

Life History Correlates of Human (*Homo sapiens*) Ejaculate Quality

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Life history strategies reflect resource allocation decisions, which manifest as physiological, psychological, and behavioral traits. We investigated whether human ejaculate quality is associated with indicators of relatively fast (greater resource allocation to mating effort) or slow (greater resource allocation to parenting effort) life history strategies in a test of two competing hypotheses: (a) The *phenotype-linked fertility hypothesis*, which predicts that men pursuing a relatively fast life history strategy will produce higher quality ejaculates, and (b) the *cuckoldry-risk hypothesis*, which predicts that men pursuing a relatively slow life history strategy will produce higher quality ejaculates. Men ($n = 41$) completed a self-report measure assessing life history strategy and provided two masturbatory ejaculate samples. Results provide preliminary support for the cuckoldry-risk hypothesis: Men pursuing a relatively slow life history strategy produced higher quality ejaculates. Ejaculate quality may therefore reflect resource allocation decisions for greater parenting effort, as opposed to greater mating effort. The findings contribute informative data on correlations between physiological and phenotypic indicators of human life history strategies.

Keywords: life history theory, ejaculate quality, humans, phenotype-linked fertility, cuckoldry-risk

Life history theory addresses organisms' resource allocation decisions for conflicting life tasks over the life span (Del Giudice, Gangestad, & Kaplan, 2015). There are three fundamental life history trade-offs to which humans must allocate their resources (Kaplan & Gangestad, 2005). The trade-off between present versus future reproduction entails allocating resources to (a) early reproduction at the cost of continued bodily growth and maintenance, or (b) continued growth and development at the cost of delaying reproduction. The trade-off between quantity versus quality of offspring entails allocating resources to (a) producing a greater quantity of offspring, which increases the chances that one or more of these offspring will survive to reproductive age, but at the cost of decreased investment per offspring, or (b) producing higher quality offspring by investing more in each offspring, but at the cost of producing fewer offspring. The trade-off between mating effort versus parenting effort entails allocating resources to (a) high mating effort to increase offspring quantity or (b) high parenting effort to increase offspring quality. These resource allocation strategies require trade-offs because individuals have limited resources to allocate to such tasks. Such strategic resource allocation "decisions" are made throughout the life span.

Resource allocation decisions manifest as phenotypic traits—including physiological, psychological, and behavioral traits

(Braendle, Heyland, & Flatt, 2011; Del Giudice et al., 2015). Phenotypic variation therefore reflects resource allocation strategies, or *life history strategies*, by which individuals attempt to optimize resource expenditure (Del Giudice & Belsky, 2011). Human life history strategies can be conceptualized on a *slow-fast continuum* (Promislow & Harvey, 1990) whereby life history strategies reflect coordinated patterns of phenotypic traits. Relatively fast life history strategies are characterized by greater allocation of resources to mating effort to increase offspring *quantity*. Relatively slow life history strategies are characterized by greater allocation of resources to parenting effort to increase offspring *quality* (Kaplan & Gangestad, 2005).

Within a life history framework, empirical work applying life history theory to humans focuses largely on identification of physiological, psychological, and behavioral traits that comprise relatively fast or slow life history strategies (Figueredo et al., 2005, 2006). For example, previous work has mapped personality traits—both normative (Figueredo, Vásquez, Brumbach, & Schneider, 2007) and pathological traits (Del Giudice, 2016)—onto the life history strategy continuum. Other suites of traits have also been identified to map onto life history strategies, such as a "covitality" component representing health and well-being (Figueredo et al., 2007), and physiological correlates including androgens, estradiol, and testosterone (Del Giudice & Angeleri, 2016; Eisenegger, Haushofer, & Fehr, 2011; Pollet, van der Meij, Cobey, & Buunk, 2011). Mapping individual differences on the slow-fast continuum of life history strategies has improved our understanding of adaptive phenotypic variation within humans.

Ejaculate quality may also be associated with phenotypic indicators of life history strategies. Human ejaculate quality has been shown in some studies to be correlated with men's trait attractiveness (see Jeffery, Pham, Shackelford, & Fink, 2016, for a review).

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Trait attractiveness, in turn, has been shown to be correlated with relatively fast life history strategy indicators in humans, including greater number of offspring and greater number of sexual partners in traditional and contemporary populations (Jokela, 2009; Waynforth, 1998). These associations accord with what is referred to as the *phenotype-linked fertility hypothesis* (Sheldon, 1994), which predicts a positive association between ejaculate quality and sex-typical male traits—traits that confer reproductive benefits to men within short-term mating contexts (e.g., fluctuating asymmetry). Situated within a human life history framework, then, the phenotype-linked fertility hypothesis suggests that men pursuing a relatively *fast* life history strategy—allocating greater resources to mating effort—will produce higher quality ejaculates to increase the likelihood of fertilization in short-term mating contexts.

Alternatively, an argument can be made that men pursuing a relatively *slow* life history strategy may produce higher quality ejaculates. Because male humans invest substantially in their putative offspring relative to other male primates (Fernandez-Duque, Vaeglia, & Mendoza, 2009), cuckoldry (unexpected nonpaternity) would have inflicted significant reproductive costs on paternally investing men over human evolutionary history (Baker & Shackelford, 2018; Pham & Shackelford, 2014; Shackelford, 2003). Ancestral men may have guarded against cuckoldry by allocating greater resource investment to a single partner and resulting offspring—indicators of a slow life history strategy. Greater resource allocation to parenting effort, rather than mating effort, therefore may be associated with higher quality ejaculates (Simmons, Lüpold, & Fitzpatrick, 2017) to ensure investment into genetic offspring. The *cuckoldry-risk hypothesis*, proposed here, suggests that men pursuing a relatively *slow* life history strategy—allocating greater resources to parenting effort—will produce higher quality ejaculates.

In summary, a theoretical focus on resource allocation decisions derived from human life history theory suggests that life history strategies may be associated with variation in human ejaculate quality. The current research offers initial tests of two competing hypotheses: (a) The *phenotype-linked fertility hypothesis*, which predicts that men pursuing a relatively fast life history strategy will produce higher quality ejaculates to facilitate successful fertilization in short-term mating contexts, and (b) the *cuckoldry-risk hypothesis*, which predicts that men pursuing a relatively slow life history strategy will produce higher quality ejaculates to reduce cuckoldry risk in long-term mating contexts. The current study presents an initial investigation of the association between life history strategies and ejaculate quality in humans. We analyze data from a larger experimental study (Pham et al., 2018) that secured several self-report measures—including a widely used measure of human life history strategy (Figueredo et al., 2006)—and obtained two masturbatory ejaculates from each participant. Using these data, we tested whether life history strategy indicators are associated with ejaculate quality across several clinical parameters.

Method

Participants

Participants were recruited via advertisements posted on the campus of a university in the Midwestern United States, and throughout the surrounding campus communities. Men were eli-

gible to participate if they (a) had not had a vasectomy, (b) had never sought treatment for infertility, (c) were aged 18–35 years, and (d) were currently in a committed, sexually active relationship lasting at least 3 months with a woman aged 18–35 years. Men's and women's age-related eligibility was implemented owing to known declines in fertility for both sexes (though fertility decline is less dramatic for men than for women). Potential participants contacted the laboratory to schedule three in-person laboratory sessions—one intake session followed by two sessions at which they delivered a masturbatory ejaculate. The original data set included responses from 66 men, with ages ranging from 18 to 34 years ($M = 22.77$, $SD = 3.83$), mostly not married (90.9%), and with relationship length ranging from 6 to 123 months ($M = 33.15$, $SD = 26.62$, $Mdn = 27$ months). The target sample size for the study at conceptualization was 100 men. The target sample size was determined based on the primary aim of the study (within-subjects design; Pham et al., 2018). After 3 years of data collection (and before data analysis), a consensus was reached to stop data collection in May 2016. Only data from men who provided ejaculate samples for both masturbatory sessions and had complete intake session data ($n = 41$) were included in analyses ($n = 14$ did not submit two masturbatory samples; $n = 11$ provided incomplete intake data [$n = 7$ owing to procedural errors]), with ages ranging from 18 to 33 years ($M = 23.3$, $SD = 3.6$) and with relationship length ranging from 6 to 123 months ($M = 35.54$, $SD = 25.57$, $Mdn = 26$ months).

Materials and Procedure

Methodological information relevant to the current study aim is reported here. Full methodological details are also reported in the article by Pham et al. (2018). All procedures were approved by the institutional review board of the university where data were collected. Data collection occurred between April 2013 and May 2016. Men arrived to the laboratory at a scheduled time to complete their intake session and were escorted to a private computer station by a researcher. Men were provided a written consent form and were shown a video describing the study procedures. Consenting participants completed an intake session that included completion of several self-report questionnaires on a desktop computer, which included the HEXACO-60 personality measure (Ashton & Lee, 2009), Raven's IQ assessment (12-item short form; Arthur & Day, 1994), reports of familial living situations (e.g., whether the participant lived with both natural parents as a child), reports on aspects of their sexual behavior (e.g., the last time they had sexual intercourse with their romantic partner), the Mate Retention Inventory—Short Form (Buss, Shackelford, & McKibbin, 2008), the Investment Model Scale (Rusbult, Martz, & Agnew, 1998), and body measurements of participants (e.g., handgrip strength and head size). Of interest to the current analysis, participants completed the Mini-K (Figueredo et al., 2006) as an assessment of life history strategy along the “slow–fast” continuum (e.g., “I avoid taking risks,” “I would rather have one than several sexual relationships at a time”) on a 7-point Likert scale (1 = *disagree strongly*, 7 = *agree strongly*). Composite scores (mean average) for the Mini-K ($\alpha = .81$) were calculated, with higher scores indicating a relatively slower life history strategy.

Before each masturbatory session, participants received materials needed to collect and transport their masturbatory ejaculate

(nonlatex, nonspermicidal condom, plastic twist-tie, screw-top specimen container, biohazard Ziploc bag, and aluminum foil). Following the guidelines provided by the [World Health Organization \(2010\)](#), participants were instructed to abstain from sexual activity for 48 hr (but not longer than 7 days) before each of their scheduled masturbatory sessions. Participants were able to reschedule their subsequent sessions or to request replacement materials (e.g., if the condom broke) without penalty. The masturbatory sessions followed a within-subject design whereby participants received written priming stimuli (order counterbalanced across participants): a scenario in which the participant discovered the sexual infidelity of their current romantic partner,¹ or a scenario in which the participant discovered that their current romantic partner lost a significant amount of money gambling² (no difference was detected for any semen parameter across the two conditions; results reported in [Pham et al., 2018](#)). Men were instructed to think about the scenario while masturbating and were asked to not use any materials that we did not provide (e.g., lubricant) and to masturbate without the help of their partner. Participants masturbated to ejaculation in a private location of their choosing while thinking about the provided scenario and wearing the provided condom. After ejaculation, participants transported their ejaculate sample to the laboratory using the provided materials within 1 hr of ejaculation. Upon delivery of the ejaculate, participants reported via paper-and-pencil survey time since last ejaculation and time of ejaculation (for the ejaculate being delivered) as a means to confirm that participants followed the instructed procedures. All participants delivered their ejaculates in accordance with the instructions provided (e.g., all ejaculates were packaged properly.).

Ejaculate quality was assessed using the Semen Quality Analyzer (SQA-V; Medical Electronic Systems, Los Angeles, California, USA)—a fully automated machine that analyzes semen along 17 clinical parameters ([Table 1](#)) using electro-optical technology, signal conversion, and the application of proprietary algorithms. Upon receipt of the participant's masturbatory ejaculate at Sessions 2 and 3, a researcher pipetted the entire ejaculate from the condom and measured the volume of the ejaculate (in ml) using the volumetric markings on the pipette. The ejaculate was then pipetted into a sterile specimen container. A test strip (Medical Electronic Systems, Los Angeles, California, USA) was dipped momentarily into the ejaculate to assess pH and white blood cell count. The ejaculate was syringed into a proprietary measurement capillary, which was inserted into a chamber in the SQA-V (Medical Electronic Systems, Los Angeles, California, USA) for automatic analysis. After completion of the automated semen analysis, all materials that directly contacted the ejaculate were discarded in a biohazard waste container.

The time between each masturbatory session ranged from 2 to 28 days ($M = 7$ days). Men were compensated US\$25 at the completion of each session.

Results

The SQA-V calculates 17 continuous semen parameters. We calculated the mean average of each semen parameter for each participant across the two samples (each participant's ejaculate sample was assessed across the 17 parameters at each session, yielding two scores on each semen parameter for each partici-

pant—one score per parameter per sample per participant) to increase reliability and power, given the small sample size available for analysis. Zero-order and partial correlation coefficients (controlling for participant age and abstinence time prior to current ejaculation) were computed between participants' scores on the Mini-K and each of the semen parameters (results displayed in [Table 1](#)). The sample size afforded adequate statistical power (>80%) to detect effects of moderate magnitude ($> .40$). Ten of the zero-order correlations reached significance, and six of the partial correlations reached significance. These correlations were uniformly positive, indicating that men pursuing a slower life history strategy produced higher quality ejaculates. Correlations between the scores on the Mini-K and the Sperm Motility Index (i.e., the comprehensive overall status of semen and its fertilization potential based on inputs from sperm motility, progressive motility, and velocity parameters; specific calculation details are not available given that the algorithms are proprietary to the SQA line of semen analyzers produced by Medical Electronic Systems, Los Angeles, California, USA) showed the largest associations ($r_s = .57-.54$; [Figure 1](#)). The results provide support for the cuckoldry-risk hypothesis: Men who reported relatively slower life history strategies also produced higher quality ejaculates.

Discussion

The current study tested two competing hypotheses with regard to associations between life history strategy and ejaculate quality in humans: (a) The *phenotype-linked fertility hypothesis*, which predicts that men pursuing a relatively fast life history strategy will produce higher quality ejaculates, and (b) the *cuckoldry-risk hypothesis*, which predicts that men pursuing a relatively slow life history strategy will produce higher quality ejaculates. The results show greater consistency with the cuckoldry-risk hypothesis (as compared with the phenotype-linked fertility hypothesis) in that men pursuing a relatively slow life history strategy produced higher quality ejaculates. Sperm Motility Index, which is an overall "quality score" based on sperm motility, progressive motility, and sperm velocity (Medical Electronic Systems, Los Angeles,

¹ "Imagine that your romantic partner confessed to you earlier today that she cheated on you two days ago by having sex with a man that she recently met. She assured you that it was only a one-night stand and that it will not happen again. Despite being upset about her infidelity, you decide to give her another chance. Now, you and your romantic partner are going to have sex for the first time since she admitted that she cheated on you. Focus on what you think that first sexual experience would be like after her confession. Your task is to think only about this sexual experience while you masturbate. Do not allow other thoughts or fantasies to distract you during your masturbation. Focus only on what it would be like to have sex with your romantic partner after learning that she had recently cheated on you."

² "Imagine that your romantic partner confessed to you earlier today that she lost a considerable amount of money when she went gambling two days ago. She assured you that it was only a one-time mistake and that it will not happen again. Despite being upset about her gambling, you decide to give her another chance. Now, you and your romantic partner are going to have sex for the first time since she admitted that she recently lost a lot of money gambling. Focus on what you think that first sexual experience would be like after her confession. Your task is to think only about this sexual experience while you masturbate. Do not allow other thoughts or fantasies to distract you during your masturbation. Focus only on what it would be like to have sex with your romantic partner after learning that she had recently lost a lot of money gambling."

Table 1
Correlations and Descriptive Statistics for Life History Strategy and Ejaculate Quality

Semen parameter	Mini-K		Reliability	M	SD
	Bivariate <i>r</i>	Partial <i>r</i> (controls: age and abstinence)	.80	5.20	.73
01. Concentration of progressive sperm that are shaped normally ^a	.42**	.35*	.72	10.72	10.78
02. Quantity of progressive sperm that are shaped normally	.41***	.30 [†]	.68	23.57	25.41
03. Percentage of progressive sperm that are shaped normally	.50***	.44**	.42	30.00	9.88
04. Concentration of rapid progressive motile sperm (a) ^b	.46***	.46***	.39	7.31	8.40
05. Percentage of rapid progressive motile sperm (a)	.45**	.41*	.08	15.05	12.80
06. Concentration of slow progressive motile sperm (b)	.15	.07	.73	9.40	8.40
07. Percentage of slow progressive motile sperm (b)	.16	.04	.64	16.40	9.32
08. Quantity of progressive motile sperm (a + b)	.30 [†]	.17	.57	41.73	41.74
09. Percentage of nonprogressive motile sperm (c)	-.07	-.07	.47	14.62	6.71
10. Concentration of motile sperm (a + b + c)	.32*	.24	.74	24.50	18.11
11. Quantity of motile sperm (a + b + c)	.26	.12	.60	60.05	55.16
12. Percentage of motile sperm (a + b + c)	.42***	.31 [†]	.04	44.42	16.60
13. Percentage of not moving or dead sperm (d)	-.43**	-.31 [†]	.03	53.94	15.62
14. Sperm Motility Index ^c	.57***	.54**	.40	90.11	78.35
15. Sperm concentration within the sample	.15	.08	.40	56.50	33.45
16. Velocity of the fastest moving cells (μ s)	.43***	.34*	.45	8.85	3.13
17. Volume of the semen sample	.04	-.04	.65	2.41	1.13

Note. Reliability analyses for Mini-K = Cronbach's α . Reliability analyses for semen parameters = Spearman-Brown coefficient (recommended for reliability estimates with only two items; Eisinga, Te Grotenhuis, & Pelzer, 2013).

^a Millions/ml. ^b Motility is subdivided into four categories: a = rapid progressive motility (forward), b = slow progressive motility (curved), c = nonprogressive motility (circles), and d = dead or not moving. ^c Sperm Motility Index is an index such that higher scores reflect higher overall quality of sperm motility.

[†] $p < .10$. * $p < .05$. ** $p < .01$. *** $p < .001$. Significant correlations are in bold.

California, USA), showed a particularly large association with scores on the Mini-K, robust to effects of age and time since last ejaculation. Among ejaculate traits typically assessed by clinicians, sperm motility is one of the traits most reliably associated with conception in humans (Zinaman, Brown, Selevan, & Clegg, 2000), suggesting that paternally investing men produce ejaculates with higher fertilization potential than men pursuing a relatively fast life history strategy.

Empirical application of life history theory to humans includes attempts to identify coordinated patterns of phenotypic traits that comprise relatively slow or fast life history strategies. In the current research, we investigated whether ejaculate quality is a phenotypic trait associated with life history strategy in humans. The results suggest that ejaculate quality reflects resource allocation decisions for greater parenting effort, as opposed to greater mating effort (Simmons et al., 2017). That men pursuing a relatively slow life history strategy produce higher quality ejaculates accords with other research documenting positive associations between human ejaculate quality and long-term (but not short-term) male attractiveness ratings (Soler et al., 2003, 2014), given that traits associated with long-term partner attractiveness and potential are indicative of a relatively slow life history strategy (Figueredo et al., 2006).

Alternatively, the association between relatively slow life history strategy and higher quality ejaculates in our sample may be owing to the relationship each of these variables has with general health. It is well-documented that there is a robust association between human ejaculate quality and various indexes of male morbidity and mortality (Eisenberg et al., 2014; Jensen, Jacobsen, Christensen, Nielsen, & Bostofte, 2009; Latif et al., 2017, 2018). Within the human life history literature (Del Giudice et al., 2015;

Ellis et al., 2009), relatively lower morbidity and mortality risk are key factors assumed to be associated with relatively slow life history strategies. Given that morbidity and mortality risk are associated with human ejaculate quality and life history strategy in humans, it is important that future research explores this potential alternative explanation for the results reported here.

That men pursuing a relatively fast life history strategy produced lower quality ejaculates may be attributable to potential trade-offs over the life span, such as (a) a developmental trade-off between investment in secondary sexual characteristics and investment in ejaculate quality (Mautz, Møller, & Jennions, 2013), or (b) a downregulation of ejaculate quality to afford production of more frequent ejaculates (Dewsbury, 1982; Preston, Jalme, Hingrat, Lacroix, & Sorci, 2011), or to potential short-term trade-offs, such as (c) diverting (sperm production) resources to courtship behaviors (Simmons et al., 2017; Warner, Shapiro, Marcanato, & Petersen, 1995) or (d) downregulating sperm production in *noncompetitive* short-term matings (Wedell, Gage, & Parker, 2002). Each of these (nonmutually exclusive) explanations has been suggested for parallel findings in nonhumans (Mautz et al., 2013; Preston et al., 2011; Simmons et al., 2017; Wedell et al., 2002). Developmental mechanisms underlying long-term and short-term trade-offs for ejaculate production in humans, however, remain a valuable arena for future exploration.

Research on human ejaculate quality has focused on testing the phenotype-linked fertility hypothesis on the assumption that ancestral men pursuing short-term mating would have produced higher quality ejaculates more capable of fertilizing ova (Jeffery et al., 2016). Guided by a life history perspective, however, the current results suggest that ejaculate quality accords more strongly with parenting effort than with mating effort (Simmons et al.,

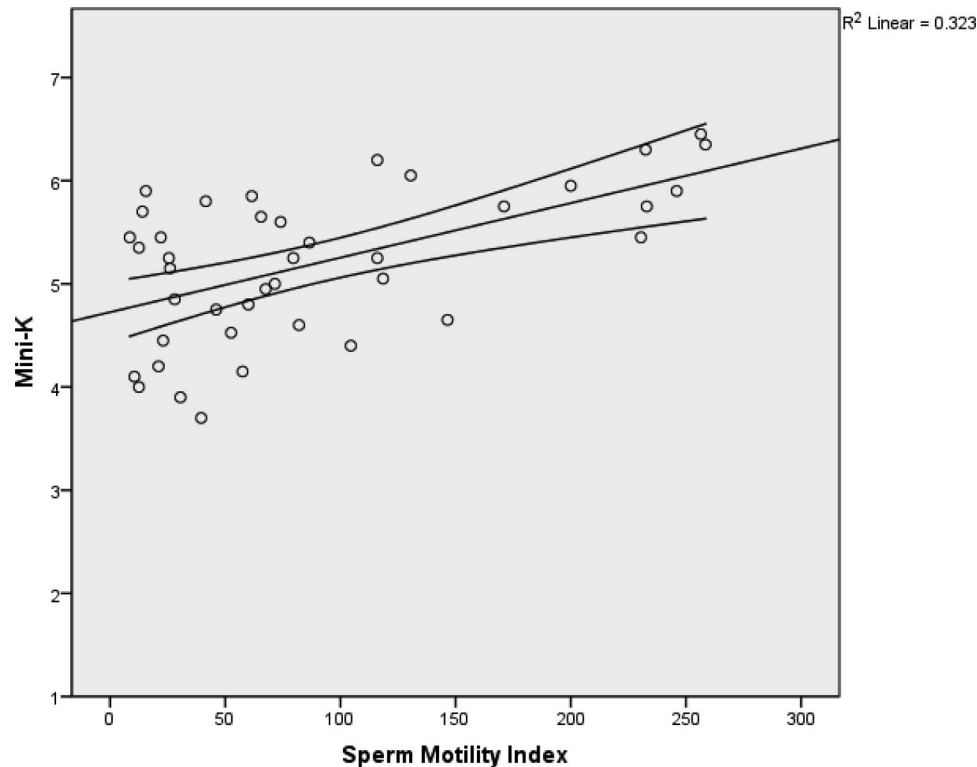


Figure 1. Zero-order correlation between Sperm Motility Index and Mini-K scores (higher scores indicating greater parenting effort). Curved lines represent 95% confidence interval.

2017). Male humans invest substantially in their putative offspring relative to other nonhuman primates (Fernandez-Duque et al., 2009) and, therefore, cuckoldry would have inflicted significant reproductive costs on paternally investing men over human evolutionary history (Pham & Shackelford, 2014). Men pursuing a relatively slow life history strategy may prioritize investment into high-quality ejaculates (rather than, perhaps, secondary sexual characteristics) to mitigate cuckoldry risk, thereby increasing the likelihood that their resources are invested into genetically related offspring (Pham & Shackelford, 2014).

Limitations

The results of the current study are preliminary. Additional research is needed to identify which phenotypic traits of men are reliably associated with ejaculate quality (see Jeffery et al., 2016, for an extended discussion) and to confirm whether ejaculate quality is reliably associated with other measures and indicators of life history strategies. Measurement of within-human variation of life history strategy has been the subject of debate since the data reported here were collected (Richardson et al., 2017). Subsequent research should use multiple measures of life history strategy to afford greater assessment of the validity of the life history construct.

Characteristics of the sample should also be considered when interpreting the results. The sample included only men currently in a committed romantic relationship and, therefore, may be biased toward men pursuing a relatively slow life history strategy. Future research could collect multiple ejaculates from a sample of men

with greater variation in life history strategy. The sample included in this study was voluntary and from a suburban community in the Midwestern United States; therefore, the results may not be generalizable to diverse populations within the United States or across cultures. The sample size was small and was limited to accurate detection of only moderate-to-large effects; smaller effects of life history strategy on ejaculate quality may have been missed. The small sample also increases the possibility that the correlations reported here are unstable, meaning that the effect may be variable in subsequent replications.

Procedural aspects of the current research also should be considered when interpreting the results (discussed in detail in Pham et al., 2018). Owing to various ethical and biosafety controls implemented at the university level, we had to rely on participants' truthful confirmation that the collection and transport protocols were followed. Although participants did confirm that instructed protocols were followed, we cannot claim the degree of certainty that could be offered if collection has been allowed in a controlled laboratory environment. The results of the current study should therefore be considered tentative and warrant replication. It is our hope that this analysis will stimulate further research investigating the connections between human ejaculate quality and life history indicators.

Conclusion

Identifying patterns of phenotypic traits associated with relatively fast or slow life history strategies can provide insights about resource allocation decisions over the life span. The current study

investigated associations between life history indicators and human ejaculate quality to test competing predictions derived from the phenotype-linked fertility hypothesis and the cuckoldry-risk hypothesis. The results accord more strongly with the cuckoldry-risk hypothesis and provide preliminary evidence that men pursuing a relatively slow life history strategy produce higher quality ejaculates, perhaps to reduce the likelihood of cuckoldry. Although broad patterns of phenotypic traits have been associated with mating and parenting outcomes, relatively little is known regarding the physiological and reproductive mechanisms underlying life history strategies in humans. The current findings contribute informative data on correlations between physiological and phenotypic indicators of life history strategies.

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