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Why Human Behavioral Ecology Needs Behavioral Genetics: The Problem of Phenotypic Gambit

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The phenotypic gambit is one of the crucial assumptions in evolutionary behavioral ecology: it asserts that a phenotypic variation of a trait represents a reasonably adequate estimation of its genetic variation. This is particularly important since one of the main goals of behavioral ecology is to analyze the patterns of natural selection on phenotypic traits—the phenotypic gambit allows only the measurement of phenotypic variance of a trait, without exploring its genetic variance. The phenotypic gambit is crucially dependent on heritability itself—if there are systematic factors that decrease heritability, there is elevated chance for phenotypic gambit to fail. We argue that there is at least one ecological condition, harsh environment, which is related to markedly lower heritability of life history and behavioral traits in humans. Hence, the measurement of phenotypic variance of a trait may generate invalid results, at least for participants who originated from harsh environmental conditions. As a solution we propose the integration of behavioral ecological and behavioral genetic research designs: this integrative design allows researchers to partition the genetic and environmental variances of an examined trait and to obtain genetic correlations between the trait and fitness proxies. Furthermore, it enables that ecological conditions can be analyzed as a moderator in this link. Due to the strengths of integrated design, we believe that this research approach may be highly fruitful for the future studies in evolutionary human sciences.

Public Significance Statement

Empirical research of behavioral evolution is often conducted only on phenotypes; however, evolutionary processes are unfolding on a genetic level. Observed phenotypic data may not hold on a genetic level, especially in certain ecological conditions. Therefore, we propose closer collaboration between human (evolutionary) behavioral ecology and behavioral genetics and emphasize that this cooperation would benefit and advance both research fields.

Keywords: phenotypic gambit, human behavioral ecology, behavioral genetics, fitness, harsh environment, life history, personality

Phenotypic Gambit in Human Behavioral Ecology

Human behavioral ecology represents a unique scientific discipline which bridges natural and social sciences. It is an extension of behavioral ecology—a subdiscipline of evolutionary biology aimed to explore morphological, physiological, and behavioral traits in the light of evolutionary theory (Birkhead & Monaghan, 2010). The central term in human behavioral ecology, similarly to evolutionary biology, is fitness. It is defined broadly as a probability of transferring individual genes from one generation to the next (Hunt & Hodgson, 2010); this probability has the highest contingency to the lifetime number of offspring—this is why reproductive success is most frequently used as the main fitness proxy. The basic method of human behavioral ecology is based on analyzing the relations between behavioral traits of interest and fitness—if such relations exist, they suggest

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that examined behavioral traits are under natural selection. Hence, the empirical research of current selection regimes on human behavioral, morphological, and physiological traits represents a fundamental research goal in human behavioral ecology—this is the only empirical way to analyze adaptive function of the trait (in an evolutionary sense) and to estimate the effects of selection to the future mean population levels of a trait. The main assumption of behavioral ecology is that populations adapt to their local environments—this means that a certain behavioral trait is not universally adaptive, but it can increase fitness only in certain ecological conditions. Having in mind that humans populate various ecological niches, human behavioral ecology can explain the diversity of human behavior both within and between populations.

Note that the definition of selection is based solely on the covariation between a trait and fitness—if this association exists, we may conclude that natural selection acts upon a trait. However, this does not mean that a trait will *respond to selection*. In fact, response to selection may occur only if there is *genetic* covariation between a trait and fitness. However, most of the research in the field of human behavioral ecology is conducted only on the phenotypic measures of analyzed traits. The underlying rationale for this is an assumption of phenotypic gambit (Grafen, 1984; Krebs & Davies, 1978). This assumption states that the phenotypic variance of a trait is reasonably valid estimation of its genetic variation (van Oers & Sinn, 2011); furthermore, it implies that the genetic architecture of a trait does not represent a constraint for its phenotypic evolution (Fawcett et al., 2013). As a result, researchers may explore only phenotypic trait values and their relations with evolutionary fitness (Rubin, 2016). If the covariation between a trait and fitness is detected, then researchers can reasonably assume that this covariation is partly based on a trait's genetic variance; consequently, we can expect phenotypic changes in the mean levels of the trait across generations due to directional selection or reduction in its variation in a case of stabilizing selection. The phenotypic gambit is one of the fundamental assumptions in behavioral ecology—it allows that empirical studies do not estimate genetic variation directly, they can rely solely on phenotypic information instead. Indeed, there are empirical findings which show that phenotypic gambit may be a solid assumption in both humans (Sodini et al., 2018) and other animals (Brommer & Kluen, 2012). On the other hand, the phenotypic gambit has been criticized on various grounds, especially because it oversimplifies the relations between the genotype and phenotype (Dall et al., 2019). Furthermore, the assumption that genetic architecture does not constrain the evolution of a trait may too be invalid (Hadfield et al., 2007; Rubin, 2016).

In the present manuscript, we aim to question the phenotypic gambit on the ground of heritability itself. Heritability is usually defined as a proportion of a phenotypic trait's variation which is explained by its genetic underpinnings. It is a population statistic that is sensitive to cohort characteristics, ecological conditions, and even the age of individuals in which is estimated. Heritability can be estimated using various methods; some of the most frequent ones are twins and family studies (where heritability is estimated via comparing phenotypic correlations between the individuals varying in genetic resemblance; e.g., Posthuma et al., 2003), pedigree data (also known as "animal" model, where heritability is derived from the similarity in phenotypic traits of individuals sharing the same biological lineage; e.g., Bochud, 2012; Milne et al., 2008; Schwartz et al., 2015) or the samples of unrelated individuals where a large number of genetic polymorphisms is used to infer heritability—genome-wide association studies or GWAS and genome-wide complex trait analysis or GCTA (e.g., Yang et al., 2011). Although natural selection potentially may act on any trait, a response to selection will crucially depend on trait's heritability because evolutionary changes are based on the change of the frequency of gene alleles which contribute to the trait's phenotypic expressions. However, heritability estimates tend to be variable: this fact represents a problem for phenotypic gambit per se, because in conditions of low heritability, the phenotypic gambit has a higher probability to fail (van Oers & Sinn, 2011). Furthermore, we would like to emphasize an additional condition which may systematically deplete heritability, the one which may be especially important in a behavioral ecological research—harsh environment. First, we would like to illustrate the problem of phenotypic gambit by analyzing heritability estimates in life history and behavioral traits.

The Problem of Phenotypic Gambit: Variation in Heritability Coefficients

Heritability Coefficients of Life History Traits

Behavioral ecologists believe that in order to understand how individuals maximize fitness we should measure various indicators related to reproductive, parental, or longevity-related behavior. The most frequently measured traits and events are reproductive success, age of first and last reproduction, pubertal timing, onset of sexual behavior, number of sexual partners, and parental investment (Belsky, 2012; Mell et al., 2018; Xu et al., 2018). A conceptual framework which analyzes the relations between these indicators using evolutionary theory is called life history theory (Bolund et al., 2016; Roff, 2002). Life histories of individuals are heavily dependent on the ecological conditions. One of the main ecological determinants of life history dynamics is environmental harshness. Generally, it is assumed that harsh, stressful, low resource, and hostile environments are related to life history patterns aimed at maximize fertility: earlier maturation, onset of sexual behavior and first reproduction, short-term mating, higher reproductive success, followed by a decrease in parental investment and overall health. In contrast, a beneficial and supporting environment, abundant with resources, is associated with the opposite trend: delayed maturation, onset of sexual behavior and first reproduction, long-term mating patterns, lower number of offspring with elevated parental investment, and increased levels of health and longevity. The former pattern of life history indicators is labeled as a “fast” life history pathway, while the latter is labeled as “slow” (Del Giudice et al., 2015). Various characteristics of harsh environment have been found to positively associate with the fast life history trajectory: frequency of violent crimes (Copping & Campbell, 2015), higher mortality rates and lower life expectancy on birth (Griskevicius et al., 2011; Wilson & Daly, 1997), lower socioeconomic status (Sheppard et al., 2016), violent intergroup conflict (Međedović, 2019a), the absence of a father (Webster et al., 2014), lack of maternal sensitivity (Dunkel et al., 2015), troubled family relations (Chisholm et al., 2005), and so on. It is important to note that the application of life history theory in explaining human individual differences and especially the existence of fast–slow continuum has been recently criticized (Međedović, 2020, 2021; Sear, 2020; Stearns & Rodrigues, 2020; Zietsch & Sidari, 2020). Still, other authors believe that the slow–fast dimension of life history dynamics is still useful in interpreting the data, although the scholars should invest more effort to refine life history framework and provide more complex models for its application in humans (Del Giudice, 2020; Galipaud & Kokko, 2020).

Life history traits are heritable, although the proportion of genetic variance in life history traits is lower than the one in morphological or behavioral traits in both humans (Stearns et al., 2010) and other animals (Visscher et al., 2008). Certainly, the most central life history trait is reproductive success itself—the number of biological children an individual has also labeled as fertility. Family and pedigree studies yielded similar results regarding the heritability of reproductive success. First, most of the twin studies found additive genetic variation in reproductive success (e.g., Colodro-Conde et al., 2013; Kohler et al., 2002; Polderman et al., 2015; Silventoinen et al., 2013; reviewed in Mills & Tropf, 2015). Furthermore, they revealed that the heritability of reproduction success highly varies between the cohorts of participants (Briley et al., 2015) or estimates of fertility in different stages of ontogeny (Rodgers et al., 2007)—this variation ranges from zero to moderate effect sizes.

Pedigree studies estimates are lower in magnitude (e.g., Bolund et al., 2013 [fertility is estimated as the number of grandchildren in this study]; Bolund & Lummaa, 2017) but importantly, the range of heritability estimates is also high—when comparing fertility in different life stages (Pettay et al., 2008) or different samples (Milot et al., 2011; Pettay et al., 2005), coefficients range from nonsignificant to moderate ones.

Quite similar empirical data exist for other life history traits. Data also show that heritability coefficients of the age of first reproduction highly vary—from near-to-zero to moderate effect sizes (Mills & Tropf, 2015). Both twin (Briley et al., 2015; Silventoinen et al., 2013; Tropf, Barban, et al., 2015) and pedigree methods converge to this conclusion (Bolund et al., 2013; Bürkli & Postma, 2014). The data on age of menarche are a bit different: estimates show higher heritability, compared to reproductive success and age of first reproduction, which ranges from 50% to 70% depending on the method of estimation and sample characteristics (Sørensen et al., 2013; Sulem et al., 2009; van den Berg & Boomsma, 2007). The heritability of other life history traits has been examined as well; however, the research on other traits is still quite scarce so we cannot reliably estimate the variability of heritability coefficients. Nevertheless, significant heritability coefficients have been found in breastfeeding (as an indicator of parental investment), the onset of sexual behavior, the number of sexual partners, and the probability of being married (Cherkas et al., 2004; Colodro-Conde et al., 2013; Trumbetta et al., 2007; Waldron et al., 2007).

Explaining Heritability Variation in Life History Traits: Implications for Current Life History Evolution

The variation in heritability coefficients certainly has multiple causes; some of the frequently detected parameters which influence this variation are the age and sex of participants (Mills & Tropf, 2015). There are environmental causes in this variation as well. It has been noted that heritability of fertility and age of first reproduction changes across the cohorts in the late 19th and whole 20th century—generally the data point to the conclusion that heritability is higher when demographic transitions started to unravel (Kohler et al., 2002); for example, heritability is higher in individuals born between 1936 and 1955 compared to the 1920–1935 cohort (Briley et al., 2015; however, in the 1956–1970 cohort the heritability of fertility persisted but not the one of the age of first reproduction). Heritability of fertility was also higher in urban, compared to rural environments (Bras et al., 2013). One of the explanations for these results is that in demographic transition populations (characterized by lower fertility partially caused via accessible methods of birth control), urban environments, and later 20th-century generations there was enhanced *choice* in making reproductive decisions (Briley et al., 2015; Udry, 1996). Perhaps it sounds counterintuitive that the elevated choice in fertility-related behavior gives rise to the genetic underpinnings of the same behavior. However, this explanation becomes apparent if we note the following: (a) the role of social and environmental factors in a broader sense has decreased in these contexts, which allowed genetic mechanisms to influence behavior in a greater extent; (b) motives for childbearing, including the number of desired children are heritable psychological traits as well (Miller et al., 2010; Pasta & Miller, 2000), hence, when individuals have a choice to make their reproductive decisions, this choice is partly a result of underlying genetic variation. The data of shared genetic variation between fertility motivation and observed number of children are clearly in line with the previous explanation (Rodgers et al., 2001).

The data on elevated heritability of fertility in urban environments can be explained by other processes postulated in behavioral genetics that have high relevance for behavioral ecology as well: genotype–environment correlations or rGEs (Meek et al., 2013). There are three types of these correlations: passive, evocative, and active (Plomin et al., 1977). Passive correlation describes the congruence between parental genotype and parental behavior toward offspring; evocative correlation highlights the responses from children toward their environment that further guides their development. Finally, active correlation describes the tendency of individuals to search for new environments that suits their genetic potentials; therefore, changing the environments may lead to a better match between ecological conditions and genetic dispositions. Furthermore, if we choose environments in order to be suited for our genetic dispositions, this would enable higher genetic expressions on behavior, and consequently the increase in heritability estimates. This is why active genotype–environment correlation can explain higher heritability of fertility in urban environments, especially in conditions of elevated migration from rural to urban ecologies. The conceptual benefits of active genotype–environment correlation for behavioral ecology are apparent—if changing environments leads to better functioning in new ecological conditions, this behavior may be viewed as an adaptation. However, as far as we are aware, there is no empirical research in humans that examine active genotype–environment correlation in the context of biological adaptation so far—this remains a fruitful topic for future research.

The magnitude of heritability coefficients is linked to environmental harshness as well—broadly viewed as the level of deprivation, lack of resources, hostile, and stressful environments versus beneficial, resource-abundant, and supporting environments. It has been noted that the genetic variation in number of children and grandchildren is higher in landowning compared to landless families (Bolund & Lummaa, 2017). Intriguing findings are obtained on the heritability of first sexual intercourse—genetic variation explained 39% of the onset of sexual behavior's phenotypic variation in females without the history of child sexual abuse; however, in women who reported sexual abuse in childhood, the genetic influences on the age of first intercourse drops to zero (Waldron et al., 2008). Hence, the percentage of genetic variation in phenotypic values of life history traits is higher in favorable environments, a finding which is obtained in other animals as well (Visscher et al., 2008). Note that the levels of harshness are probably related to the level of individual freedom discussed earlier: more supporting and beneficial environments are likely the same ones which provide higher freedom to make choices about sexual and reproductive behavior.

Thus, the variation in heritability of life history traits may represent one of the constraints for their evolution, and it may cause the failure of phenotypic gambit. There are empirical data which suggest that this indeed may be the case. For example, one study found low but significant positive association between breastfeeding and reproductive success (interestingly, life history theory would predict a negative association between these traits[1])—this finding alone could suggest that breastfeeding may be under positive directional selection; nevertheless, the genetic association between these two traits was not statistically significant (Colodro-Conde et al., 2013). A more striking example comes from the study which investigated sex differences regarding selection on several life history traits (Bolund et al., 2013). Phenotypic analysis showed that sex moderated relations between age of first and last reproduction, and fitness (i.e., reproductive success)—this finding implies sexual selection on these traits which may result in heightened differences in timing of reproduction between males and females. However, genetic correlations between life history traits and fitness were quite similar in both sexes, the finding that suggests an opposite process—a convergent life history evolution in males and females. Another study (Beauchamp, 2016) showed positive associations between body mass and fitness and negative between female height and fitness, but there were no genetic associations between these traits; phenotypic gambit held only for educational level which showed negative genetic and phenotypic associations with fitness. Finally, there is even evidence of a larger discrepancy between genotypic and phenotypic levels of analysis—associations which have opposite signs. Sanjak et al. (2018) obtained some converging links between life history traits and fitness (e.g., negative association between age of first birth and fitness) but they found positive relation between age of menopause and fitness on the phenotypic and negative on the genetic level.

Hence, there are empirical data that cast a doubt on the phenotypic gambit's reliability. Furthermore, there is reason to doubt phenotypic gambit even when there are mirroring associations on phenotypic and genetic levels. One of the key assumptions of life history theory is related to local ecologies: a harsher and depriving environment should facilitate the evolution of phenotypes which contribute to reproductive output and early fertility, including morphological, physiological, behavioral, and life history traits in a narrow sense. However, previously described data on life history traits' heritability showed lower heritability coefficients in the conditions of a harsh environment. Therefore, it is questionable whether genetic correlations between life history traits and fitness would hold in subpopulations characterized by harsh environmental conditions—the mere lack of genetic variation may constrict covariation with fitness as well. In these cases, a fast life history phenotypic response in a harsh environment would not be a consequence of genetic evolution

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[1] Breastfeeding is a form of parental investment; one of the major evolutionary tradeoffs is the one between quality and quantity of offspring—this tradeoff implies that parents cannot invest as much if they have higher number of offspring compared to fewer offspring. Parental investment can evolve if individuals with lower number of offspring can have offspring with elevated quality by increased investment in them. In the life history context, fast life history trajectory would be depicted by higher reproductive success and lower parental investment; inverse pattern should characterize slow life history. The cited study shows that this prediction cannot hold in populations where fertility is generally low —quantity–quality tradeoff can be more easily found in natural fertility populations (Gillespie et al., 2008; Meij et al., 2009).

but the processes which act on an ontogenetic level like developmental and behavioral plasticity (Nettle & Bateson, 2015).

The Case of Behavioral Traits—Personality and Cognition

A personality trait is any behavioral pattern that is relatively stable in time, and that shows considerable inter-individual differences in a population. There are many taxonomies of human personality traits; one of the most prominent is the Big Five personality model (John et al., 2008) which consists of five traits: Extraversion (sociability, activity, positive affectivity), Neuroticism (negative emotionality), Agreeableness (cooperation, empathy, altruism), Conscientiousness (orderliness, behavioral control), and Openness to experience (inquisitiveness, creativity). Personality traits are adaptive behavioral dispositions (at least at certain levels of traits' expressions)—a fact which is reflected in their relations with fitness in both humans (Allen & Robson, 2018; Gurven et al., 2014; Međedović et al., 2018) and other animals (Smith & Blumstein, 2008). In fact, it is shown that every one of the major human personality characteristics is associated with fitness, although the obtained links may vary as a function of sample characteristics (Penke & Jokela, 2016). Personality traits show moderate heritability—around 40% (Vukasović & Bratko, 2015); this fact, combined with their association with fitness, marks their potential to evolve under natural selection.

Unfortunately, there are only a few studies which examine if the link between personality and fitness exists on genetic level as well. In fact, some data showed that phenotypic gambit may apply to human personality: certain findings showed the same phenotypic and genetic associations between personality traits and fitness (Berg et al., 2016; Briley et al., 2017; the matrix of phenotypic associations between personality traits and fitness in the latter study was obtained via personal communication with the first author). However, it is highly debatable if these associations would hold in every sample. The heritability of personality is highly variable and depends on numerous characteristics of the analyzed samples (Bratko et al., 2017), including the age of the participants (Kandler et al., 2021). Furthermore, environmental harshness turned out to be an important determinant of heritability in personality as well: it has been found that the heritability coefficients are lower in participants who received more negative and stressful parental behavior (Krueger et al., 2008). There are findings showing that the heritability of the Emotional Dysregulation trait (which is similar to the trait Neuroticism) drops almost to zero in environments with high family conflict (Jang et al., 2005). The existing data imply that the heritable variation in personality may be reduced in conditions of environmental harshness.

The hypothesized role of the environment in the heritability of behavioral traits is even more convincing for cognitive abilities. Intelligence is a broad term to capture cognitive abilities related to problem solving and it has a profound influence on various behaviors and life outcomes. Furthermore, intelligence is a trait which probably has the highest heritability among the human behavioral characteristics—estimates even go to 80% (Sauce & Matzel, 2018). While it is quite plausible to hypothesize that cognitive abilities evolved as an adaptation, there is an ongoing debate whether intelligence is adaptive in contemporary humans, due to a mismatch between adaptations and environment. This debate is reflected in empirical data as well: both negative (Reeve et al., 2013; Shatz, 2008) and positive (Kolk & Barclay, 2021; Međedović, 2017) associations were detected between the phenotypic scores of intellectual performance and fitness. Hence, examining the current evolution of intelligence remains an intriguing and exciting task. Various factors contribute to the variation of heritability estimates in intelligence; for example, age seems to be an important cause of heritability coefficients' increase in cognitive abilities (Haworth et al., 2010). Furthermore, there are differences in heritability of intelligence in different environmental conditions—the data show that heritability estimates are lower in individuals who grew up in the conditions of economical poverty (Tucker-Drob et al., 2013). There are studies estimating the heritability of intelligence to be 72% in wealthy, compared to 10% in children living in economic deprivation (Turkheimer et al, 2003). Although, it must be noted that the effect of harsh environment on the heritability estimates of intelligence is more common for some countries than others; for example, the effect is ubiquitous in the United States but practically absent in Australia (Bates et al., 2016; Tucker-Drob & Bates, 2016). Hence, harsh environment may not be necessarily linked to heritability depletion in cognitive abilities and this association may be dependent on other ecological conditions. There are additional critiques of this assumption as well—some data suggest that lower heritability estimates in poorer environments are not the consequence of lower additive genetic variation but elevated shared environmental variance (Hanscombe et al., 2012). Nevertheless, such a high range in intelligence's heritability can represent a major obstacle in the research on its contemporary evolution if only phenotypic scores of cognitive abilities are analyzed: low heritability decreases the chances that the covariation between the trait and fitness will be found on a genetic level. Consequently, it diminishes the possibility that the trait would respond to natural selection.

Particularly Vulnerable Traits—Adaptations to Harsh Environment

Behavioral ecologists often explicitly analyze ecological conditions as factors which moderate the links between a trait and fitness, that is, there are traits which may be adaptive only in certain conditions. In fact, there are behavioral traits which are assumed to be adaptive especially in harsh environments. An example of such a trait is psychopathy—it represents a behavioral syndrome consisting of several traits: diminished tendency to generate negative emotions (especially fear, guilt, and empathy), manipulative and deceitful behavior, and lower behavioral control based on impulsivity and disinhibition (Hare, 2003; Lilienfeld & Andrews, 1996; Patrick et al., 2009). Similarly to other personality traits, psychopathy was shown to have moderate heritability (Tuvblad et al., 2019). Evolutionary ecological analysis suggested that psychopathy may positively contribute to evolutionary fitness although the adaptiveness of psychopathy may be dependent on its frequency in a population—psychopathic phenotypes may be adaptive only if they are rare (Mealey, 1995). Furthermore, it is assumed that psychopathy can increase fitness especially in the harsh environmental conditions (Glenn et al., 2011). Psychopathic affectivity may represent a trait which enables individuals to overcome adaptive challenges more successfully in such environment because it elevates stress tolerance. Despite the fact that psychopathy is mainly viewed as a maladaptive, even pathological trait, empirical data confirmed behavioral ecological predictions: manipulative and affective traits were found to elevate reproductive fitness (Međedović, 2019b; Međedović & Petrović, 2019) and adaptive potentials of psychopathy are indeed more expressed in a harsh, depriving, and stressful environment (Međedović, 2019c; Međedović et al., 2017). However, the above-mentioned associations were obtained only on the phenotypic level. Since the possibility that psychopathic traits have lower heritability in a harsh environment is at least plausible, we can pose a question whether these links can be replicated on a genetic level as well. Unfortunately, there are no empirical research studies that examine genetic associations between psychopathy and fitness, especially the ones which explore these links in various environments so far.

A Possible Solution: Integration of Behavioral Ecology and Behavioral Genetics

Behavioral Genetics and Its Application to Human Behavioral Ecology

It seems that the phenotypic gambit cannot be sustained in all circumstances; furthermore, there are environmental conditions, such as harsh environment, which elevate the probability of phenotypic gambit's failure. The solution seems apparent: behavioral ecologists need genetic information which could allow them to more validly and reliably infer if the trait under natural selection would indeed respond to selection. Molecular genetics has been largely unsuccessful in determining gene variants which participate in a phenotypic expression of behavioral traits (Jarnecke & South, 2017), mostly due to their highly polygenic nature; gene-candidate studies showed to be particularly prone to fail in replicating the findings about the specific genetic polymorphisms related to behavioral traits, while GWAS studies have higher chance to find and replicate the findings on molecular genetic basis of behavior (Chabris et al., 2015). Among several methods, behavioral genetics, as a quantitative genetics applied to behavior, seems to have the highest analytic potential since it can partition the phenotypic variation of a trait into the genetic and environmental variance components, allowing analyses to be performed on both variances (Plomin et al., 2008). Furthermore, compared to some other methods of heritability estimation, behavioral genetics provides higher genetic variation estimates: other methods such as GWAS are characterized by missing heritability, which results in lower heritability estimates (Manolio et al., 2009; although it must be said that GWAS studies have substantial contribution to understanding genetics of reproductive-related traits: Gajbhiye et al., 2018). The integration of behavioral genetics in evolutionary human sciences has been proposed on several previous occasions (see Barbaro et al., 2017). These appeals came mostly from evolutionary psychology (Zietsch et al., 2015); however, due to their theoretical assumptions (e.g., evolutionary mismatch hypothesis; Li et al., 2018), evolutionary psychologists do not aim to empirically estimate current selection regimes on behavioral traits (i.e., they do not measure current fitness). Hence, we are focused on ways behavioral genetics can help behavioral ecologists analyze the relations between behavioral traits and fitness.

Behavioral genetics uses information about the genetic similarity between individuals to estimate heritability. The most prominent behavioral genetic methodology is based on the examination of the phenotypic traits in twin pairs: heritability is estimated by comparing correlations of phenotypic traits in monozygotic and dizygotic twins (Plomin et al., 2008). But more importantly, this method allows for decomposing the phenotypic trait's variation into genetic, shared environmental (the environment which is common for both twins such as family context), and unique environmental variation (the events and experience which is unique for every member of a twin pair). Shared environment results in heightened similarity between the twins, whereas non-shared environment contributes to the differences between the twin-pair members. Hence, every analysis may be performed on phenotypic, genetic, and environmental variation of examined phenotypical measures (shared environmental variance is quite low for many traits, therefore, for such traits only unique environmental variation is suitable for separate analyses).

The main benefit of behavioral genetics is the ability to perform direct testing of phenotypic gambit. The majority of behavioral genetics studies compare phenotypic and genetic correlations of the examined variables. But in behavioral ecology, the baseline research design should be a bit more complex. The integration of behavioral ecology and behavioral genetics must include at least four sets of variables: (a) the traits which represent target concepts of the research—life history, physiological, morphological, or behavioral traits; (b) fitness proxies—reproductive success (number of children and grandchildren), longevity, parental investment, and so on; (c) genetic information—in this case, represented as genetic variation in general, not specific alleles or other polymorphisms; (d) environmental conditions—harsh environment or other ecological variation of interest. Thus, the method is not simply based on conducting separate analyses on genetic and environmental variation of certain traits—the crucial hypotheses involve testing the environmental conditions as a moderator in the link between certain traits and fitness. This means that the analysis must involve two steps: first, a researcher removes the environmental variation of analyzed variables, leaving only genetic variation for further examination; afterwards a researcher should analyze if the genetic links between the trait and fitness exist in different environments (e.g., harsh and beneficial). For example, if we want to obtain unambiguous evidence of natural selection's influences on psychopathy we analyze the genetic link between psychopathy and reproductive success; subsequently, we examine if this (genetic) link holds for various environmental conditions or if it exists only in certain ecologies.

Basic conceptual frameworks for these analyses already exist in behavior genetics. The hypothesis that genetic links between a trait and fitness exist only in certain environments is congruent with the concept of gene—environment interaction (Manuck & McCaffery, 2014; Shanahan & Hofer, 2005). It is often defined as genetic control of sensitivity to various environments, or equivalently, as the environmental control of differential gene effects. In behavior genetics research, the particularly important design incorporates genetic variation operationalized as a latent variable (e.g., additive genetic variance) with environment as a measured variable (e.g., socioeconomic status, childhood stress, social ostracism). Behavior geneticists typically examine if heritability coefficients for a given trait vary across different environments

(Purcell, 2002). In a behavioral ecological context, we could examine genetic associations between traits and fitness across different environments.

This said, it is important to mention the limitations of behavioral genetics as well. The most common criticisms point to two problems; firstly, the assumption of shared environment may be invalid - do parents have the same behavior toward twins, especially dizygotic ones? Because if they not, the shared environmental influences are not the same for dizygotic twines as the model expects. Secondly, twin samples may not be representative for the whole population; hence a problem of findings' generalizability emerges (e.g., Burt & Simons, 2014; Jarnecke & South, 2017). Another problem refers to assortative mating: if couples' pairing is based on similarity in certain traits, this may influence biometric parameters by increasing the heritability estimates (Ruby et al., 2018). However, other researchers pointed out that possible violations of biometric modeling assumptions do not invalidate the results of behavioral genetic analyses. For example, it is shown that the hypothesis of equal shared environment for monozygotic and dizygotic twins is rarely violated, and even if it is it has very low and unsystematic effect on heritability estimates (for a detailed discussion on this topic, see Barnes et al., 2014). Still, some specific aspects of generalizability criticism can be especially important for behavioral ecology: by examining only twins, behavioral genetic studies exclude families with low fertility; furthermore, dizygotic twinning is genetically based which means that including dizygotic twins in a study sample may produce biased estimations of fertility-related traits (Tropf, Stulp, et al., 2015).

Additional Potentials of a Behavioral Ecology/Genetics Integrated Design

The partition of a trait's variation into genetic and environmental ones is the most basic behavioral genetic design. The methodology provides more complex designs based on structural modeling that are of clear importance for behavioral ecology. Therefore, although we were focused on a harsh environment as a factor which decreases heritability and consequently questions phenotypic gambit, we would like to provide other reasons for the integration of behavioral ecology and genetics. We do not aim to present a comprehensive review, but examples of heuristic powers embedded in integrated design.

In behavioral ecology it is very rare to explore the link between a single trait and fitness—multivariate designs are frequently applied, the ones where associations between the suits of traits and fitness are estimated simultaneously (Sinervo & Calsbeek, 2010). This is of utmost importance since various characteristics of individual differences are related between themselves, both on a phenotypic and genetic level. The latter associations are the result of genetic pleiotropy—a situation where a single genetic variant or a suit of variants are associated with several phenotypic traits. Pleiotropy has an important implication for behavioral ecological analysis; for example, a trait does not need to be directly genetically related to fitness in order to be under natural selection—it may be affected by selection if it is genetically associated with other traits linked with fitness. An example comes from one of the rare research which explored genetic associations between personality traits and fitness: the data showed that the Neuroticism trait is not related to reproductive success on a genetic level; however, Neuroticism was genetically negatively associated with Extraversion, a trait found to elevate the number of children on a genetic level (Berg et al., 2016). Therefore, if we analyzed only bivariate genetic associations between personality traits and fitness we may erroneously conclude that Neuroticism is selectively neutral; however, it may be under negative directional selection via its genetic associations with Extraversion. Multivariate models provide another advantage besides biologically more valid estimation of traits' evolution due to the presence of pleiotropy and correlational selection—exploration of multivariate genetic constraints on traits' change under natural selection (Walsh & Blows, 2009).

The problem of causality is present in behavioral ecological research as well—the most valid information on selective forces acting on a trait should demonstrate that trait affects fitness, not vice versa (but vice versa is plausible as well, for example, having children may change personality traits of parents: Jokela et al., 2009). Hence, longitudinal designs enable more convincing data in behavioral ecology, similar to other scientific disciplines. Behavioral genetics provide an additional piece of information to these designs: by using Cholesky models behavioral geneticists may analyze if genetic variation of a trait obtained at an earlier age can predict variation in fitness at a later age (preferably in a post-reproductive period of ontogeny). For example, Rodgers et al. (2007) found that genetic factors which are positively associated with early fertility (at the age of 20 years) are negatively associated with later fertility (at the age of 30 and 35 years). This finding suggests that the same genetic variants may have opposite effects on fitness in different stages of ontogeny.

There is another exciting paradigm in animal behavioral ecology which examines social evolution of the traits—it is labeled as indirect genetic effects or interacting phenotypes (Bailey et al., 2018; Wolf & Moore, 2010). Indirect genetic effects emerge if the phenotype of a focal individual is influenced by the genotype of its social partners. Hence, the environmental variation examined in this framework is social, not the physical environment—in principle, every individual that has interactions with the focal individual can be analyzed as a source of indirect genetic effects. One of the apparent social partners analyzed in empirical research are mating partners (Danielson-François et al., 2009) and parental dyads (Head et al., 2012). Unfortunately, interacting phenotypes are not yet studied in human behavioral ecology, at least as far as we are aware. This is unfortunate because they provide a unique theoretical perspective which may provide more valid and precise estimations of traits' evolution since interactive phenotypes can bias evolutionary trajectories and elevate traits' response to selection (Bailey et al., 2018). Behavioral genetics can provide an adequate platform for examining indirect genetic effects in humans. The logic of a research design is similar to previously described studies focused on environmental harshness. We could use twin designs to decompose the variation of a trait into genetic and environmental components; afterwards we can analyze if the genetic variation of a trait is related to fitness of their mating partners—for example, their fertility, longevity, or parental investment.

Concluding Remarks

Behavioral genetics and behavioral ecology had distinct developmental trajectories as scientific disciplines and even today they remain relatively separate. This state of affairs is not surprising since the main research focus and questions are different in these two disciplines. In the present manuscript, we focused on a problem of phenotypic gambit as a potentially critical condition which may jeopardize the findings in behavioral ecology; however, the integration of two fields has an extraordinary explanatory potential in general and it can help both fields to further develop and grow. Behavioral genetic methodology can help human evolutionary ecology to obtain unambiguous answers of selective regimes acting on phenotypic traits, and to pose more complex questions regarding the interactions between individuals and their ecologies, physical and social environments. On the other hand, behavioral ecological approach can open new doors of scientific inquiry for behavioral geneticists—the latter mostly estimated genetic and environmental variation of phenotypic traits and analyzed its consequences so far. Behavioral ecology can help them to study the causes of this variation and its evolutionary dynamics; this can provide deeper insight into the complex evolution of behavioral traits and help estimate future changes in phenotypic characteristics. Therefore, evolutionary social sciences would gain large benefits if these two research fields would integrate: this may help in opening new and even more exciting chapters in the story of contemporary human evolution.

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