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RELATIONSHIPS BETWEEN BASIC EMOTIONS AND REPRODUCTIVE FITNESS ARE MODERATED BY SEX AS AN INTERNAL STATE[3]

One of the key features of personality is the existence of inter-individual differences in motivation, emotions and behavior. Individual differences may be maintained in a population if personality traits are linked to states – conditions which affect the fitness-related outcomes of personality. We tested this assumption using the participants' sex as an internal state. Personality was operationalized via basic emotional systems: FEAR, ANGER, SADNESS, SEEKING, PLAYFULNESS and CARE. We measured several fitness-related outcomes like reproductive success, residual reproductive value, reproductive timing, the onset of sexual activity and short- term mating frequency. The data were collected in a community sample via an online study (N = 635; M_{age} = 29.4; 69.4% females). We used linear regression to predict fitness-related outcomes by basic emotions and tested interactions between sex and emotions to the prediction of these criteria measures. Predictable sex differences in basic emotions were obtained: males had lower scores on CARE, FEAR and SADNESS traits. Findings also showed that basic emotions can have an adaptive role in a biological sense – this was particularly true for CARE and ANGER traits. Finally, five interactions were detected, which showed that the adaptive benefits of emotional traits are different for males and females in a conceptually expected manner. Research results showed that personality traits operationalized as basic emotional systems can contribute to evolutionary fitness. These results furthermore expand the knowledge of human personality as a state-dependent behavior.

Keywords: basic emotions; human behavioral ecology; reproductive fitness; sex differences; state-dependent behavior

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[2] The second author of this paper, Boban Petrović, has passed away during the process of writing this manuscript.

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Introduction

Personality as a State-dependent Behavior

Behavioral ecology is a sub-discipline of evolutionary biology which attempts to understand behavior through its relation to evolutionary fitness (reproductive success, residual reproductive value, longevity, parental investment etc.) and fitness-related outcomes (e.g., pubertal timing, onset of sexual behavior, mating, and the timing of reproduction). Recently, the field has broadened to include the study of personality in this framework. Indeed, the very existence of individual differences in stable behavioral traits represents one of the major evolutionary questions of personality (Međedović, 2018a), which emerges from the fact that personality traits are related to fitness in many animal taxa (Smith & Blumstein, 2008). Consequently, stabilizing selection should diminish genetic variance in personality which would lead to a decrease in phenotypic variation as well. However, this is obviously not the case, since the variation (both genetic and phenotypic) in personality is high in natural populations. Hence, behavioral ecology tries to answer a fundamental question of personality itself: why there are individual differences in behavioral traits.

There are several candidate processes which could maintain the variation in personality traits. One of them is described by *state-dependent behavior models* (Sih et al., 2015). State is defined as any condition which influences fitness-related outcomes of behavior (Dingemanse & Wolf, 2010). These conditions can be external, like various characteristics of the physical and social environment, and internal, like body mass, energy reserves, metabolism etc. State-dependent behavior models assume that behavior cannot be equally beneficial in different state conditions. For example, aggressiveness should not be equally adaptive for individuals with large and small bodies: aggressiveness may be positively related to fitness only in individuals with large body size; however, non-aggressive behavioral tactics can increase fitness in low body size individuals (perhaps through cooperative behavior). Hence, body size may preserve genetic (and consequently phenotypic) variance in aggressiveness since both aggressive and non-aggressive phenotypes can acquire high fitness, dependently of their body size. Obviously, one of the apparent internal states could be the sex of the individual itself.

Are there Sex Differences in the Relationships between Personality Traits and Fitness in Humans?

The research linking personality and fitness (commonly operationalized as reproductive success) in human behavioral ecology was usually done using the Big Five/Five Factor personality taxonomy (Costa & McCrae, 1992; Goldberg, 1993). It is based on five broad personality dimensions named Neuroticism

(emotional instability, tendency to feel aversive emotions like fear, sadness and anxiety), Extraversion (sociability, activity, gregariousness, positive affect), Openness (originality, creativity, aesthetic appreciation), Agreeableness (cooperation, patience, flexibility in interpersonal relations) and Conscientiousness (orderliness, enhanced impulse control, long-term planning). Many empirical studies showed significant relationship between these personality traits and fitness (reviewed in Penke & Jokela, 2016). Furthermore, these links are frequently obtained for one sex and not the other. For example, the links between Extraversion, Neuroticism, and fitness (positive for the former and negative for the latter) are particularly present in males (Berg et al., 2016; Gurven, von Rueden et al., 2014; Skirbekk, & Blekesaune, 2014). Some studies found positive correlations between Agreeableness and fitness in males (Međedović et al., 2018) while others obtained it for females (Berg et al., 2013). Finally, Conscientiousness may be beneficial for male fitness (Gurven et al., 2014) but detrimental for females (Skirbekk & Blekesaune, 2014). Thus, the existing data do not display a coherent and straightforward picture of the sex differences in the relationship between personality and fitness, but it certainly suggests that sex could be a heuristically important moderator of this link.

Personality Operationalized by Basic Emotional Systems

Leaning on the crucial role that emotions play in personality, Jaak Panksepp with his colleagues conceptualized the taxonomy of personality traits based on the affective neuroscience research framework (Panksepp, 2005). Basic emotional systems are defined mostly by using deep brain stimulations: excitation of different subcortical structures revealed distinct neural systems which serve as the biological basis of primal emotions. Seven basic emotional systems were detected in this line of research: FEAR, SEEKING, RAGE, PANIC, LUST, CARE and PLAY (Panksepp, 2005; Panksepp & Watt, 2011). In order to facilitate the research on emotions in humans, these primal emotions (all except LUST) were operationalized by a self-report questionnaire which was termed the Affective Neuroscience Personality Scales (ANPS: Davis & Panksepp, 2011; Davis et al., 2003). The content of the traits is as follows: SEEKING describes the search for positive stimuli, gathering information, foraging in animals and resource acquisition in humans; FEAR represents a reaction to potential danger; ANGER depicts an emotional response to frustration or a fighting reaction in situations with competitive characteristics; SADNESS is based on separation anxiety and is activated when we are separated from loved ones; CARE is expressed in warm emotional feelings and protective attitude towards others; PLAYFULNESS depicts emotionally positive interactions with others, sociability which is a basis for learning of social dynamics. Basic emotions tend to be grouped into two higher order factors – positive and negative emotions (Barrett et al., 2013). Previous research is relatively unequivocal

regarding the sex differences in emotional traits: males tend to score lower on FEAR, SADNESS and CARE traits (Davis et al., 2003; Pingault et al., 2012).

So far, there are no data regarding the relationship between basic emotions and fitness. However, as we have described previously, there are data on the associations between the Big Five/Five Factor traits and reproductive success (Penke & Jokela, 2016). On the other hand, the relationships between ANPS scales and five lexical factors are well established: PLAY corresponds to Extraversion, CARE associates positively, while ANGER is negatively associated to Agreeableness; FEAR, ANGER and SADNESS have positive correlations with Neuroticism, while SEEKING is positively related to Openness to experience (Barrett et al., 2013; Davis et al., 2003). These relationships can be used to examine and compare the links between ANPS traits and fitness with the ones which were found in previous research.

Goals of the Present Research

It was argued recently that human personality psychology could have high theoretical benefits if the behavioral ecological framework could be applied to a greater extent (Međedović, 2018a). In the present research we tried to advance our knowledge of the behavioral ecology of human personality by exploring the relationships between basic emotions and fitness-related outcomes. These emotional systems are partially genetically transmitted from parent to children in contemporary humans (Montag et al., 2016), which means that they could represent a target for natural selection. Certainly, we do have grounds for the assumption that primal emotions are adaptive, even in contemporary humans: they represent *general behavioral dispositions* which are activated in the presence of adaptive challenges (Montag & Panksepp, 2017).

We believe that the present research may contribute to the existing knowledge in human personality ecology in three ways. Firstly, majority of the research regarding personality-fitness link explored associations between Big Five/Five factor personality traits and reproductive success (Penke & Jokela, 2016). In the present study we expand the existing data on the personality-fitness link by including several fitness-related indicators in the research: 1) reproductive success – as a crucial fitness component; 2) onset of sexual behavior – to capture the initiation of sexual activity during ontogeny; 3) short-term mating frequency[4]; 4) timing of first reproduction – for two reasons: it captures one of the major trade-offs in fitness optimization (Del Giudice et al., 2015); furthermore it is negatively correlated to fertility (e.g., Međedović et al., 2018) and thus it represents another estimation of reproductive success; 5)

[4] Earlier onset of sexual behavior and higher short-term mating frequency are thought to be markers of so-called fast life history trajectory (e.g., Kogan et al., 2015) which should maximize fitness by increasing reproductive output (Del Giudice et al., 2015). This was the main reason why we examined these indicators in the present study.

the total expected number of children (residual reproductive value; e.g., Wolf et al., 2007). It is especially important in modern humans since humans have intentional and willful control over reproduction via contraception and other practices of conception control (Berg et al., 2013) - hence, motivation and planning to have children is positively correlated to the observed fertility (Miller et al., 2010). Analyzing all these indicators should provide us with a more comprehensive picture of the associations between basic emotions and fitness.

Secondly, we have chosen ANPS because it operationalizes personality in a manner which can be especially suitable for a behavioral ecological research. It depicts personality traits as functions of basic emotional systems which are present in various taxa. Thus, the research on these emotional systems can more easily bridge the knowledge on personality ecology in humans and other animals, i.e., they are fruitful for comparative research. Findings on complex, culturally- affected descriptions of personality (e.g., lexical models of personality) can be more difficult to compare between the species (Međedović, 2018a).

Finally, we wanted to advance the current knowledge of the role of personality in fitness optimization by analyzing personality traits as a state-dependent behavior. Previous research showed that this theoretical framework may be fruitful in explaining why there are inter- individual differences in personality traits (Međedović, 2018b; Međedović & Kovačević, 2020). In the present research we assumed that the adaptive benefits of basic emotions may be dependent on the sex of the individual. Building on the current state of knowledge regarding the links between the Big Five/Five Factor traits and fitness we assumed that the traits similar to Extraversion (i.e., PLAYFULNESS) may be beneficial for fitness in males, while the traits that correspond to Neuroticism (i.e., FEAR and SADNESS) may buffer fitness in males.

Our general hypotheses regarding the links between emotions and fitness are: 1) Adaptive potentials could be expected for CARE and PLAYFULNESS since the former represents a source of parental effort while the latter should facilitate mating effort. CARE system should be related to positive emotions toward children and toddlers (Montag & Panksepp, 2017) and thus associated to higher expected number of children and earlier reproduction; PLAYFULNESS is expected to have similar effect to fitness with the addition of positive associations with short-term mating (similarly to the Big Five/Five Factor trait of Extraversion: Gurven et al., 2014; Jokela et al., 2011; Schmitt, & Shackelford, 2008). 2) FEAR and SADNESS could have detrimental consequences for fitness optimization. More precisely, these are expected to show negative associations with observed and expected reproductive success (similarly to the Neuroticism trait of the Big Five/Five Factor model: Berg et al., 2016, Skirbekk, & Blekesaune, 2014).

Method

Sample and Procedure

The data were collected via an on-line study. The link with the questionnaire was shared among a community sample of participants on social networks and via informal contacts. The total number of participants was 635. All of the participants were of Serbian nationality and the survey was displayed in Serbian language. We wanted to increase the sample size as much as we could, having in mind that some of the expected associations can have low effect size. The questionnaire was online for approximately two weeks – since there were no new responses after that time, we stopped with data collection. The majority of the participants were females (69.4%). Majority of the participants were adults in their twenties and thirties (M_{age} = 29.4; *SD* = 10.38), however, the age range of the participants was very high (from 18 to 55). Most participants had a high school degree (44.7%), some participants had a university degree (37.5%), while the rest had a primary school education (17.8%). The research was conducted on a voluntary basis. Subjects were told that they would be participating in research which explores psychological characteristics associated with decisions to have and raise children. The informed consent form was present on the first page of the questionnaire. The data was collected in 2017.

Instruments and Measures

Short Version of ANPS

Short version of ANPS (Pingault et al., 2012) is a self-report inventory which contains 36 items, 6 items per every primal emotion: SEEKING, RAGE, FEAR, SADNESS, PLAYFULNESS and CARE. We used a five-point Likert type scale for responding where 1 stands for "*I disagree completely*" while 5 denotes "*I agree completely*"[5]. The higher score indicates a higher level of emotional expressions.

Fitness and Life History Indicators

We collected several fitness and life-history indicators: 1) *reproductive success* - as a binary variable coded with 0 if a participant does not have children and 1 if he/she does (31% of the participants declared they have children); 2)

[5] The original scale has a four-point Likert scale for item responding. Due to a procedural error we attached the five- point scale for the responding ANPS. However, existing data show that there are no differences in psychometric properties (including the validity and reliability) between the four and five-point scales for the same instrument (e.g., Adelson & McCoach, 2010; Leung, 2011; Preston & Colman, 2000). This is why we firmly believe that the method of measurement did not compromise the validity of the current data.

onset of sexual activity – age at which a participant had their first sexual intercourse (*M* = 18.25; *SD* = 2.76); 3) *short-term mating frequency* – measured by three items from the Revised Sociosexual Orientation Inventory – Behavior facet (Penke & Asendorpf, 2008): 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 = 2.22; 73.91% of original indicators variance explained] labeled as short-term mating frequency– the scores on this variable were saved in a database and used further in the analyses); 4) *residual reproductive value* – total expected number of children (*M* = 2.11; *SD* = 0.88), and 5) *reproductive timing* – planned or observed age for having the first child. Since some of our participants had children while others did not, we analyzed this last variable on these subsamples separately. The variable obtained on a subsample of parents was labeled as Observed reproductive timing (*M* = 28.24; *SD* = 5.17), while the variable collected on a subsample of participants without children was named Planned reproductive timing (*M* = 29.90; *SD* = 4.99).

Results

Descriptive Statistics and Sex Differences on Analyzed Measures

First we showed descriptive statistics and sex differences for ANPS scales. Males had significantly lower scores on CARE, FEAR and SADNESS measures. We calculated the reliabilities (Cronbach's α statistics) of Affective Neuroscience Personality Scales as well. All scales had satisfactory reliabilities except PLAYFULNESS, whose α coefficient is somewhat lower (but still acceptable). All these results can be seen in Table 1.

Table 1
*Sex diff*erences in basic emotional systems

	Males		Females		*t*	*d*	α
	M	*SD*	*M*	*SD*			
SEEKING	3.99	0.66	3.97	0.72	0.45	0.03	.76
CARE	3.47	0.79	3.75	0.72	-4.47**	0.37	.73
PLAYFULNESS	3.62	0.58	3.59	0.68	0.53	0.05	.62
ANGER	2.80	0.86	2.92	0.83	-1.65	0.14	.77
FEAR	2.59	0.73	2.77	0.87	-2.74**[e]	0.22	.79
SADNESS	2.65	0.80	2.92	0.85	-3.69**	0.33	.77

Notes. *M* – mean; *SD* – stadard deviation; *d* – Cohen's d (effect size); [e] – *t*-test where equal variances in groups are not assumed (Levene's statistic was significant); α - Cronbach's α statistics.
* $p < .05$. ** $p < .01$.

Correlations between the Administered Measures

In order to explore the relationships between the primal emotions and fitness-related measures we calculated bivariate correlations between the variables. Since the continuous fitness- related indicators showed deviation from normal distribution (which could be expected since they are count variables) we normalized them (using Blom's algorithm: Blom, 1958) and used normalized scores in all analyses. Pearson's correlation coefficients are obtained for all variables, except for reproductive success: since it is a binary measure we calculated the point-biserial correlation coefficient (the measure of association between binary and interval variables). The correlation coefficients are shown in Table 2.

Table 2
Correlations between the examined variables

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
1. SEEKING	1										
2. CARE	.19**										
3. PLAYFULNESS	.27**	.18**									
4. ANGER	-.06	-.04	.02								
5. FEAR	-.22**	-.04	-.19**	.33**							
6. SADNESS	-.15**	.09*	-.21**	.25**	.57**						
7. Onset of sexual behavior	-.04	.11**	-.01	-.11**	.01	.04					
8. Short-term mating frequency	.03	-.11**	.06	-.01	-.07	-.04	-.28**				
9. Observed reproduction timing	-.02	-.11	-.02	-.12	.01	-.15*	.31*	-.02			
10. Planned reproduction timing	.06	-.08	-.03	-.11*	-.08	-.05	.10	.14*	/		
11. Residual reproductive value	.05	.18**	.16**	-.01	-.12**	-.09*	-.09*	-.00	-.13	-.32**	
12. Reproductive success	-.07	.18**	-.06	.07	-.04	.01	.08	-.06	/	/	-.05

Notes. * $p < .05$. ** $p < .01$

We can see in Table 2 that positive emotions generally correlate positively between themselves and the same could be said for negative emotions as well. The correlations between these two sets of measures are mostly negative. Criteria measures are associated in a predictable fashion as well. Individuals with an earlier Onset of sexual activity tend to delay reproduction and expect a lower total number of children. A higher number of instances of sexual intercourse is positively correlated to the postponement of reproduction. Finally, individuals who delay reproduction have a lower expected number of offspring.

The main goal of this analysis was to estimate the relationships between basic emotions and fitness outcomes. CARE is positively correlated to Residual reproductive value, Reproductive success and the Onset of sexual behavior while it is negatively correlated to the Timing of reproduction and Short-term mating frequency. Individuals with higher PLAYFULNESS have a higher expected total number of children. ANGER is negatively correlated to the Timing of reproduction. Fearful individuals tend to expect a lower number of offspring. Finally, SADNESS is negatively correlated to Residual reproductive value and the Observed timing of reproduction. Most of the detected associations were small in effect size, according the criterions set by Cohen (1992).

Basic Emotions as Predictors of Fitness

Next, we analyzed the relationships between emotions and fitness-related indicators in a multivariate fashion. We set six regression models with basic emotions, sex (males were coded by 0 and females by 1) and age as predictors and fitness-related measures as criteria variables. Linear regression was used for all criteria except reproductive success – we used binary logistic regression for this criterion. All regression models were statistically significant. The contributions of predictors and the characteristics of the regression functions are provided in Table 3.

Table 3
Basic emotions as predictors of fitness/life-history outcomes

	Onset of sexual behavior		Short-term mating frequency		Observed reproduction timing		Planned reproduction timing		Residual reproductive value		Reproductive success	
	β	*se*	β	*se*	β	*se*	β	*se*	β	*se*	*exp B*	*se*
sex	.13**	.09	-.26**	.09	-.11	.24	-.15**	.08	-01	.08	0.26**	.32
age	.13**	.00	.07	.00	-.17*	.01	.54**	.01	-.27**	.00	1.24**	.02
SEEKING	-.03	.06	.03	.06	.05	.12	.10*	.06	-.07	.05	0.83	.19
CARE	.06	.06	-.11**	.06	-.08	.14	-.17**	.05	.26**	.05	1.12	.20
PLAYFULNESS	.02	.07	.08	.07	-.03	.14	.00	.06	.06	.06	1.10	.22
ANGER	-.14**	.05	.03	.05	-.19*	.12	-.07	.05	.03	.04	1.58**	.17
FEAR	.04	.06	-.08	.06	.22*	.15	.07	.05	-.12*	.05	1.02	.20
SADNESS	.02	.06	.06	.06	-.17	.13	.02	.06	-.05	.05	0.82	.20
$F(df1.df2)/\chi^2$	$4.99_{(8, 584)}$**		$7.75_{(8,603)}$**		$2.47_{(8,184)}$*		$23.52_{(8,396)}$**		$11.05_{(8,593)}$**		$349.58_{(8.327)}$**	
R^2	.06		.09		.10		.32		.13		.43	

Notes. * $p < .05$. ** $p < .01$.; χ^2 was used as a statistic for the evaluation of the reproductive success prediction's significance; Cox & Snell R^2 was showed in the prediction of reproductive success.

Percentages of criteria's explained variance varied highly, from 6% of explained variance regarding the Onset of sexual activity, to 43% of explained variance in reproductive success (however, it should be noted that the contribution of the participants' age and sex plays a major part in this prediction, as could be expected). We can see in Table 3 that CARE is negatively correlated to Short-term mating frequency and the Planned timing of reproduction, while it positively predicts Residual reproductive value. The emotion of ANGER negatively predicted the Onset of sexual activity and Observed reproductive timing with positive contributions to the prediction of Reproductive success. FEAR had a negative independent association with Residual reproductive value while it positively predicts Observed timing of reproduction.

Interactions between the Primal Emotions and Sex in the Prediction of Fitness-related Criteria

Our final analysis was aimed at exploring the moderating role of individual sex in the link between emotions and fitness-related outcomes. We calculated interaction terms as products of centered measures of basic emotions and the participants' sex. These new variables are entered in the abovementioned regression models on the second hierarchical level. We found five interactions between sex and emotions. They are graphically plotted using the values of

unstandardized regression coefficients (excel worksheets for interaction plots, both for continuous and binary criteria measures, can be found at: http://www.jeremydawson.co.uk/slopes.htm).

Graphical representations of interactions can be seen in Figure 1. Obtained interactions showed that males with higher PLAYFULNESS (β = -.18; p = .03; marked by "a)" on Figure 1) and lower FEAR (β = .19; p = .02; marked by "b)" on Figure 1 have higher Short-term mating frequency. Furthermore, males with low expressions of the ANGER trait tend to delay reproduction to a larger extent, although with the marginal contribution of the interaction in the prediction of the Observed timing of reproduction (β = .18; p = .009 for the Planned timing of reproduction; marked by "c)" on Figure 1, and β = .29; p = .063 for the Observed timing of reproduction; marked by "d)" on Figure 1;). Finally, males with low manifestations of SADNESS have an elevated Reproductive success (exp(B) = 2.46; p = .034; marked by "e)" on Figure 1).

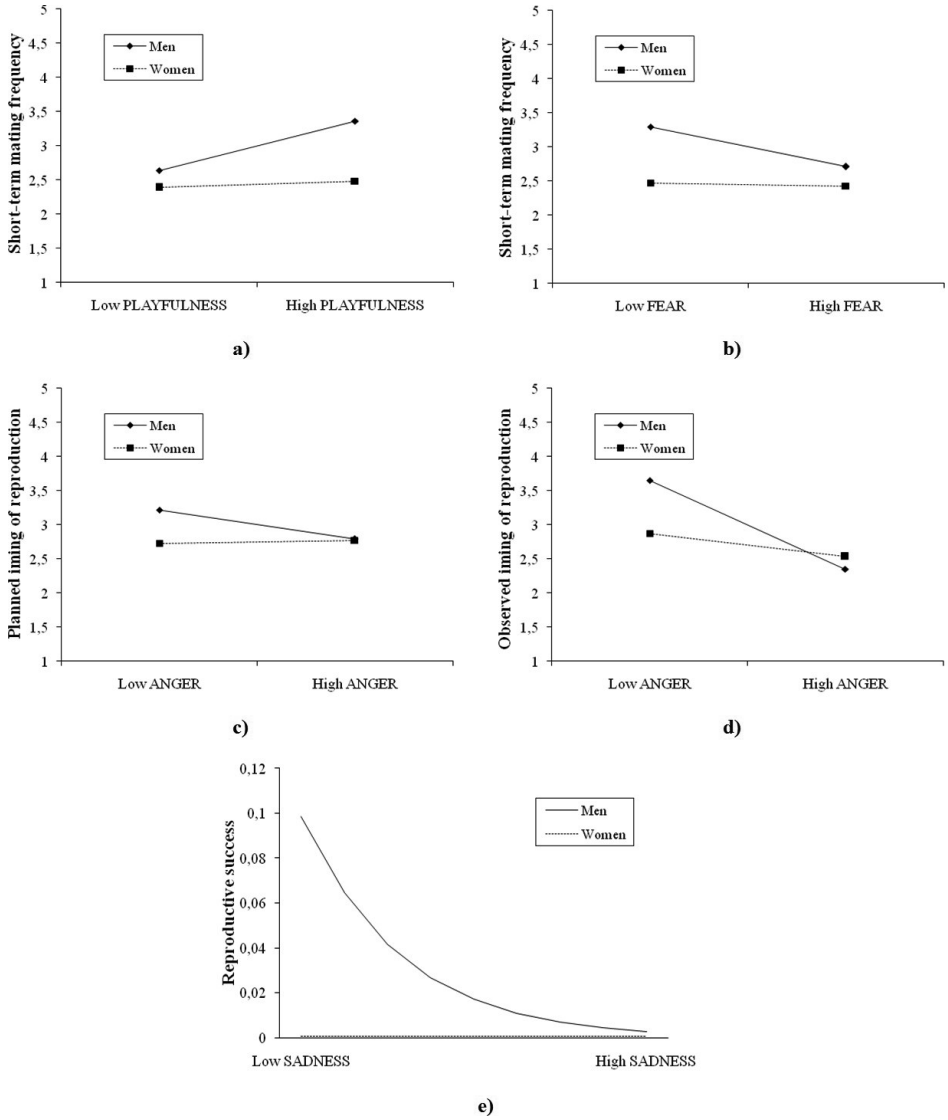

Figure 1. Interactions between basic emotions and participants sex in the prediction of fitness/life-history outcomes

Discussion

Applying the behavioral ecological conceptual framework in personality research would be beneficial in many aspects, including the insight into adaptive potentials of personality traits, ecological and individual constraints which moderate the adaptiveness of a behavior and the explanation of the variance in the behavior itself (Međedović, 2018a). Choosing the ANPS personality model for the present research was motivated by the fact that it is based on primal emotions which represent evolutionary homologies common for all mammals and with a known neurobiological and pharmacological basis (Panksepp, 2005; Panksepp & Watt, 2011). These features make the ANPS model particularly suitable for explorations based on an evolutionary and behavioral ecological framework. Indeed, the present study findings mostly confirmed the hypotheses of the relations between basic emotions and fitness-related outcomes. Furthermore, these associations are moderated by sex in a theoretically congruent fashion. Hence, the present findings are in line with the assumption that individual sex represents an internal state condition which moderates the adaptive benefits of personality.

Behavioral Ecology of Basic Emotional Systems

In our research we detected patterns of correlations between ANPS scales showing that the emotions we studied can be divided into two groups – pleasant (SEEKING, CARE and PLAYFULNESS) and aversive (FEAR, SADNESS and ANGER). This finding is in the line with previous studies which found two higher order factors in primal emotions – positive and negative emotions (Barrett et al., 2013). Furthermore, the pattern of sex differences is completely in line with previous data: males had lower scores on FEAR, SADNESS and CARE traits (Davis et al., 2003; Pingault et al., 2012). Replicating these findings in the current study suggests the validity of the data described in the present report.

Obtained findings showed that individuals with elevated CARE emotions have lower short-term mating frequency and they plan to have their first child earlier in their lifetime. Furthermore, they expect a higher number of children and they have larger observed fertility. These findings suggest that CARE is the most important basic emotion in regard to fitness optimization. They are in line with the conceptualization of CARE as a major source of parental and kin investment (Montag & Panksepp, 2017). They are also congruent with data showing that caring feelings for children or family correlate negatively with short-term mating but positively with parental status (Neel et al., 2016). Finally, these findings correspond with the positive links between the Agreeableness trait and fitness found in previous studies (Berg et al., 2013; Međedović et al., 2018). It seems that individuals with high CARE tendencies invest less in short-term mating but they compensate that in parental and reproductive ef-

forts. Long-term mating is probably their crucial mating pattern, a hypothesis which could be explored in future research.

PLAYFULNESS depicts positive reinforcement in a social interaction which facilitates the learning of social roles and understanding of social hierarchies. Hence, it is not surprising that it represents an affective basis for the Extraversion personality trait (Barrett et al., 2013). Previous findings showed that Extraversion represents a disposition towards short-term mating (Schmitt & Shackelford, 2008) and a facilitator of reproductive success (Penke & Jokela, 2016). Present data confirmed these findings to a certain extent: PLAYFULNESS had a positive association with the total desired number of children.

Former data and theoretical accounts of animal behavior showed that aggressiveness is an important personality characteristic with regard to fitness-related behavior (Smith & Blumstein, 2008). Present findings are in line with this view on aggressiveness: ANGER accelerates the onset of sexual activity and reproductive timing in males. Furthermore, the results of the regression analyses showed elevated reproductive success in aggressive individuals. Our data showed ANGER is the emotion which had the highest number of associations with fitness- relevant outcomes, together with CARE. However, it should not be forgotten that aggressive individuals may have elevated mating and fertility but experience fitness cost in parental effort or longevity (Smith et al., 2004).

FEAR is a basic emotion which generates avoidance behavior in the presence of a threat. However, in contemporary humans its evolutionary role is often biased by maladaptive feelings of anxiety (Panksepp et al., 2011). Our results show that the role of the FEAR system is mostly detrimental to fitness-related outcomes since it decreases residual reproductive value. Furthermore, low FEAR is beneficial to male short-term mating frequency. These findings are in line with the studies of romantic attachment which posit that anxiety is one of the fundamental dimensions of dysfunction in romantic and sexual relationships (Brennan et al., 1998) and short-term mating (Jackson & Kirkpatrick, 2007).

Similarly to FEAR, SADNESS is mostly negatively related to fitness. The data showed negative associations between SADNESS, residual reproductive value, and observed age at first birth. The correlation between SADNESS and reproductive success is moderated by sex: males with a low expression of SADNESS had elevated fertility. This finding is in line with the existing data which suggest that psychopathic affectivity, a trait depicting *low levels of negative emotions*, including sadness, can be positively related to fertility in males (Međedović & Petrović, 2019; Međedović et al., 2017). Finally, we can assume that certain psychological processes mediate the link between low basic emotional systems and fitness. When facing the problem of starting the family and having children, individuals have positive motives for having a child but they face a variety of obstacles, problems and fears related to raising a child as well. These incentives for childbirth and fears and doubts are frequently labeled as positive and negative motives (Miller, 1995) or reasons for or against having

a child (Langdridge et al., 2005), respectively. It is plausible to assume that individuals with elevated levels of positive emotions (especially CARE) and low levels of negative emotions (like FEAR and SADNESS) have more positive reasons for childbirth and more easily overcame obstacles for having a child, which could facilitate various reproductive outcomes.

Sex Moderates the Link Between Emotions and Fitness-related Outcomes

If a trait positively contributes to fitness, natural selection would eventually erode its variance in a population. However, if a given trait is related to states, various conditions which moderate its correlations with fitness, then natural selection cannot deplete its variance (Dingemanse & Wolf, 2010). In the present research we tested the hypothesis that sex, as an internal state, may moderate the link between basic emotions and fitness. The present data confirm this assumption to a certain extent – more pronounced ANGER and PLAYFULNESS followed by a lower expression of FEAR and SADNESS can be beneficial for fitness-related outcomes in males. These data are in accordance with the previous findings regarding the links between Big Five/Five Factor Extraversion and Neuroticism traits and fitness – the existing data also showed that Extraversion may be more beneficial to fitness in males while the opposite stands for Neuroticism (Berg et al., 2016; Gurven et al., 2014; Skirbekk, & Blekesaune, 2014). Furthermore, these data are congruent with sex differences on FEAR and SADNESS – if these traits facilitate fitness in males than they should be more expressed in men, a finding which is frequently obtained in past studies (Davis et al., 2003; Pingault et al., 2012), including the present research as well. However, following the same logic, the same should stand for ANGER and PLAYFULNESS; an assumption which is not corroborated by empirical data. The reason for this may lie in evolutionary trade-offs: ANGER and PLAYFULNESS may decrease other fitness components (which are not measured in the current study, e.g., longevity or parental investment) which may prevent the rise of their phenotypic mean levels in males.

Limitations and Future Directions

The limitation of the present study is the sample structure: our participants were still in their reproductive stage, and consequently we did not analyze completed fertility. This means that we should be cautious in interpreting the results in an ultimate fashion. Additionally, different fitness-related measures we used have different explanatory potential as operationalizations of biological adaptation: reproductive success and observed timing of first reproduction are most closely related to actual fitness, while the other indicators are associated to fitness, but cannot be viewed as fitness itself. The correla-

tions examined in the present study should be explored in post-reproductive samples as well – this would enable researchers to measure lifetime reproductive success, together with parental investment as fitness measures. Another limitation of the present study is reflected in its design. The current research is based on a cross-sectional data; this prevented us from inferring causal relationships from the data, which could only be provided by longitudinal research. Finally, it should be mentioned that a common critique of human behavioral ecology is that it rarely explores the mechanisms which increase fitness in individuals with certain traits (see for example Nettle et al., 2013). Hence, it would be fruitful if future research devote more attention to proximate mediators which could explain the associations between behavioral traits (including personality characteristics) and fitness.

Despite the limitations, the present study provided initial evidence that: 1) basic emotions may be related to evolutionary fitness in contemporary humans, which makes them probable targets for natural selection; 2) the data provided further support for the state-dependent models of personality revealing sex differences in the links between emotions and fitness-related outcomes. The latter finding suggests that exploring states could be fruitful in understanding the ways emotions contribute to biological adaptation in humans. Thus, future research could benefit from including more states, both external and internal, in empirical research. Furthermore, other mechanisms that could maintain inter-individual variation in emotions, such as evolutionary trade-offs, should be included in research as well. This strategy may provide highly needed answers regarding the fundamental features of personality by further advancing the implementation of behavioral ecological framework in human personality psychology.

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ODNOSI IZMEĐU BAZIČNIH EMOCIJA I ADAPTIVNE VREDNOSTI MODERIRANI SU POLOM KAO INTRINZIČKIM STANJEM

Jedan od ključnih problema ličnosti je postojanje inter-individualnih razlika u motivaciji, emocijama i ponašanju. Individualne razlike se mogu održavati u populacijama ukoliko su crte ličnosti povezane sa stanjima - uslovima koji utiču na posledice ponašanja koje su povezane sa adaptivnom vrednošću. U ovom radu testirali smo tu pretpostavku analizirajući pol ispitanika kao intrinzičko stanje. Ličnost je operacionalizovana preko bazičnih emocionalnih sistema: STRAH, BES, TUGA, POTRAGA, IGRA i BRIGA. Merili smo nekoliko indikatora koji su povezani sa adaptivnom vrednošću kao što su reproduktivni uspeh, rezidualna reproduktivna vrednost, tajming reprodukcije, početak seksualne aktivnosti i frekventnost kratkoročnog sparivanja. Podaci su prikupljeni na prigodnom uzorku iz zajednice dobijenom pomoću procesa "snežne grudve" (N = 635) a sam upitnik je zadavan online. Dobijene su predvidive polne razlike u izraženosti bazičnih emocija: muškarci su imali niže skorove na sistemima BRIGA, STRAH i TUGA. Nalazi su takođe pokazali da bazične emocije imaju adaptivnu ulogu u biološkom smislu (u smislu asocijacija između emocija i indikatora adaptivne vrednosti), ovo se pokazalo tačno pogotovo za emocije BRIGE i BESA. Na kraju, detektovano je pet interakcija koje su pokazale da se adaptivni benefiti emocionalnih sistema razlikuju za muškarce i žene na konceptualno očekivan način: za muškarce su visoko izražena IGRA i nisko izražen STRAH i TUGA imali pozitivne asocijacije sa sparivanjem i reprodukcijom; sa druge strane nisko izražen BES kod muškaraca je bio maladaptivan jer je bio pozitivno asociran sa planiranim i observiranim uzrastom prve reprodukcije. Rezultati istraživanja pokazali su da crte ličnosti operacionalizovane kao bazični emocionalni sistemi mogu pozitivno doprineti adaptivnoj vrednosti. Dobijeni nalazi proširuju razumevanje ljudske ličnosti kao ponašanja zavisnih od stanja i potvrđuju benefite primene modela iz animalne bihejvioralne ekologije u ljudskoj ekologiji ponašanja.

Ključne reči: adaptivna vrednost, bazične emocije, ljudska bihejvioralna ekologija polne razlike, ponašanje zavisno od stanja