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ORIGINAL ARTICLE

Under pressure: human adolescents express a pace-of-life syndrome

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Abstract

The pace-of-life syndrome (POLS) hypothesis posits that life-history characteristics, among individual differences in behavior, and physiological traits have coevolved in response to environmental conditions. This hypothesis has generated much research interest because it provides testable predictions concerning the association between the slow-fast life-history continuum and behavioral and physiological traits. Although humans are among the most well-studied species and similar concepts exist in the human literature, the POLS hypothesis has not yet been directly applied to humans. Therefore, we aimed to (i) test predicted relationships between life history, physiology, and behavior in a human population and (ii) better integrate the POLS hypothesis with other similar concepts. Using data of a representative sample of German adolescents, we extracted maturation status for girls (menarche, $n = 791$) and boys (voice break, $n = 486$), and a set of health-related risk-taking behaviors and cardiovascular parameters. Maturation status and health-related risk behavior as well as maturation status and cardiovascular physiology covaried in boys and girls. Fast maturing boys and girls had higher blood pressure and expressed more risk-taking behavior than same-aged slow maturing boys and girls, supporting general predictions of the POLS hypothesis. Only some physiological and behavioral traits were positively correlated, suggesting that behavioral and physiological traits might mediate life-history trade-offs differently. Moreover, some aspects of POLS were sex-specific. Overall, the POLS hypothesis shares many similarities with other conceptual frameworks from the human literature and these concepts should be united more thoroughly to stimulate the study of POLS in humans and other animals.

Significance statement

The pace-of-life syndrome (POLS) hypothesis suggests that life history, behavioral and physiological traits have coevolved in response to environmental conditions. Here, we tested this link in a representative sample of German adolescents, using data from a large health survey (the KIGGs study) containing information on individual age and state of maturity for girls and boys, and a set of health-related risk-taking behaviors and cardiovascular parameters. We found that fast maturing girls and boys had overall higher blood pressure and expressed more risk-taking behavior than same-aged slow maturing girls and boys. Only some behavioral and physiological traits were positively correlated, suggesting that behavioral and physiological traits might mediate life-history trade-offs differently and not necessarily form a syndrome. Our results demonstrate a general link between life history, physiological and behavioral traits in humans, while simultaneously highlighting a more complex and rich set of relationships, since not all relationships followed predictions by the POLS hypothesis.

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Introduction

The pace-of-life syndrome (POLS) hypothesis seeks to characterize phenotypic attributes that mediate the trade-off between current and future reproductive success (Réale et al. 2010; Careau and Garland 2012). As such, it extends one of the core trade-offs in life-history theory (Stearns 1989), to

include behavioral and physiological attributes, whereby the assumption is that these attributes have coevolved resulting in a suite of co-varying, functionally relevant traits, depending on the local ecology (Réale et al. 2010). Following the introduction of the POLS hypothesis in animal and behavioral ecology, there has been a rapid accumulation of studies testing the original POLS predictions in a wide range of animal species with conflicting results (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes). Whereas there is an abundance of studies investigating POLS in animals, the POLS hypothesis has not yet been directly applied to the domain of human ecology although many similar concepts have been developed (for more details, see below).

Humans show a relatively slow life history, in comparison to most other mammal species, with late maturation, long life span, senescence, but short inter-birth intervals in comparison to same sized primates (Smith 1992; Hill and Kaplan 1999; Kaplan et al. 2000). Substantial variation in several key human life-history traits (e.g., growth velocity, age of menarche, onset of puberty) has been reported, both on the within and the between population level (Eveleth and Tanner 1990; Worthman 1999; Walker et al. 2006; Pettay et al. 2007). The main focus of the POLS hypothesis is on the trade-off between current and future reproductive success; however, specific characteristics of humans (e.g., longevity, extended parental care, and intergenerational effects) create several more important trade-offs (see "Discussion").

In the human ecology literature, several conceptual frameworks have been introduced, which bear close resemblance to the POLS hypothesis. One of the earliest theories, integrating life-history traits, behavior, and physiology in humans, was proposed by Rushton (Rushton 1985; Figueredo et al. 2013): In his differential K theory, Rushton categorizes humans along a continuous dimension K, with higher K values representing individuals coming from small families with higher parental investments and longer inter-birth intervals and these individuals are predicted to also mature slower and show higher behavioral constraint and altruism (see also Ellis 1988; Figueredo et al. 2004). As such, Rushton's theory is an application of the "r/K selection" theory introduced by MacArthur (MacArthur 1962; MacArthur and Wilson 2015). Belsky et al. (1991) developed an influential evolutionary-based theory of social organization and lifespan interpersonal development. Their theory postulates that a range of early social contexts, rearing, and physiological and behavioral orientations, predict markers of reproductive strategy (e.g., pubertal timing, sexual activity, and pair bonding) in an adaptive manner. More specifically, the experiences during early life (5–7 years) are predicted to give individuals an estimate of the availability and predictability of resources and trustworthiness of their social environment in the future. Individuals experiencing scarce and/or unpredictable resources and untrustworthy others are expected to advance their sexual maturation and invest less in social bonds. Building on these insights, Ellis et al. (2009) introduced a developmental theory of inter-individual variation in humans proposing a cluster of correlated life-history traits lying on a slow-to-fast continuum, crucially mediated by environmental harshness and unpredictability. Other frameworks have also integrated physiological attributes [e.g., stress response (Del Giudice et al. 2011)] and/or behavioral attributes [e.g., extraversion (Nettle 2005), risk-taking (Ellis et al. 2012)] with life-history traits (see also Belsky 2012). Moreover, numerous empirical studies have investigated potential links between behavior and/or psychological attributes (e.g., Figueredo et al. 2004; Figueredo and Rushton 2009; Jokela et al. 2009, 2011; Ellis et al. 2011; Griskevicius et al. 2011) and life-history traits (see also discussion), though few empirical studies integrate behavior, physiology, and life-history traits within one study. Thus, many concepts similar to POLS are in the extant human literature but they are either specified for humans with their unique life history, differing from most other animals, and their specific socio-cultural environmental conditions and/or use psychosocial instead of biological measures for POL (e.g. Figueredo et al. 2004, 2005, 2007; Figueredo and Rushton 2009). In our opinion, the POLS hypothesis goes beyond these other frameworks by conceptually explaining the evolution of within-species variation in life-history strategies along the current versus future reproduction trade-off by the mediating function of behavioral and physiological traits (Dammhahn et al. 2018, topical collection on Pace-of-life syndromes). Here, we aim to test specific predictions of the POLS hypothesis with an exemplary data set for humans and to contribute to joining these overall similar conceptual frameworks.

Specifically, we investigated several of the key predictions of the POLS hypothesis (Réale et al. 2010) within a human population. To this end, we used data from the German Health Interview and Examination Survey for Children and Adolescents (KiGGS). The KiGGS data set contains information on maturation status, risk-taking behavior, and physiology from a representative sample of German adolescents (Hölling et al. 2007, 2012; Kurth et al. 2008). As an indication of pace-of-life, we used maturation status in same-aged children questioned at an age when half of them were mature and studied how presence and absence of the life-history marker covaried with behavioral and physiological traits. Age of sexual maturation has been used as an indicative measure of pace-of-life in many inter- and intra-specific studies in vertebrates (Stearns 1992; Oli 2004). Menarcheal age is commonly used as a biological marker of female development (Susanne and Bodzsar 1998) and occurs usually between Tanners pubertal stages of breast development B3 and B4 (Tanner 1962; Marshall and Tanner 1969; Harries et al. 1997). Biological characteristics of male sexual maturity are pubic hair development, a characteristic with different stages and high variability

over the whole pubertal time, and voice break (a deepening of the voice); a characteristic rarely used as a clinical or biological marker. In contrast to pubic hair development voice break occurs around one year after spermarche (first motile spermatozoa) (Bogin 1999) and between Tanners pubertal stages of genital development G3 and G4 (Harries et al. 1997). Voice break is therefore better comparable (in absence of information of age of spermarche) with menarcheal age in girls and can, as such, be seen as a proxy for the pace-of-life in boys (e.g., Juul et al. 2007).

As behavioral traits, we focused on risk-taking behavior as part of the possible syndromes provided by the POLS hypothesis and because of the characterization of the adolescent transition through increased rates of risky and reckless behavior with potentially severe consequences including disability and death due to, for example, violence, suicide, accident, eating disorders, and drug and alcohol use (Steinberg 2008; National Research Council 2011; Ellis et al. 2012). As physiological traits, we focused due to limitations of the KiGGS data set on a set of cardiovascular parameters. We used these parameters as a proxy for the sympathetic/parasympathetic nervous system reactivity, which has been suggested to align with pace-of-life (Réale et al. 2010). For humans, the Adaptive Calibration Model (ACM; Del Giudice et al. 2011, Ellis et al. 2017) would allow to make more nuanced predictions regarding physiological regulation of life histories, which cannot be tested, however, with our limited data set (see also "Discussion").

Based on the POLS hypothesis (Réale et al. 2010; Dammhahn et al. 2018, topical collection on Pace-of-life syndromes), we expect covariation between life history, risk-taking, and cardiovascular physiology. Specifically, based on the verbal framework presented in Fig. 1 of Réale et al. (2010), we expect that individuals who mature faster show (i) increased risk-taking behavior and (ii) score higher on cardiovascular parameters, compared to individuals who mature slower. Moreover, if risk-taking behaviors and physiology mediate the trade-off between current and future reproduction similarly, we expect (iii) a positive correlation between risk-taking behaviors and cardiovascular parameters.

Methods

Study population

The KiGGS study is a health survey of 17,641 children and adolescents of both sexes, aged between 0 and 18 years, and was performed between 2003 and 2006 in Germany (Hölling et al. 2007, 2012; Kamtsiuris et al. 2007; Kurth et al. 2008; Rosario et al. 2010). This cross-sectional study gathered representative data through medical health examinations and questionnaire-based assessments and it uniquely encompasses data on physiology, risk-taking behavior, and life history. All information for one person was collected within 1 day (Hölling et al. 2007). Data collection (detailed explained in Hölling et al. 2007, 2012, Kamtsiuris et al. 2007 and Kurth et al. 2008) and data analysis by the authors were performed independently of each other which minimize observer bias. For more information about study design and quality management within the KiGGS study, please see the literature mentioned above.

Life history

The KiGGS study provides data on the exact age of the adolescents, as well as information about the occurrence of menstruation of girls and voice break of boys, both quantified as yes or no at the time of questioning. Because the exact timing of the onset of either maturation events was not available, we selected one homogeneous age group for each sex and compared individuals who did mature with those that did not mature within this age group. We decided against the opposite approach: grouping children of the same state but different ages (young mature versus old mature) since we assume that the social environment and behavior of contemporaries is strongly associated and behavior, especially to risk-taking behaviors, may overlay differences due to differential POL. In addition, we first removed data of children with migration background from the data set. Because the developmental tempo (age of maturation) between different human populations can differ because of various genetic as well as socioeconomic conditions (Susanne and Bodzsar 1998). We further removed age groups below 11 years because they were not included in the questionnaire-based assessment to assess risk taking (see below).

In the remaining data set (2804 girls and 2205 boys between 11 and 18 years), we searched for the age with a 50% probability of having reached maturity, using logistic regression models with binomial residual distribution and a "logit" link function. Girls reached the 50% probability of having menarche with 12.89 years (± standard error (SE) = 0.04). Boys reached the 50% probability of voice break experience at an age of 14.35 years (± SE = 0.05 years). Next, we formed homogeneous age groups by including all individuals that were up to 1 year younger or older than the age at which 50% of all individuals reached maturity. This procedure allowed us to compare slower (absence of maturity sign) with faster (presence of maturity sign) pace-of-life groups while controlling for age. Our final sample comprised 791 girls (378 without menarche (slow maturing) and 413 with menarche (fast maturing), age range 11.89–13.89) and 486 boys (226 without voice break (slow maturing) and 260 with voice break (fast maturing), age range 13.35–15.35). By categorizing girls and boys into these age-homogenous groups depending on their maturational status, we largely controlled for age in all further analysis.

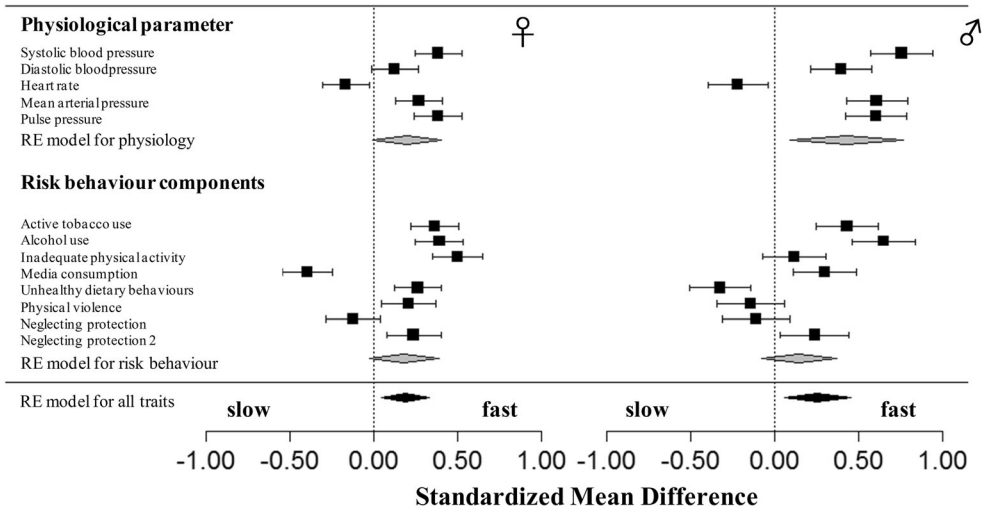


Fig. 1 Standardized mean difference (Hedges' g) and 95% CI between same-aged fast maturing and slow maturing girls and boys. Positive values indicate that the fast life-history group showed higher values for this variable (either higher values of cardiovascular parameters, or higher risk-taking behavior). Negative values indicate that the slow life history group showed higher values for this variable. Overall effect strengths within trait domains (gray diamonds) and over all traits (black diamonds) were calculated using random-effects meta-analysis models

Risk-taking behavior

For quantifying different categories of adolescents' risk-taking behavior, we used the behavioral categories described by the *Youth Risk Behavior Surveillance System* (YRBSS) of the Centers for Disease Control and Prevention (CDC) of the United States (Brener et al. 2002; Kann et al. 2016). This program distinguishes six broad categories of health-risk behaviors: (a) tobacco use, (b) alcohol and other drug use, (c) inadequate physical activity, (d) unhealthy dietary behaviors, (e) behaviors related to unintentional injuries and violence, and (f) risky sexual behaviors.

The parental and child questionnaire of the KiGGS study contains detailed information on a range of health-risk behaviors, including tobacco use, alcohol and drug use, diet, violence, and quality of life of German adolescents of both sexes, aged between 11.00 and 18.00 years (Hölling et al. 2007, 2012; Kamtsiuris et al. 2007; Kurth et al. 2008; Rosario et al. 2010). To the best of our knowledge, only Höpker et al. (2014) used the KiGGS data set to analyze adolescent risk behavior. Since no validated measures of behaviors were available yet, we screened the KiGGS questionnaires and identified questionnaire items comprising information falling into the six categories of health-risk behaviors of the YRBSS. In total, we identified 85 (continuous or categorical) such questionnaire items distributed as follows: (a) tobacco use ($n = 5$), (b) alcohol and other drug use ($n = 13$), (c) inadequate physical activity ($n = 9$), (d) unhealthy dietary behaviors ($n = 6$), and (e) behaviors related to unintentional injuries and violence ($n = 52$) (more details in supplement Table S1). There were no questions related to risky sexual behaviors in the survey.

To reduce the amount of heterogeneous questionnaire items to a smaller set of interpretable components, we used a categorical principal component analyses (catPCA) (Linting and van der Kooij 2012). We used this data reduction step instead of directly applying confirmatory analyses because many questionnaire items were ordinal or nominal with very heterogeneous distributions, which hampered fitting complex models directly (for further confirmatory steps of the analysis see below). The catPCA is similar to a linear principal component analysis but allows modeling non-linear relationships and including numeric, ordinal, and nominal variables. In a first step, we sorted all risk behavior-related questionnaire items according to the degree of risk, whereby a small value encoded low risk and vice versa, except for inadequate physical activity behaviors. For using catPCA, we followed the guidelines of Linting and van der Kooij (2012), which recommend an initial analysis to evaluate analysis level, variable selection, and the number of components. We ran a two-dimensional initial analysis treating all variables as spline nominal level, except dichotomous variables which were set as nominal. Based on transformation plots, we chose the appropriate analysis level of each variable; for ordinal and nominal spline level, we used the default settings of splines with two interior knots and two degrees of spline. Questionnaire items were considered meaningful variables if they accounted for more than 10% of the total variance (VAF > 0.1). To determine the final number of dimensions (components), we used the following recommended criteria: (i) elbow criterion in a scree plot (Fabrigar et al. 1999), (ii) Eigenvalue larger than one (Kaiser Criterion), and (iii) interpretability of the components. We also compared the results of different dimensionalities for evaluation of the chosen number of components (Linting et al. 2007; Linting and van der Kooij 2012).

Because catPCA requires only integer variables, we chose [following Linting and van der Kooij 2012] appropriate discretizing procedures. Ranking procedure was used for continuous variables which were treated as ordinal (spline) or nominal (spline) in the analysis level. Variables, treated as numeric, were discretized with a multiplying procedure. In case of non-responding participants for particular questionnaire items, we followed the missing value strategy of excluding those ones for each variable separately. Because rotation methods in catPCA are not available, we re-analyzed all transformed variables in a linear PCA to perform oblique (oblimin with $\delta = 0$) rotation. Pattern matrix and structure matrix (results of oblique rotation) were only used for increasing interpretability. For each combination of sex and risk-taking category, we conducted a separate catPCA using the outcomes to define health-related risk behavior components (Table 1).

Applying this procedure to the completed 85 questionnaire items of 2802 girls and 2896 boys aged between 11 and 18 years, we extracted 11 risk-taking components for girls and 10 for boys (Table 1, supplement Table S2 for girls and Table S3 for boys). Of those, we excluded "drug use behaviors" for further analyses due to an unrepresentative amount of positive drug use statements (within our subsample less than 10% of the participants reported to have used drugs at least once). Further, we excluded one component representing the psychosocial state of an individual (e.g., fear, peer pressure) because it fell outside of the scope of the six categories of health-risk behaviors of the YRBSS. Finally, we excluded health-risk behaviors that were not actively performed (e.g., exposure to smoking "passive tobacco use").

Our final data set for health-related risk behaviors thus encompassed only actively performed behavior and included the following variables: active tobacco use, alcohol use, inadequate physical activity, media consumption, unhealthy dietary behaviors, physical violence, and two components of neglecting protection (i.e. not using a helmet when riding a bike) (details in supplement Tables S2 and S3). Using Pearson correlations of components with original questionnaire items, we checked for interpretability of components and if necessary recoded variables so that each component increased in value with increasing risk-taking. This was achieved by multiplying the following risk-taking components by − 1: inadequate physical activity and media consumption in both sexes and neglecting protection in boys only (see supplement Tables S2 and S3). For example, a high value of active tobacco use indicates that the individual smokes a lot and started to use tobacco at an early age; a high value in physical violence behavior signaled a higher willingness to be physically violent.

Physiological parameters

The KiGGS data set comprises five cardiovascular parameters: systolic and diastolic blood pressure, mean arterial pressure, pulse pressure, and heart rate. Full details on the methods employed to measure these parameters are provided in Neuhauser and Thamm (2007) and Neuhauser et al. (2011). All parameters, except heart rate, were measured twice at the same day; we used the mean value of these two measurements.

Statistical analyses

To test whether fast and slow maturing boys and girls differ in a set of physiological and risk-taking behavioral traits, we calculated the standardized mean difference Hedges' g to compare both life-history groups for each trait for girls and

Table 1 Summary results of catPCAs for girls and boys on the questionnaire items (QI) of the KIGGS study

	Risk-taking behavior	Number of QIs	Number of components	Eigenvalues	Percent variance explained
Girls	Tobacco use	5	2	4.12	82.38
	Alcohol and other drug use	13	1	3.41	48.64
	Inadequate physical activity	9	2	3.76	47.02
	Unhealthy dietary behaviors	6	1	1.87	46.76
	Behaviors related to unintentional injuries and violence	52	5	15.49	37.79
	Total	85	11		
Boys	Tobacco use	5	2	4.13	82.53
	Alcohol and other drug use	13	1	3.57	50.93
	Inadequate physical activity	9	2	3.84	42.61
	Unhealthy dietary behaviors	6	1	1.73	34.53
	Behaviors related to unintentional injuries and violence	52	4	12.91	35.85
	Total	85	10		

boys, respectively. A positive value of Hedges' g implies a higher mean estimate for the fast life-history group than for the slow life-history group, and vice versa. Confidence intervals (95% CIs) of the standardized mean difference are based on the sampling variance. We calculated (for visual representations) overall effects using random-effects meta-analyses models, running separate analyses including (i) all physiological parameters, (ii) all health-related risk-taking behaviors, and (iii) all variables.

To test whether physiological and behavioral traits were correlated at the phenotypic level, we used Pearson correlations for each pair of physiological and behavioral traits within the selected subsample of 791 girls and 486 boys. We considered correlations as significant, if 95% CIs excluded 0; all 95% CIs are given in square brackets.

To examine the relationships between physiological, behavioral, and life-history traits under the POLS hypothesis, we used confirmatory factor analysis (CFA). CFA is a structural equation modeling technique that allows us to measure latent variables (Hoyle 1995; Kline 2011) and to test our hypothesized structure of POLS. For our analysis, we followed the guidelines for constructing structural equation models by Ullman (2006) and Fan et al. (2016). We constructed a model including three latent variables representing behavior, physiology, and life history in accordance with POLS theory. In our model, the latent behavior variable represents health-related risk behavior. For the CFA, we limited the set of behavioral indicator variables to those which most strongly represent health-related risk behavior; these four indicator variables were alcohol use, active tobacco use, inadequate physical activity, and physical violence behavior. Due to our data set structure (only one variable expressing life history), highly correlated cardiovascular characteristics (systolic blood pressure and diastolic blood pressure ($r > 0.67$, $p < 0.001$ in girls; $r > 0.65$, $p < 0.001$ in boys)) and the once measured variable heart rate the latent variables expressing life history and physiology were formed by only one indicator variable each. Physiology was expressed by systolic blood pressure and life history by the occurrence of maturation (girls menarche and boys voice break, for more explanation please see above) (see also Fig. 3).

To perform a CFA, we prepared and re-structured the data as follows: as indicator variables expressing health-related risk behavior, we used the factor scores generated by catPCA of alcohol use, active tobacco use, physical violence behavior, and inadequate physical activity (for more details please see above) which were log-transformed, except for active tobacco use. Active tobacco use was used in the CFA model as a binary variable (active smoking: yes or no). Furthermore, maturational status was used as a binary indicator variable and systolic blood pressure used as a z-scored continuous variable. We checked our data set for multivariate normality, one important assumption when modeling with maximum likelihood procedures (Fan et al. 2016), with Mardia's Multivariate Normality Test (Mardia 1970; Korkmaz et al. 2014). Due to the non-multivariate normality, neither in girls ($p_{skewness} < 0.001$ and $p_{kurtosis} = 0.79$) nor in boys ($p_{skewness} < 0.001$ and $p_{kurtosis} < 0.001$), and the complex structure of the data set (a mixture of continuous and binary variables) the appropriated estimation method "WLSMV" was used to get robust standard errors (SE) and adjusted test statistics (Rosseel 2012). In accordance with SEM guidelines (Ullman 2006; Fan et al. 2016), we used the X^2 test and the recommended indices RMSEA (root mean square error of approximation), CFI (comparative fit index), and SRMR (standardized root mean square residual) for assessing model fit. We conducted separate CFAs for boys and girls.

All analyses were calculated using R 3.1.2 (R Development Core Team 2014). For the calculation of Hedges' g, we used the "Metafor" package (version 1.9–7 + Viechtbauer (2010)). CFA models were built using the "lavaan" package (version 0.5–20 + Rosseel (2012)), while the analysis of multivariate normality was done within the "MVN" package (0.1–2 + Korkmaz et al. (2014)). Descriptive statistics (mean and standard deviation (SD)) of cardiovascular characteristics and risk-taking components for girls and boys, catPCA modeling and correlation analyses were done with IBM SPSS Statistics for Windows (version 22). CIs were estimated with bootstrapping using percentile-method with 1000 bootstrap samples within SPSS. For all traits in boys and girls, sample sizes differed due to missing information within questionnaires (for full information on sample sizes for each analyses see supplement Tables S4 and S5).

Results

Mean age of 791 girls was 12.89 years (SD = 0.59); girls of the fast life-history group ($n = 413$) had a mean age of 13.09 years (SD = 0.55), whereas girls of the slow life-history group ($n = 378$) showed a mean age of 12.68 years (SD = 0.56). Boys ($n = 486$) were on average 14.38 years old (SD = 0.61), whereby "fast" boys ($n = 260$) had a mean age of 14.67 years (SD = 0.54) and "slow" boys ($n = 226$) of 14.04 years (SD = 0.51). Further descriptive statistics for all physiological parameters and all risk behavioral components separated by sex and life-history group are presented in supplement Table S4.

Comparison between fast and slow life-history groups

Overall, fast maturing girls and boys had higher cardiovascular parameter values than slow maturing girls and boys (Fig. 1, Table S4). Particularly, blood pressure was higher in fast than in slow life-history groups; except for diastolic blood pressure, which only tended to differ between fast and slow maturing

girls. In contrast, fast maturing individuals of both sexes had lower heart rates.

Overall, boys and girls who matured faster tended to express higher scores of health-related risk-taking behaviors than those that matured slower (Fig. 1, Table S4). In girls, fast maturing individuals showed higher levels of substance use (active tobacco use and alcohol use), inadequate physical activity, unhealthy dietary behaviors, physical violence, and neglecting protection 2. Girls belonging to the slow life-history group showed higher media consumption behavior. There were no differences in neglecting protection between both life-history groups in girls (Fig. 1, Table S4). Boys with a fast life history showed more risk-taking concerning active tobacco use, alcohol use, media consumption, and neglecting protection 2 and a slight tendency to have more inadequate physical activity behaviors. In contrast, "slow" boys neglect protection to a higher degree, and indicated more unhealthy dietary behaviors and tended to show more physical violence (Fig. 1, Table S4).

Correlations between health-related risk-taking behaviors and physiology

Overall, pair-wise correlations between physiological and behavioral traits revealed a mixed pattern (Fig. 2). For girls, three components of risk-taking were positively correlated phenotypically with most cardiovascular parameters, namely inadequate physical activity (all $p < 0.05$, except pulse pressure $p > 0.1$), media consumption (all $p < 0.05$, except mean arterial pressure $p < 0.1$, systolic blood pressure and pulse pressure $p > 0.1$), and unhealthy dietary behavior (all $p < 0.05$, except diastolic blood pressure $p > 0.1$ and heart rate $p > 0.1$). In addition, physical violence was positively correlated with pulse pressure ($p < 0.05$). For alcohol use, we found no significant correlations with cardiovascular parameters. Neglecting protection was negatively correlated with most cardiovascular parameters (all $p < 0.05$, except pulse pressure $p > 0.1$). For active tobacco use, we found negative correlations with diastolic blood pressure and mean arterial pressure ($p < 0.05$). Physical violence was also negatively correlated with diastolic blood pressure ($p < 0.05$). Neglecting protection 2 was negatively correlated with heart rate ($p < 0.05$) (Fig. 2, Table S5).

In boys, inadequate physical activity was positively correlated phenotypically with most cardiovascular parameters (all $p < 0.05$, except pulse pressure $p > 0.1$). Four components of risk-taking were negatively correlated with at least one cardiovascular characteristic, namely physical violence (all $p < 0.05$, except pulse pressure $p > 0.1$), alcohol use (heart rate $p < 0.05$), neglecting protection (all $p < 0.05$, except systolic blood pressure $p < 0.1$ and pulse pressure $p > 0.1$), and media consumption (heart rate $p < 0.05$). For the remaining risk-taking behaviors (neglecting protection 2, active tobacco use and unhealthy dietary behaviors), no significant correlations were found (Fig. 2, Table S5).

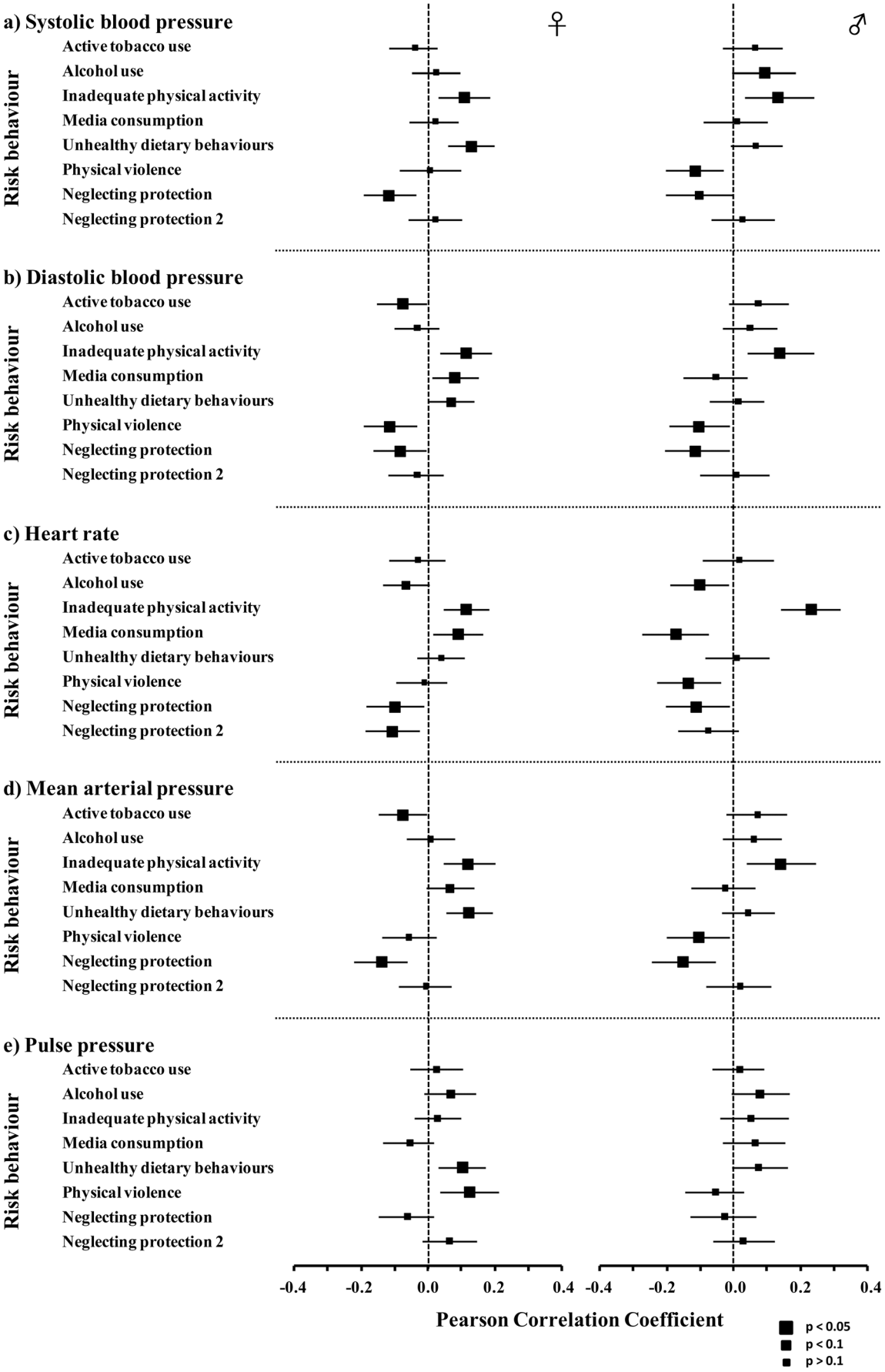
Confirmatory factor analysis for girls and boys

The fit of the CFA model of the girls sample ($n = 524$) revealed a slight deviation of the implicit covariance matrix of the indicators of our chosen model structure from the real one ($X^2 = 16.58$, df = 8, $p = 0.04$). Further CFA model fit indices for the girls' sample were quite good; RMSEA = 0.045 ($p = 0.553$; 90% CI = 0.012–0.076) and SRMR = 0.03. Only the CFI of 0.93 indicated a poor fit. Overall, model fit for the boys sample ($n = 328$) was poor ($X^2 = 32.55$, df = 8, $p < 0.001$; RMSEA = 0.097, $p = 0.012$; 90% CI = 0.06–0.133; CFI = 0.799, SRMR = 0.056). Therefore, all results of the CFA, particularly for the boys' sample, have to be interpreted with caution.

The latent factor solutions for our CFA models for girls and boys are shown in Fig. 3 and Table 2. For girls, standardized structure coefficients (SSC) for indicator variables of health-related risk behavior ranged between 0.28 (for active tobacco use) and 0.43 (for alcohol use). The latent variable life history was correlated with health-related risk behavior (cov = 0.44) and to a lower degree with physiology (cov = 0.15). In girls, physiology and health-related risk behavior were not correlated (Fig. 3, Table 2). In boys, alcohol use (SSC = 0.77), active tobacco use (SSC = 0.60), and physical violence behavior (SSC = 0.37) support the latent variable health-related risk behavior. Only physical activity seemed to have no influence. In boys, life history was correlated with health-related risk behavior (cov = 0.30) and with physiology (cov = 0.23). We found no support for the relationship between physiology and health-related risk behavior (Fig. 3, Table 2).

Discussion

The POLS hypothesis posits that phenotypic attributes mediate the trade-off between current and future reproduction (Réale et al. 2010; Dammhahn et al. 2018, topical collection on Pace-of-life syndromes). This hypothesis has generated much research interest in animal and behavioral ecology (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes) because it provides testable predictions concerning the association between the slow-fast life-history continuum and behavioral and physiological traits. Here, we tested several of these predictions using data of a contemporary human population. We found covariation between maturation status and health-related risk behavior as well as between maturation status and cardiovascular physiology for both boys and girls, supporting a general POLS. Further, we found that fast maturing boys and girls had overall higher blood pressure and tended to express more risk-taking behavior than same-aged slow maturing boys and girls. Thus, general predictions of the


a) Systolic blood pressure
b) Diastolic blood pressure
c) Heart rate
d) Mean arterial pressure
e) Pulse pressure
♀
♂
Risk behaviour
Active tobacco use
Alcohol use
Inadequate physical activity
Media consumption
Unhealthy dietary behaviours
Physical violence
Neglecting protection
Neglecting protection 2
-0.4
-0.2
0.0
0.2
0.4
Pearson Correlation Coefficient
p < 0.05
p < 0.1
p > 0.1

◀**Fig. 2** Correlation coefficients and 95% CI of all possible pair-wise combinations of physiological parameters (a–e) and health-related risk-taking behaviors for girls (aged 11.89–13.89 years) and boys (aged 13.35–15.35 years)

POLS hypothesis are partly supported for a human population. Only some of the single physiological and behavioral traits were positively correlated (Fig. 2, Table S5) and the CFA did not support covariation between cardiovascular physiology and health-related risk behavior (Fig. 3, Table 2). Hence, behavioral and physiological traits might mediate life-history trade-offs differently and not necessarily form a syndrome. Moreover, we found commonalities but also interesting differences between the sexes, suggesting that some aspects of POLS are sex-specific (Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes), and that some sex-specific feedbacks between life history and behaviors exist. Below, we discuss our findings in more detail and attempt to integrate the POLS hypothesis with similar conceptual frameworks from the human literature.

Life history and physiology

As predicted by the POLS hypothesis, individuals on a slow life-history trajectory had lower blood pressure (except girls for diastolic blood pressure) than those expressing a faster life history. Moreover, the present CFA results indicate a, albeit weak, relationship between life history and physiology (expressed by cardiovascular characteristics). Cardiovascular parameters, such as blood pressure, can serve as a proxy for the sympathetic/parasympathetic nervous system reactivity (Réale et al. 2010). Furthermore, high systolic blood pressure is positively linked to basal metabolic rate (Snodgrass et al. 2008), a physiological trait assumed to covary with POL (Réale et al. 2010). In the animal ecology literature, most studies investigating the link between physiology and POL have focused on metabolic parameters (Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes), and to the best of our knowledge, none of these studies used cardiovascular parameters. In human medicine, the determinants of blood pressure are well known and include age, sex, testosterone levels (Huisman et al. 2006), parent health-risk behavior, birth weight, and obesity (Huisman et al. 2006; Simonetti et al. 2011; Patel and Walker 2016; van der Steen and Hokken-Koelega 2016). By creating homogeneous age groups and treating the sexes separately, we attempted to control for key components of variation in blood pressure. Moreover, blood pressure during childhood and adolescence appears to be a good predictor of blood pressure later in life (Chen et al. 2007). We found higher blood pressures in fast maturing girls and boys than in slow maturing ones. Sexual maturity had an influence on cardiovascular characteristics during adolescence. Our results are in line with Cho et al. (2001), they found a relevant contribution of sexual maturity status on systolic blood pressure (when controlling for height and body mass index) within the Heartfelt study, but also pointed out that the literature is not clear about contribution of sexual maturity on variation in cardiovascular characteristics. In addition, systolic and diastolic blood pressure values are higher in adult women with earlier menarcheal age (Dreyfus et al. 2015; Jelenkovic and Rebato 2016).

In contrast to blood pressure, heart rate was lower in boys and girls maturing fast, as compared to those maturing slower and, thus, the pattern for heart rate was against our prediction.

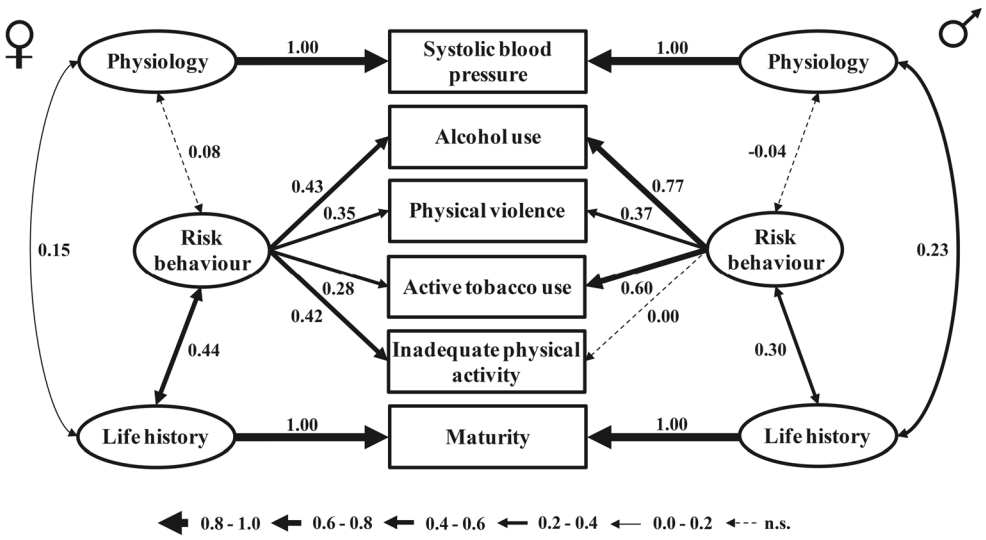


Fig. 3 Structure of confirmatory factor analysis (CFA) and strength of associations (based on standardized structure coefficients) in the model of life history (maturity), health-related risk-taking behaviors and physiology in two separate models, one for girls (left) and one for boys (right). Indicator variables (observed variables) were illustrated with rectangles and latent variables with ellipses. Single arrowheads express a direct effect of the latent variable on the indicator variables; two-headed arrows indicate covariance between latent variables. Solid arrows illustrate significant relationships, dashed arrows non-significant relationships

Table 2 Results of the confirmatory factor analysis (CFA) testing the complex structure of POLS with a life history trait, physiological characteristic and health-related risk-taking behaviors for girls (n = 524) and boys (n = 328)

	Trait	Girls								Boys							
		ES	SE	95% CI		Z	p	R^2	SSC	ES	SE	95% CI		Z	p	R^2	SSC
				lower	upper							lower	upper				
Risk behavior	Alcohol use*	1.00						0.18	0.43	1.00						0.59	0.77
	Physical violence	0.84	0.20	0.44	1.24	4.10	< 0.0001	0.13	0.35	0.42	0.09	0.24	0.60	4.53	< 0.0001	0.14	0.37
	Active tobacco use	1.63	0.44	0.76	2.49	3.69	< 0.0001	0.08	0.28	0.68	0.11	0.46	0.90	6.00	< 0.0001	0.36	0.60
	Inadequate physical activity	0.89	0.21	0.48	1.31	4.21	< 0.0001	0.17	0.42	0.00	0.07	−0.14	0.14	0.03	0.976	0.00	0.00
Life history	Maturity*	1.00						1.00	1.00	1.00						1.00	1.00
Physiology	Systolic blood pressure*	1.00						1.00	1.00	1.00						1.00	1.00
Covariance	Risk behavior—life history	0.01	0.00	0.01	0.02	5.04	< 0.0001		0.44	0.02	0.01	0.01	0.030	4.54	< 0.0001		0.30
	Risk behavior—physiology	0.01	0.01	−0.01	0.01	1.03	0.303		0.08	−0.01	0.01	−0.02	0.01	−0.57	0.567		−0.04
	Life history—physiology	0.07	0.02	0.03	0.11	3.37	0.001		0.15	0.12	0.03	0.07	0.17	4.32	< 0.0001		0.23

*Fixed estimates for CFA

ES, estimate; *SE*, standard error; *CI*, confidence interval; *Z*, *Z* value; *p*, *p* value; *SSC*, standardized structure coefficients

Heart rate variation is an indicator of the stress response in animals and humans (e.g. Koolhaas et al. 1999, 2010; Thayer et al. 2012). Unfortunately, the KiGGS data set contained only one measurement of heart rate, preventing us from assessing heart rate variation in response to stress. Heart rate is under regulation of the sympathetic- and parasympathetic antagonists' system. The parasympathetic control increases from infancy to adulthood. Hence, earlier puberty could be associated to increased parasympathetic tone; consequently, heart rate is lower (Graziano and Derefinko 2013; Ellis et al. 2017) and reflects acceleration towards a slower maturation schedule. Similarly, under the adaptive calibration model of stress responsivity (ACM: Del Giudice et al. 2011; Ellis et al. 2017) low basal heart rate could be linked to a faster life history under certain local environmental condition. Without further data on early environmental conditions and repeated physiological measures of the subjects testing, these more nuanced predictions remain outside the scope of our study.

Overall, our results bear some similarity to the findings of Figueredo et al. (2004): Using data of the National Survey for Midlife Development in the USA, they found that a set of correlated psychosocial traits (K), their measure for POL was highly correlated with a general factor for overall physical and mental health (see also below). Though this study did not focus on age of maturation per se, it lends support for a tight association between POL and physiological parameters. Taken together, in humans, age of maturation, a key life-history trait, appears to covary with non-metabolic physiological traits, such as cardiovascular parameters, that are known to affect physical activity and are part of animal coping styles.

Life history and behavior

Generally, fast maturing boys and girls tended to display higher levels of health-related risk-taking behaviors than their same-age peers. Particularly, tobacco and alcohol use and inadequate physical activity were substantially higher in fast maturing girls and boys. In girls, fast maturing individuals also displayed higher levels of unhealthy dietary behavior and physical violence. Fast maturing boys had higher levels of media consumption than their slower maturing peers. Proximately, these differences are likely due to elevated sex hormones in matured individuals as compared to immature peers, driving both POL and the expression of health-related risk-taking behavior. Still, it remains to be explained, why hormones are upregulated earlier in some individuals than others.

Among our set of risk-taking components, some represent health-risk behavior more directly than others. Particularly for active and direct risk-taking behaviors, such as smoking and drinking alcohol, we found support for our prediction of higher risk taking in faster life histories. Thus, following the predictions from the POLS hypothesis, same-aged individuals with a faster life history showed increased risk-taking

behavior in terms of unhealthy substance use, reduced physical activity and increased physical violence risk. Similar to the POLS hypothesis, (Ellis et al. 2012) proposed in their "evolutionary model of risky behavior in adolescence" that engaging in risky behavior can be beneficial in concert with a fast life history and under certain environmental conditions. Human psychological literature provides a wealth of studies demonstrating various links between personality and life history (summarized, e.g., in Réale and Dingemanse 2010; Figueredo et al. 2013). Particularly, fast maturing boys and girls display higher levels of aggressive and delinquent behavior than slow maturing (Najman et al. 2009) and sensation seeking and drug use during adolescence compared to same-aged peers (references in Ellis et al. 2012). Some of these differences between slow and fast maturing adolescents can persist through adulthood, such as initial differences in physical strength, body height and dominance in boys carrying over to manhood (references in Ellis et al. 2012). In sum, girls and boys pursuing a fast life-history trajectory score higher in various risk-taking behaviors during a critical transition phase in life, a phase characterized by a substantial increase in morbidity and mortality (Ellis et al. 2012).

Given that much is at stake and that several characteristics expressed in adolescence can have long-lasting consequences, risk-taking behavior might be one mediator of the trade-off between current and future reproduction in humans. However, the above-described differences in physiological and behavioral traits between slow and fast life-history groups could also be the result of state-dependent plasticity based on the developmental status of an individual. For instance, cardiovascular characteristics or the amount of risk taking could change when individuals advance from pre-puberty to puberty and adolescence. A longitudinal study with several consecutive measurements of risk-taking behavior, cardiovascular characteristics and life-history traits is required to rule out this possibility.

Behavior and physiology

We also explored potential links between health-related risk-taking behavior and physiology at the phenotypic level, assuming that positive correlations would indicate that both sets of traits mediate the trade-off between current and future reproduction in a similar way (direction) and, thus, would form suits of integrated characteristics along a slow-fast POL continuum. We found mixed support for this prediction. Within our CFA analysis neither in girls nor in boys' health-related risk-taking behavior was linked to physiology at the phenotypic level. But among all single risk-taking behaviors, only inadequate physical activity correlated positively at the phenotypic level with all (except pulse pressure) cardiovascular parameters in girls and boys. Other single risk-taking parameters (unhealthy dietary behavior, media consumption, alcohol use or physical violence) correlated positively with at least one single cardiovascular characteristic in girls or in boys. In addition, physical violence, active tobacco use, alcohol use, neglecting protection, neglecting protection 2, and media consumption showed negative correlations with at least one cardiovascular characteristic. Notably, the direction and strength of these phenotypic correlations varied between the sexes.

Although not directly predicted by the POLS hypothesis, behavioral and physiological traits are often forming syndromes. Within the framework of POLS, correlations between aspects of energy metabolism and behaviors related to energy acquisition (e.g., foraging) or energy expenditure (e.g., mating) have received much attention (Careau et al. 2008; Mathot and Dingemanse 2015). Another well-known syndrome in animal behavior are coping styles, which are correlated behavioral and physiological traits characterizing the stress response of an individual, jointly regulated by sympathetic and parasympathetic reactivity (Koolhaas et al. 1999; Koolhaas et al. 2010). For example, risk-taking ("proactive") individuals are assumed to have a different coping style than less risk-taking ("reactive") individuals. Proximately, a high sympathetic reactivity and low parasympathetic reactivity lead to a high but consistent heart rate under stressors in proactive individuals (Koolhaas et al. 1999; Ellis et al. 2006), allowing them to cope with the source of stress through a "flight-or-fight" response. Reactive individuals are assumed to show the opposite physiological patterns and tend to react by freezing. In animals, cardiovascular parameters are considered a part of coping styles. For example, proactive individuals develop hypertension more often than reactive animals due to increased sympathetic reactivity (Koolhaas et al. 2010 and references therein). In humans, cardiovascular parameters have been found to correlate with personality; for example, the amplitude patterns of electrocardiogram (ECG) correlated with various personality scores in healthy individuals (Koelsch et al. 2012). Thus, although personality and physiology covary in many species, there is only mixed support for cardiovascular physiology traits and risk-taking mediating the life-history trade-off between current and future reproduction in the same way, at least based on the set of traits used in our study.

Sex-specific POLS in humans

Although the overall link between age of maturation and physiology and behavior was largely similar in both sexes, we found several sex differences: for physiology, POLS was better supported in boys than in girls, whereas for risk-taking behavior POLS was better supported for girls than boys. In addition, CFA results revealed slight differences between girls and boys in terms of health-related risk behavior (inadequate physical activity, active tobacco use and alcohol use) and the strength of the association between physiology with life history (weaker in girls than in boys) and between health-related risk-taking behavior and life history (weaker in boys than

in girls) (see Fig. 3, Table 2). Moreover, differences between fast and slow maturing individuals were sex-specific for a number of single risk-taking behaviors. Against the POLS hypothesis and in contrast to boys, fast maturing girls had lower scores in media consumption than slow maturing peers. In our data set, boys had much higher values for this variable. For example, 6.4% of boys reported playing video games for more than 2 h/day, compared to only 1.1% in girls. Hence, this variable might reflect unhealthy behavior better for boys than girls. Conversely, unhealthy dietary behavior was expressed more in fast maturing girls than slow maturing girls, but in boys, the pattern was reversed. For this behavior, sex differences are well known (Croll et al. 2002; Swanson et al. 2011) and, in agreement with previous studies, we also found a lower propensity of eating disorders in boys.

Apart from sex-specific importance of certain risk-taking behaviors, the differences between the sexes might be due to two, non-mutually excluding, causes. First, the differences between life-history groups might increase with age and boys are on average 1 year older than girls in our life-history groups. Although this might explain why the differences between fast and slow maturing boys are stronger than between fast and slow maturing girls in physiological parameters, it is unlikely to explain differences between the sexes for health-related risk-taking behaviors. Second, sex differences in POLS might have an adaptive value (Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes). In humans and many other species, males and females differ in life history, physiological and behavioral traits (summarized in Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes; Immonen et al. 2018, topical collection on Pace-of-life syndromes, see also Del Giudice and Belsky 2011) and sex-specific selection pressures might generate differences in mean trait expressions, strength of trait correlations and covariance structures (Hämäläinen et al. 2018, topical collection on Pace-of-life syndromes). Exploring sex differences in POLS in humans in more detail and from an evolutionary perspective (see, e.g., Ellis et al. 2011), will be a fascinating area of future research.

A human pace-of-life syndrome?

Several conceptual frameworks exist that are similar to the POLS hypothesis (Réale et al. 2010). For example, Rushton's (1985) *differential K theory* posits that among-individual variation in behavioral and physiological traits is related to slow-fast life-history strategies. This framework has stimulated much empirical work (summarized in Figueredo et al. 2013), revealing that (i) suites of psychosocial measures form a higher order life-history factor (termed *K*), representing a slow-fast continuum; (ii) an integrated, general factor of personality (termed *GFP*) phenotypcially correlates with *K*; (iii) an integrated, general factor of overall physical and mental health (termed *covitality*) phenotypcially correlates with *K*; and (iv) these correlations have a significant genetic component (e.g., Figueredo et al. 2004, 2005, 2007; Figueredo and Rushton 2009). Further, Ellis et al. (2009) proposed a developmental theory of inter-individual variation in humans, which posits that correlated life-history traits form a slow-fast continuum and evolved in response to environmental harshness and unpredictability. Subsequently, risk-taking behavior, particularly during adolescence, was incorporated into this view of human life-history syndromes (Ellis et al. 2012). Brumbach et al. (2009) provided support for this framework by showing that frequent changes or ongoing inconsistency in childhood environments negatively affected health and risk taking (their proxies for life-history strategies) in a representative sample of adolescents and young adults in the USA. Moreover, resource availability during childhood determined how mortality cues affected gambling decisions: individuals who grew up relatively poor favored risky but immediate rewards when confronted with mortality cues, whereas individuals who grew up relatively wealthy favored future rewards (Griskevicius et al. 2011). Other researchers also highlighted that physiological characteristics, particularly stress response, should covary with life-history strategies because they evolved in response to the same environmental conditions that shaped life-history variation (e.g., Del Giudice and Belsky 2011; Del Giudice et al. 2011). Thus, many ideas present in the human literature bear close resemblance to the POLS hypothesis, but they also differ in some key details. All of these frameworks are based on life-history theory (Pianka 1970; Stearns 1982) and view life-history strategies as evolved adaptive responses to certain environmental conditions (e.g. Ellis et al. 2009; Del Giudice and Belsky 2011). However, all concepts in the human literature are either specified for humans with their unique life history, differing from most other animals, and their specific socio-cultural environmental conditions and/or use psychosocial instead of biological measures for POL (e.g., Figueredo et al. 2004, 2005, 2007; Figueredo and Rushton 2009). In our opinion, the POLS hypothesis goes beyond these other frameworks by conceptually explaining the evolution of within-species variation in life-history strategies along the current versus future reproduction trade-off by the mediating function of behavioral and physiological traits (Dammhahn et al. 2018, topical collection on Pace-of-life syndromes).

Our results of links between a key life-history parameter, physiology and health-related risk-taking behavior in a contemporary German population, are plausible under the POLS hypothesis. However, formally testing POLS in humans and other animals is difficult because it requires experimental manipulation of environmental conditions and disentangling within- from between-individual correlations (Montiglio et al. 2018, topical collection on Pace-of-life syndromes). In general, raw phenotypic correlations (or simple group differences, as used in this study) are not well suited to reveal syndromes between traits because other sources of variation (e.g., within-individual variation) are not controlled for. Ideally, behavior, physiology, and life history should all be measured repeatedly and simultaneously over the course of

a life time to estimate pure between-individual correlations among traits (Dingemanse et al. 2012). Only these correlations will reveal additive genetic, permanent environment or maternal effects, which can be shaped by evolution (see e.g. Figueredo and Rushton 2009). However, many life-history traits (namely age at maturity, age at first reproduction) occur only once in a lifetime. Moreover, repeated measures of complex traits, such as personality in humans, in concert with physiological measures are often not available, partly because they are studied in very different research areas (e.g., psychology and medicine), and partly because of logistic challenges of following humans over the course of their lifetime. Several governmental organizations do collect large representative data sets, such as KiGGS and MIDUS, which—although not perfect in sampling design for testing POLS theory—might provide valuable data of a large sample. Including crucial life-history traits in these surveys and applying a repeated measures design for subgroups, would allow testing POLS predictions more rigorously in the future.

Humans are special in their life history and their cultural environment (Bogin 1999), but despite human universals, we find support for the POLS hypothesis in humans. Better multivariate data sets of repeatedly measured traits, in concert with fitness data (e.g., Alvergne et al. 2010; Jokela et al. 2011), would allow ultimately testing whether behavior and physiology mediate the trade-off between current and future reproduction in humans. Combining data sets of human populations living under environmental conditions that vary in harshness and predictability (e.g., Brumbach et al. 2009) would additionally help testing the environmental drivers of POLS evolution. Previous conceptual frameworks of the human literature are more anthropocentric but can be well integrated with the POLS hypothesis. Further, uniting these concepts more thoroughly would be fruitful for the study of POLS in humans and other animals, akin to the integration of behavioral ecological approaches to animal personality and approaches and tools of personality psychology (e.g., Gosling 2001; Nettle and Penke 2010; Uher 2011).

Conclusions

Using data on life history, health-related risk-taking behavior and cardiovascular physiology of contemporary human adolescents, we found some support for key predictions of the POLS hypothesis. We are aware that our comparisons between life-history groups have some limitations and cannot replace multi-trait (co)variance analyses, but repeated measures of physiological traits in concert with behavioral traits and biological measures of life history are rare, even in the rich human literature. We hope that our work can familiarize animal ecologists with the developments taking place in human ecology; for instance, by showing that the trade-off between current and future reproductive success is only one out of several key processes that could underlie covariance between life history and behavior/physiology (Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes).

For human ecologists, we hope this introduction to the POLS can stimulate future research exploiting other long-term data sets. Throughout, we have highlighted similarities and differences between the key approaches in animal and human ecology. By pointing out parallels and distinctions, we hope to stimulate cross-fertilization between these two research domains, which have evolved largely independent (see also Nettle 2006; Nettle and Penke 2010).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants performed by any of the authors. The KiGGS survey was reviewed and approved by the responsible ethics committee at the University Hospital of the Charité of the Humboldt University in Berlin.

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