Response to Commentaries: Life History Genetics, Fluid Intelligence, and Extended Phenotypes

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Published online: 6 February 2019

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Dixon (2019) contextualizes, qualifies, and extends the research and ideas I presented in a recent article on extended phenotypes, human sexual selection, and life history theory (Luoto 2019). He notes that since age at first intercourse has a significant genetic component, genetic factors may influence the cross-national association between adolescent fertility and economic complexity. Dixon (2019) calls for further genetically informed research on extended phenotypes.

To offer a preliminary response to this research call, I collected data on the national life history strategy genetic factor index from Minkov and Bond (2015) and compared it with economic complexity and adolescent fertility rates.¹ The androgen receptor gene AR, the dopamine receptor gene DRD4, and the 5-HTTLPR VNTR of the serotonin transporter gene have been associated with national variation in life history outcomes and time orientation (Minkov and Bond 2015, and references therein). Following Minkov and Bond (2015), national scores on the life history strategy genetic factor index were defined by average AR CAG repeat length, DRD4 7 + 8 allele frequency, and 5-HTTLPR S-allele frequency. The national life history strategy genetic factor index was significantly correlated with the Economic Complexity Index ($r_s = .51$, $p < .001$, $n = 52$, Fig. 1). As expected, countries with a “slower” life history genetic factor index had higher economic complexity. The genetic factor index was also significantly correlated with adolescent fertility rates ($r_s = -.57$, $p < .0001$, $n = 52$).² Countries with a “faster” life history genetic factor index had higher adolescent fertility rates, as expected.

Building on prior research (Figueredo et al. 2004; Minkov and Bond 2015; van der Linden et al. 2018), these results indicate that life history strategies and more proximal

¹The genetic factor index consists of data on 52 countries (Minkov and Bond 2015). Data on Economic Complexity Index (The Atlas of Economic Complexity 2017) and adolescent fertility rates (UN Statistics Division 2017) are subsets ($n = 52$) of the dataset used in Luoto (2019).

²Spearman’s rank correlation coefficient was used in these analyses because of non-normal distribution of data for the life history genetic factor index and adolescent fertility rates.

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Fig. 1 A positive relationship between the national life history strategy genetic factor index and Economic Complexity Index ($r_s = .51$, $p < .001$, $n = 52$). A low value on the genetic factor index indicates a genetic predisposition for faster life history strategies (Minkov and Bond 2015). Data points are scaled per country-specific adolescent fertility rate (calculated as births per 1000 women ages 15–19: min. = 1.66 in South Korea, max. = 114.85 in Uganda, $M = 34.27$, $SD = 30.23$)

behavioral outcomes such as economic complexity can have a significant genetic component. Dixon (2019) notes that a genetic confound could reflect non-adaptive mutational drift rather than localized responses to competing life history processes. Future research may reveal the extent to which these findings represent random mutations or whether they constitute directional selection based on local ecologies (Luoto 2019).

Dixon calls into question the empirical validity and theoretical utility of the sexual strategies theory (Buss and Schmitt 2019), suggesting that it “may not be relevant to understanding how sexual selection has shaped male investment in phenotypic extensions” (Dixon 2019). Dixon cites studies on facial masculinity preferences to support his argument. However, viewing morphed faces on a computer screen, with shoulders and the rest of the body cropped out, is hardly an ecologically valid mate choice scenario. Actual mate choice zeroes in on a range of phenotypic, behavioral, and extended phenotypic traits over a long time period (Luoto 2019; Miller and Todd 1998). Recent evidence also indicates that facial masculinity is not a condition-dependent male ornament and does not reflect MHC heterozygosity (Zaidi et al. 2019). It therefore appears that Dixon (2019) prematurely rejects the sexual strategies framework based on facial morphometric studies. Sexual strategies theory is supported in various ways by other evidence from anthropological and psychobehavioral studies (Arslan et al. 2019; Buss and Schmitt 2019; Flegr et al. 2019; Scelza and Prall 2018) that have higher ecological validity than the facial morphometrics research paradigm. A

careful evaluation of the extended phenotype theory (Luoto 2019) reveals that it does not hinge upon women's preferences for facial masculinity in any meaningful way.

Dinh and Gangestad (2019) provide additional questions to direct future research on the role of extended phenotypes in human sexual selection. They correctly point out that most extended phenotypes that may influence human sexual selection are unlikely to do so via specialized psychological adaptations for evaluating *those particular traits*. Dinh and Gangestad (2019) note that evolved mate choice adaptations that take into account extended phenotypic productions “must be capable of extracting information that is represented at a level that would have been recurrent during the period in which the adaptations evolved”. Importantly, however, this is not how evolved psychological mechanisms work (Al-Shawaf et al. 2019). Evolutionarily novel extended phenotypic traits can be cues (not evolved signals) of underlying characteristics, and humans are cognitively sophisticated enough to associate such novel cues with desirable phenotypic and/or genotypic characteristics in potential mates. Evolved psychological mechanisms are not inflexible: they are highly context-sensitive, requiring environmental input at every stage of their emergence (Al-Shawaf et al. 2019).

A significantly fluid component in *Homo sapiens* intelligence enables humans to assess evolutionarily and situationally novel traits that inform overall mate value evaluations. Humans regularly apply fluid intelligence to make rational decisions, overcoming more rudimentary motivational forces by using higher-order cognitive processing (Duncan et al. 2017; Kenrick et al. 2010; Yang et al. 2019). Thus, the degree to which extended phenotypes exploit sensory biases, constitute sensory traps (such as pets and food gifts) (Luoto 2019), or evoke higher-order cognitive processes to evaluate distal traits (Luoto 2017; Miller and Todd 1998) is a question for future research to explore. None of these scenarios presupposes the existence of functionally specific evolved cognitive mechanisms for appraising specific modern traits such as cars and apartments.

I offered a broad overview of extended phenotype theory and applied it in cross-cultural analyses of innovation and economic complexity (Luoto 2019). Future research can now focus on any aspect of the complex interrelationships between ecology, genetics, human life histories, sexual selection, and extended phenotypes, including those emphasized by Dixon (2019) and Dinh and Gangestad (2019). Zooming in (Krams et al. 2019; Luoto and Rantala 2018) and out (Luoto 2019; Luoto et al. 2019) between various levels of analysis can be immensely valuable when researching complex topics such as human evolution and its present-day behavioral manifestations.

Acknowledgements The author is grateful for Peter K. Jonason's comments on an earlier draft of this article.

Funding This work was supported by the Emil Aaltonen Young Researcher Grant.

Compliance with Ethical Standards

Conflicts of Interest The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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