Network approach in psychology and social sciences see Borgatti et al., 2009; Borsboom & Cramer, 2013; Costantini et al., 2015). Recent research has suggested that Network analysis is especially suitable for analyzing life history data, both conceptually and statistically (Međedović, 2020a, 2021a, 2021b). Conceptually, Network approach offers a view of life histories as dynamic systems which exist on a population level (Međedović, 2021b). Network analysis explores the variables of interest as nodes in a network; the associations between variables are

depicted as edges – the thickness of every edge represents the strength of an association (Costantini et al., 2015; Epskamp et al., 2018; Hevey, 2018). The networks are graphically plotted with the distance between the nodes being respectful of the associations between them; this way we can visualize a system of life history dynamics. Network analysis can provide centrality metrics for every node: these indices show how important the particular node is in the network. This last feature of Network analysis is quite useful in the context of the present research: by analysing centrality metrics we can evaluate the relative position (or importance) of the body mass in the network of life history parameters.

Method

Participants

An online survey was used to collect the data; the research was conducted in 2015. The link with the questionnaire was sent to various social networks; furthermore, students of psychology from Singidunum University and the University of Nikšić shared the link as a part of their tasks on the psychometrics course they attended (Serbia and Montenegro were the part of the same country until 2006; they share very similar cultural background including the language). Total sample size was 1,504 participants ($M_{age} = 27.20$; SD = 9.20), majority were females (68%). Most of the participants had finished high school/secondary education (51%) but there were many participants with a university degree as well (32%), with a smaller percentage of those with only primary school (17%). The research was conducted on a voluntary basis. The informed consent was presented on the first page of the online questionnaire. The data presented in the current manuscript were part of a larger survey. For this set of data there were only 23 participants with missing data – due to a large sample size, the missing data were not replaced with estimated values, these participants were removed from the analyses.

Measures

Firstly, the information about the weight and height of the participants was gathered; Body mass index (BMI) was calculated as the mass divided by squared height in meters.

The psychosocial-biodemographic set of measures (Međedović, 2020a) was used in order to assess participants' life history. This inventory of measures contains three sets of life history indicators: *environmental conditions* in childhood, *mating effort*, and indicators related to *reproduction*. The following measures are administered to the study participants: *Harsh environment* was measured via two scales (Međedović, 2020b). The first one is *Family dysfunctions*. It is based on a shortened scale of Weak Socialization ($\alpha = .81$) from the AMORAL 9 inventory (Knežević, 2003). It measures dysfunctional family relations in participants' childhood and it captures both maltreatment (e.g. "My parents beat me frequently when I was a child") and neglect (e.g. "My parents did not care much about what I did when I was a child"). It has 5 items. The second one ($\alpha = .71$) is a four-item scale which measures *Childhood poverty* (e.g. "My family never had enough money", "Growing up, there was always a threat that my parents would be out of work"). These scales are based on a selfreport methodology with a standard Likert-type scale ranging from 1 to 5 (1 – *I disagree completely*).

Short term mating success was explored via three items from the revised version of Sociosexual Orientation Inventory (SOI; Penke & Asendorpf, 2008). These three items belong to the Behavioral facet of the SOI. They assess the number of sexual partners in the last 12 months, the number of "one-night stands" and the number of partners with whom one had sex despite a lack of long-term relationship interest. The scores on these three items were subjected to Principal Component Analysis which resulted in the extraction of a single latent variable (Eigenvalue = 2.10; 70.07% of original indicators variance explained) – the scores on this variable were saved in a database and used in further analyses.

Reproductive success was measured as a binary variable where participants with children (22.4% of participants) were coded by 1, while participants without children were coded by 0. Note that this measure cannot operationalize fitness in the narrow sense, because the participants have not finished their reproductive stage. But in fact, early reproduction is a particularly good indicator of faster life history dynamics and therefore suits the goals of the present research. *Planned age at first birth* was measured with the following question: "When would you want to have your first child (please provide your answer as the number of years you will have at the time when you have your first child)?". To assess *Observed age at first birth* the participants who already have children were asked how old they were when they had their first child. Furthermore, all participants were asked what was their *Desired number of children* (total number of children they would like to have).

One of the most important reasons against having a child, or delaying reproduction is the economic concern, i.e. not having enough money to raise a child (Langdridge et al., 2005). This is why the participants were asked "How important for you is to be economically situated before having your first child?". Participants who already had children were asked "How important was it for you to be economically situated before having your first child?". The answers were provided on a five-point Likert-type scale where 1 denotes *Not at all* while 5 stands for *Very important*. This variable is labelled as *Reasons against reproduction*.

Finally, the information about the age at which the participants had their first sexual encounter (*Onset of sexual behaviour*) and the *Age of the first menarche* for

female participants were collected. The participants were asked to self-assess their *Physical health* by providing an answer on a 10-point Likert-type scale where 1 stands for *Very bad* while 10 stands for *Very good*. All collected data are based on self-report methodology.

The Plan for Data Analysis

The main goal of the present research was to analyse the associations between body mass and various life history indicators. Hence the correlation analysis between all administered measures is presented first. Note that when analysing bivariate relations between the variables, we calculated the correlations for height and weight beside the BMI measure; this was done in order to see if associations obtained for BMI can be attributed to height or mass. Furthermore, we calculated the same associations for males and females separately; however, since sex differences were not the primary goal of the present research, these correlations are shown in the Supplementary material. Afterwards, the quadratic associations between BMI and life history were analysed in order to test if individuals with average body mass have the highest scores on mating or reproduction measures. These analyses were conducted in SPSS statistical package (version 17). Finally, the associations between the analysed variables were explored in a multivariate fashion using the Network analysis; centrality indices were calculated for the network nodes as well. The network analysis was conducted in R statistical program using the ",ggraph" package (Epskamp et al., 2012).

Results

Descriptive Statistics and the Correlations between the Examined Variables

First, we show descriptive statistics and bivariate associations between the variables. These data are shown in Table 1. We can see that the majority of our participants fall into the range of normal body mass since the range for normal BMI is between 18.5 and 24.9 (World Health Organization, 2012). Furthermore, BMI was positively related to Reproductive success, Childhood poverty, Planned age of first reproduction and Short-term mating success, while it showed negative associations with Physical health, Age of the first menarche and Reasons against reproduction. Note that these associations can be attributed to the raw measure of weight because weight has identical associations with the life history indicators as BMI; height even shows some opposite-sign correlations with the life history variables.

The associations between the life history parameters were mostly in accordance with expectations. Short-term mating success was positively related to harsh environment and Planned age at first reproduction. Reasons against reproduction showed high negative correlation with reproductive success as hypothesized; this measure negatively correlated with economic poverty in childhood and the Onset of sexual behaviour. Desired number of children was positively associated with Age of the first menarche and Physical health and negatively with both measures of reproduction timing. Planned and Observed age of the first birth were positively related to the Onset of sexual behaviour as well; the latter measure was positively associated with Reproductive success too. Individuals with higher Physical health had lower Reproductive success and they originated from more beneficial environment. Finally, Childhood poverty showed high positive correlation with Family dysfunctions and a positive association with Reproductive success. The majority of obtained associations have low effect sizes with only few correlations with medium effect sizes; this could be expected based on the previous data regarding psychosocial-biodemographic life history data (e.g. Međedović, 2020a, 2021a).

It could be argued that the relations between body mass and life history indicators may be different for males and females (e.g., Frederick & Jenkins, 2015; Međedović & Bulut, 2019). The main goal of the present research was not to examine sex differences in body mass's role in life history, but we calculated these correlations and showed them in the Supplementary material. These analyses showed that relations between BMI and life history indicators were more similar than different in males and females. For example, BMI positively correlates with reproductive success and negatively with reasons against reproduction for both sexes. Apparently, there is a higher number of significant associations in the subsample of females; but one of the main reasons for this could be the fact that there were much more female participants than males in the present research.¹

Since previous studies found quadratic relations between BMI and fitnessrelated outcomes, we explored these associations as well. We found nonlinear associations between BMI and two life history indicators – Short-term mating success ($R^2 = .06$; $F_{(2, 1501)} = 46.87$; p < .001; $\beta_{\text{linear}} = .23$; p < .01; $\beta_{\text{quadratic}} = -.07$; p <.01) and the Observed age of first reproduction ($R^2 = .02$; $F_{(2, 334)} = 3.82$; p < .05; $\beta_{\text{linear}} = .13$; p < .05; $\beta_{\text{quadratic}} = -.14$; p < .05). Individuals with average body mass had the highest scores on these life history outcomes. These associations are shown in Figure 1 and 2.

¹ This said, it should also be noted that there are differences in general patterns of correlations between males and females. For example, the differences are present with regard to the major fitness component - reproductive success: there are more significant associations in a subsample of females compared to males. Again, this could be due to the large differences in sample sizes, but some of the associations are in accordance with the existing data and theory: e.g. childhood poverty is negatively related to reproductive success only in females. This is in line with the data suggesting that socioeconomic status decreases fitness in females but not in males (Hopcroft, 2021). This suggests that the life history traits may be under different selection regimes for males and females. While this is certainly important for future life history research, in-depth analysis of the sex differences in life history covariation is beyond the scope of the present manuscript.

Table 1														
Descriptive Statistic	cs and Correlati	ons betwe	en the E	xamined	Measu	res								
	M(SD)	1	2	з	4	5	9	L	8	6	10	11	12	13
1. RSUC	/													
2. FDYS	1.84 (0.79)	.03												
3. CPOV	2.36 (0.89)	$.10^{**}$.42**											
4. PHEA	8.16 (1.70)	16**	24**	18**										
5. AFM	12.94 (1.70)	02	08*	07*	.08*									
6. OSBH	16.79 (6.20)	.11**	.03	.03	02	.07*								
7. Planned AFR	28.08 (5.93)	/	01	04	.03	01	.13**							
8. Observed AFR	27.23 (6.21)	/	02	00.	-00	11	.22**	/						
9. DCHIL	2.32 (0.96)	08**	07*	02	.12**	.13**	06*	20**	26**					
10. REAR	4.28 (0.84)	40**	05	10**	.07**	05	10**	01	.08	05				
11. STMS	/	.02	$.10^{**}$	$.10^{**}$	03	08*	08**	.20**	.05	.01	01			
12. BMI	22.88 (3.56)	.19**	.04	$.10^{**}$	11**	11**	01	$.10^{**}$.07	-00	15**	.23**		
13. Height	174.46 (10.00)	12**	03	.02	.03	.07**	04	.09**	.08	.12**	.06*	.30**	.19**	
14. Weight	69.87 (14.69)	$.10^{**}$.02	$.09^{**}$	09**	09**	04	$.12^{**}$	60.	.04	08**	.33**	.85**	.67**
Note. RSUC – Repro	ductive success;]	FDYS – F	amily dys	sfunction	s; CPOV	r – Chilo	lhood pc	verty; PI	HEA – H	hysical	health; A	FM - A	Age of th	e first
menarche; OSBH - (Onset of sexual b	ehaviour; .	AFR – A	ge of fir	st reprod	luction;	DCHIL	- Desired	l numbe	r of chil	dren; RE	AR – R	easons a	gainst
reproduction; STMS - is a standardized meas	- Short-term matir	e of the second states of the	BMI – B	ody mass	s index; S	short terr onificant	n mating	success i	is represe	ented by	its factor	score –	conseque	ently it
matte matematime p et	Jurve P Nove, P		·····			6			·>> 1 1 2 1					

Figure 1



Nonlinear Association between Body Mass and Short-Term Mating Success

Figure 2

Nonlinear Association between Body Mass and Observed Age of First Reproduction



Body Mass as a Node in Life History Network

We estimated the network of life history parameters using partial correlations to analyze the edges between the notes. Furthermore, we applied adaptive lasso optimization in order to buffer spurious associations between the nodes (Zou, 2006). We excluded both Planned and Observed age of first reproduction from the analysis since these measures are collected on different participants. Age of the first menarche is removed from the similar reason: if we analysed this measure, the network could be estimated on female participants only. Finally, before building the network, we partialled out the variance of participants' sex, age, and education from the variation of all measures, because they represent confounding variables. The network is shown on Figure 3.

Figure 3

The Position of Body Mass in the Network of Life History Parameters



Note. Solid edges represent positive associations; dashed edges represent negative associations. STMS – Short-term mating success; RSUC – Reproductive success; REAR – Reasons against reproduction; PHEA – Physical health; OSBH – Onset of sexual behavior; FDYS – Family dysfunctions; DCHIL – Desired number of children; CPOV – Childhood poverty; BMI – Body mass index.

As we can see, four associations between body mass and life history indicators obtained in the correlation analysis are confirmed in the network. Body mass index is positively related to Short-term mating success and Reproduction success, while it is negatively related to the economic reasons against reproduction and physical health. BMI had no direct edge to the Childhood poverty in the network – the closest pathway from Childhood poverty to elevated BMI was diminished physical health.

We calculated several centrality statistics to evaluate the relative importance of every node in the network (Borgatti, 2005). We showed three centrality indices: 1) 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); 2) closeness – estimation of the position of the target node in the network based on direct and indirect connections with other nodes; 3) 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). Centrality indices are shown on Figure 4. We can see that Family dysfunctions measure is estimated as the most central node in the network; this variable is followed by physical health which has the highest closeness and betweenness. Body mass had low strength, average betweenness and a slightly above-average closeness.

Figure 4



Centrality Indices for the Network Nodes

Note. z-scores are shown on x-axis rather than raw centrality indices; STMS – Short-term mating success; RSUC – Reproductive success; REAR – Reasons against reproduction; PHEA – Physical health; OSBH – Onset of sexual behavior; FDYS – Family dysfunctions; DCHIL – Desired number of children; CPOV – Childhood poverty; BMI – Body mass index.

Discussion

Life history theory is an important theoretical framework in analyzing the role of physiological, morphological, and behavioral characteristics in biological adaptation. It represents an ecological theory of evolutionary tradeoffs – it can provide detailed pathways of fitness optimization dependent of local ecologies and various characteristics of organisms. Previous findings indicated that human body mass may indicate faster life history – a pattern of fitness optimization aimed to maximize reproductive output with a potential tradeoff in decreasing physical health and longevity. The present data were largely in accordance with this hypothesis: slightly higher body mass (but below obesity levels) is probably an adaptive response to harsh ecological conditions that accelerate maturation, increase mating, and reproductive output. However, not all detected associations were in line with the hypothesis: body mass was mostly unrelated to the reproduction timing; furthermore, individuals with average body mass had the highest observed age of first reproduction, which was not predicted. Finally, the relations between body mass, the onset of sexual behavior, and desired number of children were also not detected.

The Evolution of Body Mass

Increased body size, which is highly correlated with body mass, has been linked to earlier maturation and higher reproductive success in many animal taxa (Roff, 2000). There are tradeoffs associated with elevated somatic growth as well: increased mortality based on heightened predation risk or compromised immune function (Mangel & Stamps, 2001). These fitness-relevant outcomes of body mass are highly similar in humans too: the data shows negative associations between body mass, pubertal timing (Hochberg et al., 2011; Sheppard et al., 2016; Xu et al., 2018) and physical health (Mell et al., 2018), and positive relations between body mass and reproductive success (Ellis & Haman, 2004; Schooling et al., 2011). We confirmed all of these associations in the present research.

Elevated body mass may be beneficial for fitness in several ways. Nutritional status is an important condition for menarche and conception. Organisms need to acquire certain levels of body growth in order to successfully reproduce; in fact, there is probably a threshold in body mass which serves as a signal that body can begin with reproductive function (Wells, 2006). Furthermore, humans were highly exposed to uncertainty in energy supply in our recent evolution, which represented a selection pressure favorizing individuals with higher body mass. In this case, body mass elevates fitness by serving as an energy storage (Pond, 1998; however, note that the evolutionary mismatch between ancestral and contemporary environment may produce maladaptive responses like obesity and diabetes – a hypothesis labeled as "thrifty genotype", Neel, 1962). On the other hand, the tradeoff of elevated body mass reflects a higher predation risk: individuals with increased BMI have higher risk of being killed. However, there is relaxed selection on predation in contemporary

humans, which is probably one of the evolutionary factors that contribute to increased levels of obesity in human populations (Speakman, 2018). Obesity, similarly to underweight and malnutrition, is detrimental for both core fitness components: reproductive success and physical health (Jokela et al., 2007, 2008; Staub et al., 2018). This could indicate that body mass is currently under stabilizing selection which favors mean phenotypic levels of body mass. However, we did not obtain this result in the present data: the association between body mass and reproductive success was linear and positive. It is possible that slightly above-mean levels of body mass are the most beneficial for fitness – this assumption is in line with the findings that only severe obesity is detrimental for reproductive potential (Chavarro et al., 2010).

Body Mass as a Morphological Indicator of Fast Life History

The associations between body mass, health and reproduction are already indicative for the hypothesis of body mass as a fast life history marker. In order to test this hypothesis, we analyzed the relations between body mass and a broader set of life history indicators. First, we analyzed harsh environmental conditions in childhood as a major ecological trigger for fast life history development. Earlier research found that individuals with higher body mass originate from families with dvsfunctional relations (Međedović & Bulut, 2019); furthermore, lower maternal investment was associated with higher adiposity in offspring (Wells et al., 2016). We were unable to confirm these relations: body mass was not associated with dysfunctional family relations in the present data – possible reason is the low variation of Family dysfunctions measure in the present sample. However, we did obtain positive associations between body mass and economic deprivation in childhood, which is in accordance with the previous data (Wang et al., 2007). Individuals who lived in harsh environments (Hill et al., 2013) or were experimentally exposed to the cues of environmental harshness (Laran & Salerno, 2013) show greater preference for high calorie food; this is probably an adaptive mechanism with a function to store fat in the scarce resource environment. However, the tradeoff becomes immediately apparent: high calorie food is often unhealthy (Drewnowski & Specter, 2004). In sum, individuals originating from poorer households gain body mass at an expense of decreasing health by consuming unhealthier food and the fact that a higher BMI can compromise the immune system (Wells, 2006). This link can explain the data produced in the network analysis: BMI was not directly associated with Childhood poverty in the network; the shortest path between elevated BMI and economic poverty in childhood was via diminished physical health.

Hence, the present data showed that BMI is positively related to childhood economic poverty and to earlier pubertal timing. Furthermore, higher body mass is positively associated with short-term mating success as well: individuals with higher BMI have more short-term sexual partners. This is in accordance with previous research (Frederick & Jenkins, 2015; Međedović & Bulut, 2019). In fact, we obtained curvilinear, inverse-U shaped association between short-term mating and body mass, which was obtained in earlier studies as well (Frederick & Jenkins, 2015). These data suggest that individuals with average BMI have the highest short-term mating success (or to be more precise, slightly above average, at least according to the present and the data of Frederick & Jenkins, 2015). Interestingly the same association has been found between BMI and the indicators of long-term mating – likelihood of having ever lived with a partner (Jokela et al., 2007), while the overweight individuals had lower likelihood of being married (Gortmaker et al., 1993). Thus, near-average BMI may be beneficial for mating in general – both short and long-term.

Measuring conscious and intentional motives for reproduction is very important for analyzing contemporary humans' reproductive ecology (e.g., Guedes et al., 2015; Miller, 1995). The reason for this is that humans have elevated levels of reproduction control, via contraception and other methods for conception control. One of important reasons which prevent individuals from having children is financial insecurity (Langdridge et al., 2005). Our data confirmed this as well – individuals who need to feel financially secure before having their first child had lower reproductive success. Furthermore, these participants had lower BMI. Thus, elevated body mass has another characteristic which facilitates reproductive success – individuals with higher BMI do not have a need to be economically secure before having children. However, the nature of this relationship remains elusive so far. Future research may try to explain this association, perhaps by using current socioeconomic status, or other measures of social status as mediator variables.

Finally, the centrality analysis showed that BMI had relatively low centrality indices - this suggests that BMI is a relatively peripheral node in the network of life history indicators (we base this conclusion primarily on the result that BMI has an belowe-average strength in the life history network). However, we must be cautious about this conclusion. Two important life history indicators were excluded from the network since they were not obtained from the whole sample. At least one of them, Age of the first menarche, showed bivariate associations with BMI, which means that the centrality indices of BMI would be probably higher if this variable was analysed in the network as well. Furthermore, it is possible that the centrality of BMI could be different in individuals who originated from a more harsh environmental conditions or if the network was built in a sample of post-reproductive individuals. This may be the focus of future research as well. In any case, the present data confirmed the fruitfulness of applying the Network approach to the analysis of human life history dynamics (Međedović, 2020a, 2021a, 2021b). The inclusion of body mass in the network with childhood environmental conditions, mating, and reproduction-related variables provided additional insights into the dynamics between reproductive success, reproductive motivation, health status, and harsh childhood ecologies.

The Life History of Body Mass: Differences Within and Between Species

We would like to address the additional implications of the present findings which can bear theoretical significance. Recently, a critique of life history framework's implementation in explaining inter-individual differences in humans has been published (Zietsch & Sidari, 2020). The authors highlight that life history evolution emerged in evolutionary biology as a framework aimed to explain interspecies differences, and that slow and fast life history trajectories are found between species (e.g., Pianka, 1970). They argue that evolutionary processes which lead to species differences are crucially different from the ones which generate interindividual differences; hence, the usage of slow and fast life history framework in the inter-individual context may be problematic. We believe that the case of body mass may represent a clear example of this incongruence between inter-individual and inter-species level of analysis. The present and former findings of the relations between BMI and life history indicators in humans suggest that BMI is a morphological trait associated with fast life history. Note that the same conclusion can be made not just for BMI but for raw measure of body mass (weight) as our correlation analyses show. However, when inter-species differences are analysed, higher body mass reliably indicates slower life history (reviewed in Del Giudice, 2019)! Large species have higher maturation rates, later reproduction, smaller number of offspring and higher longevity - clear indications of slow life history pace. This apparent contrast in body mass's associations with life history indicators between and within the species is in line with the arguments of Zietsch and Sidari (2020): we must be cautious in applying the slow-fast life history framework at the inter-individual level and invest more resources in developing theoretical arguments which may explain the similarities and differences between the two levels of life history framework's application.

Limitations and Future Directions

The present study is based on a cross-sectional design which prevents us from drawing inferences about the causal relations between the measures. The problem of cross-sectional design is particularly important regarding the associations between body mass and reproductive success itself, since the causation may go in both directions. Furthermore, the participants were young adults; consequently, we could not measure completed fertility and other important life history indicators like the age of last reproduction. The sample structure was biased toward more educated individuals, which represents an obstacle towards generalizing results to the whole population. Finally, the design would be certainly strengthened if some measures like physical health and environmental harshness were operationalized in a more objective fashion.

Beyond overcoming these obstacles, future research can additionally explore the role of additional factors which may help us understand the link between body mass and life history in humans. The first one is assortative mating: there is assortative mating on body mass (Silventoinen et al., 2003) but, as far as we are aware, there is no data if assortative mating speeds up life history or elevates fitness in individuals with higher body mass (e.g. by elevating reproductive success). The other quite important criterion for examining the life history role of body mass is parental investment, as one of the core fitness components. The data shows positive effect of maternal body mass on offspring growth (Wells, 2006), which does not align with the view of elevated body mass as a fast life history trait. However, this link certainly deserves more empirical exploration. Future studies should analyse different components of body mass (i.e. body fat and muscle mass) together with the additional environmental factors related to variation in body mass (i.e. extrinsic mortality or environmental unpredictability).

Concluding Remarks

The present data confirmed that elevated body mass shows signals of a fast life history phenotype. It may represent an adaptive reaction to the harsh environmental conditions during childhood, especially to economic poverty. BMI is positively associated with earlier maturation, higher mating and reproductive success, but with a trade-off in diminished physical health which may decrease longevity. This pattern of fitness-related outcomes points to fast life history dynamics. Our data, together with previous findings suggest that the associations between body mass and fitnessrelated outcomes may be curvilinear and that slightly above-average body mass may confer the highest fitness. If this is proven to be the fact it would mean that body mass is not under stabilizing, but mild positive directional selection. Thus, we believe that the present data, with all of the current study limitations, represent a strong incentive for future behavioural ecological research of human body mass. Present findings show the fruitfulness of applying life history theory in order to explore body mass's role in fitness optimization. Finally, the present study highlighted the benefits of Network analysis as a framework to conceptualize and empirically analyse human life histories.

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Položaj indeksa tjelesne mase u mreži indikatora strategija životnih putova

Sažetak

Tielesna je masa široko prepoznata kao morfološka osobina koja je važna za optimizaciju sposobnosti opstanka i kod ljudi i kod drugih životinja. Ovdje predlažemo da je tjelesna masa dio brzih strategija životnih putova – obrasca optimizacije sposobnosti opstanka koji se pojavljuje u nepogodnome okolišu s funkcijom maksimalizacije reproduktivnoga uspjeha. Da bismo testirali tu hipotezu, mjerili smo indeks tjelesne mase (ITM) i skup indikatora strategija životnih putova na velikome uzorku sudionika reproduktivne dobi (N = 1504; 32 % muškaraca; $M_{dob} = 27.20$; SD =9.2). Podaci su prikupljeni online-upitnikom. Bivarijatne korelacije pokazale su da je BMI pozitivno povezan s reproduktivnim uspjehom, siromaštvom u djetinjstvu i kratkoročnom reproduktivnom strategijom; dodatno, negativno je povezan s tjelesnim zdravljem, dobi prve menarhe i ekonomskim razlozima protiv reprodukcije. Mrežna analiza potvrdila je da je ITM pozitivno povezan s kratkoročnom reproduktivnom strategijom i reproduktivnim uspjehom, a negativno s tjelesnim zdravljem i ekonomskim razlozima protiv reprodukcije. Nadalje, parametri centralnosti pokazali su da ITM ima relativno niske indikatore centralnosti te stoga predstavlja periferni čvor u mreži. Rezultati potvrđuju da je tjelesna masa morfološka osobina koja sudjeluje u brzim strategijama životnih putova za optimizaciju sposobnosti opstanka. Tjelesna masa koja je blago iznad populacijskoga prosjeka (ali ispod razina pretilosti) vjerojatno predstavlja adaptivni odgovor na deprivirajuće ekonomske uvjete u djetinjstvu te doprinosi maksimalizaciji reproduktivne sposobnosti opstanka. Nakraju, naglašavamo da je moguće da se odnos između tjelesne mase i strategija životnih putova razlikuje unutar vrsta i između njih.

Ključne riječi: tjelesna masa, teorija životnih putova, nepogodan okoliš, mrežna analiza, ljudska bihevioralna ekologija

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Supplementary Material

Table S1

Correlations between the Examined Measures (Including Height and Weight) In a Subsample of Males

	1	2	3	4	5	6	7	8	9	10	11	12
1. RSUC												
2. FDYS	00											
3. CPOV	.06	.38**										
4. PHEA	07	19**	08									
5. OSBH	.04	.04	03	05								
6. Planned AFR	/	.02	05	04	.07							
7. Observed AFI	R /	24*	18	.17	.19	/						
8. DCHIL	.00	- .11*	00	.08	07	13*	38**					
9. REAR	34**	03	08	.05	07	02	02	09				
10. STMS	.08	04	.03	.07	13**	.12*	01	.05	01			
11. BMI	$.18^{**}$	07	00	05	.09	.03	01	.05	14**	.09		
12. Height	07	07	09	06	.02	.01	.18	.12**	.05	.14**	.01	
13. Weight	.13**	09	05	08	.08	.02	.05	$.10^{*}$	08	.14**	.85**	.52**

Note. RSUC – Reproductive success; FDYS – Family dysfunctions; CPOV – Childhood poverty; PHEA – Physical health; OSBH – Onset of sexual behaviour; AFR – age of the first reproduction; DCHIL – Desired number of children; REAR – Reasons against reproduction; STMS – Short-term mating success; BMI – Body mass index. *p < .05; **p < .01.

Međedović, J.: Life History of Body Mass

Table S2

0													
	1	2	3	4	5	6	7	8	9	10	11	12	13
1. RSUC													
2. FDYS	.05												
3. CPOV	.13**	.43**											
4. PHEA	20**	27**	24**										
5. AFM	02	05	06*	$.08^{*}$									
6. OSBH	.12**	.03	$.06^{*}$.00	$.07^{*}$								
7. Planned	/	05	08*	.06	01	.18**							
AFR													
8. Observed	/	.05	.04	08	16*	.25**	/						
AFR													
9. DCHIL	.11**	05	03	.14**	.13**	04	28**	24**					
10. REAR	43**	06	12**	$.08^*$	05	11**	.01	.13*	03				
11. STMS	$.07^{*}$.17**	$.08^{*}$	13**	04	01	.18**	.00	06	02			
12. BMI	.27**	$.07^{*}$.10**	19**	12**	00	.04	.06	07*	18**	.13**		
13. Height	07*	09**	05	.02	.13**	.03	05	03	$.07^{*}$	$.07^{*}$.01	10**	
14. Weight	.22**	.02	$.07^{*}$	17**	06	01	.01	.04	04	12**	.12**	.86**	.43**

Correlations between the Examined Measures (Including Height and Weight) In a Subsample of Females

Note. RSUC – Reproductive success; FDYS – Family dysfunctions; CPOV – Childhood poverty; PHEA – Physical health; AFM – Age of the first menarche; OSBH – Onset of sexual behaviour; AFR – age of the first reproduction; DCHIL – Desired number of children; REAR – Reasons against reproduction; STMS – Short-term mating success; BMI – Body mass index. *p < .05; **p < .01.