



Commentary

# Reactive heritability of extraversion: where do we stand?



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Researchers have puzzled over the “missing heritability” problem for quantitative traits, including personality dimensions such as the Big Five. Specifically, although all human personality traits exhibit substantial additive genetic variance, large gene association studies with immense statistical power have failed to discover specific genes that explain even a fraction of this estimated heritability (e.g., Service, Verweij, Lahti, Congdon, et al., 2012). Because such effects are prerequisite for the maintenance of personality differences via fluctuating (including frequency-dependent) selection on specific polymorphic genotypes, this initially promising type of evolutionary genetic model would seem to be rendered untenable by the empirical data as an explanation for the heritability of personality (Lukaszewski & von Rueden, 2015; Verweij et al., 2012).

Recently, Lukaszewski and Roney (2011) hypothesized that part of extraversion's genetic variance reflects its facultative calibration to highly heritable, condition-dependent phenotypic features that would have predicted the cost–benefit ratio of extraverted strategies across ancestral environments. Specifically, we predicted that extraversion would have been a more beneficial strategy on average for more physically attractive and stronger individuals. If strength and attractiveness are in turn heritable due to genetic effects on condition — for instance, individuals with lower mutation loads develop both stronger and more attractive phenotypes — then extraversion would be heritable even if no specific genes directly encode for it. Such “reactive heritability” (see Tooby & Cosmides, 1990), if confirmed, could provide both a partial explanation for the missing heritability problem and a functional explanation for why individuals differ in extraversion.

In *prima facie* support of the reactive heritability hypothesis, multiple empirical studies have found that measures of physical strength and attractiveness, respectively, positively predict individual differences in extraversion and related interpersonal dimensions (for a review of these findings, see Lukaszewski & Roney, 2011; Lukaszewski & von Rueden, 2015). As such, we have advocated for quantitative genetic studies to provide a proper test of extraversion's reactive heritability.

In the current issue of *Evolution and Human Behavior*, Haysom et al. (2015) report a quantitative genetic test of the hypothesis that extraversion exhibits reactive heritability in relation to condition-dependent phenotypic features. Using a classical twin study design, they tested for phenotypic and genetic correlations of extraversion with other-rated facial attractiveness (from headshot photos), body

mass index (BMI), height (as a proxy for strength) and intelligence test scores. Overall, results were not very supportive of the reactive heritability hypothesis: Of the phenotypic features examined, only facial attractiveness exhibited the predicted positive association with extraversion, and this effect explained at most a few percent of extraversion's additive genetic variance.

Haysom et al. concluded that their findings cast some doubt on the viability of the reactive heritability hypothesis of extraversion. We do not entirely disagree. This was in some ways the most sophisticated test of the reactive heritability hypothesis ever conducted, and it appears to indicate that putative measures of condition-dependent phenotypic features collectively explain very little of the heritable variance in extraversion. At the very least, then, this study reports empirical patterns that must be accounted for.

However, we believe that the Haysom et al. study is inconclusive as a falsification of the reactive heritability hypothesis in light of several substantive (but understandable) limitations. Most importantly, the operational definitions of condition-dependent features employed in this study do not compellingly tap the most theoretically relevant aspects of strength, intelligence, and attractiveness:

- i. Height is only weakly-to-moderately correlated with physical strength. In our own data sets, measured upper-body strength has shown robust positive correlation with extraversion and related traits in both college undergraduates (Lukaszewski, 2013; Lukaszewski & Roney, 2011) and Amazonian forager–horticulturalists (von Rueden, Lukaszewski, & Gurven, 2015). However, height is much more weakly (and non-significantly) associated with extraversion in these same data sets. Therefore, a direct measure of physical strength might well have produced different results that increased the collective contribution of condition-dependent features to extraversion's genetic variance.
- ii. We do not doubt that intelligence test scores likely reflect mutation load and components of phenotypic condition, but we are not convinced that psychometric test performance would have been the most ancestrally predictive of one's ability to accrue benefits through extraverted strategies. Within small-scale societies, the most socially valued skills and abilities are often those that enhance one's capacity to manage coalitional alliances or excel in food production (von Rueden, Gurven, & Kaplan, 2008). Correspondingly, recent evidence suggests that the ability to detect and accommodate shifting contingencies is a narrow facet of intelligence that predicts peoples' effectiveness in accruing benefits via social exchange and competition — an effect that is not explained

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by general intelligence (Ronay & von Hippel, 2015). Thus, it remains entirely possible that extraversion is in fact calibrated to certain domain-specific mental abilities that are not tapped by general intelligence batteries.

- iii. Although other-rated facial attractiveness was (as in previous studies) positively correlated with extraversion in both sexes, these effects would likely have been larger if more complete information regarding overall attractiveness were available in the stimuli. Facial attractiveness as rated from neutral headshots explains part of the variance in overall attractiveness, but cues present in the body, the voice, and patterns of dynamic motion explain a substantial amount of additional variance (e.g., Confer, Perilloux, & Buss, 2010; Saxton, Burriss, Murray, Rowland, & Roberts, 2009). This suggests that the true association of other-rated attractiveness with extraversion was likely underestimated when using ratings of a single static headshot for each research subject. Consistent with this, previous studies that have employed composite scores based on ratings of standardized total body photos have reported attractiveness–extraversion associations that are much larger than those reported by Haysom et al. (e.g., Lukaszewski & Roney, 2011).
- iv. Finally, this study did not include self-perceptive measures of strength, intelligence, or attractiveness. This is problematic from our theoretical perspective, which posits that personality strategies should be most directly calibrated to internal representations of one's relative bargaining power, which are computed via comparisons of oneself with others on phenotypic dimensions that influence one's ability to confer benefits or inflict costs on others (see Lukaszewski, 2013). Consistent with this, (i) self-perceptions of condition-dependent phenotypic features are more strongly and consistently associated with extraversion than are more 'objective' measures and (ii) associations of other-rated attractiveness and measured physical strength with extraversion are mediated via self-perceptions (Lukaszewski, 2013; Lukaszewski & Roney, 2011).

The omission of self-perceptive measures of phenotypic features could have produced particularly misleading results given that Haysom et al. compared subjects sampled from different geographical regions and time periods. Because these individuals did not come from the same face-to-face populations, subjects' internal estimates of their own bargaining power were presumably based on social comparisons with essentially non-overlapping groups of other people. As such, this could have resulted in comparing externally valid measures of individuals' phenotypic features that do not closely correspond to their cue-based internal representations (i.e. self-perceptions) that theoretically drive personality calibration. These considerations imply that self-perceptive measures of condition-dependent features, if included in the study, would likely have exhibited robust positive associations with extraversion.

In sum, a consideration of the limitations of the operational definitions and sampling methods of Haysom et al.'s study supports the assessment that it could have easily underestimated the true magnitudes of the calibrational effects of condition-dependent phenotypic features on extraversion levels. In this context, we note that associations of condition-dependent features with extraversion would not need to be large in order to help solve important theoretical problems. For example, condition-dependent reactive heritability could help elucidate why extraversion remains highly heritable within populations despite its consistent positive association with fitness-related outcomes — even if extraversion's calibration to all condition-dependent features combined only explained a minority of its genetic variance on average. Thus, in evaluating this hypothesis, it is crucial for research to employ theoretically appropriate measures and sampling techniques that are able to detect even fairly small phenotypic and genetic correlations.

Indeed, a recent study (von Rueden et al., 2015) lacks some of the limitations of the Haysom et al. study and provides support for the reactive heritability hypothesis. This investigation examined condition-dependent phenotypic features in relation to personality in a large sample of Tsimane' forager–horticulturalists indigenous to the Bolivian Amazon. Most importantly, it was found that (i) measured upper-body strength and the possession of locally valued knowledge, respectively, exhibited independent positive associations with extraversion and prosocial leadership orientation and (ii) controlling for physical strength and locally valued knowledge significantly reduced the estimated heritability of these extraversion-related dimensions. Although this study was limited in that its pedigree-based heritability estimates do not fully control for possible effects of shared environment, it successfully demonstrated that familial resemblance on extraversion-related dimensions is explained in part by condition-dependent phenotypic features.

These two recent investigations (Haysom et al., 2015; von Rueden et al., 2015) are the only two of which we are aware that directly test for genetic correlations between condition-dependent features and extraversion. Each of these studies contains a unique set of methodological strengths and limitations, and they come to somewhat contradictory conclusions. It will therefore be left to future research to arbitrate between them. Overall, we remain tentatively encouraged by the state of the evidence in supporting the viability of the reactive heritability hypothesis as applied to extraversion.

We will close by highlighting a humbling truth: Even under the best-case scenario for our hypothesis — wherein future studies find compelling support for extraversion's reactive heritability — most of the genetic variance in extraversion and all other human personality dimensions would remain unexplained. The missing heritability problem thus persists as a major unsolved mystery in behavioral and evolutionary genetics. In a recent article, Lukaszewski and von Rueden (2015) reviewed the state of the evidence and concluded that much of the genetic variance in personality likely reflects noisy (i.e. directionally random) organizational effects of low frequency genotypes maintained in the context of mutation–selection balance and pathogen–host coevolution (see also Verweij et al., 2012). If this conclusion stands up to future research — such that the heritability of personality largely reflects some combination of noisy genetic effects and reactive heritability — then the arguments advanced by Tooby and Cosmides (1990) a quarter century ago would be vindicated. These very arguments have been roundly criticized in the past decade as theorists characterized the adaptationist approach as being inconsistent with the existence of heritable personality differences (e.g., Buss & Hawley, 2011; Penke, Denissen, & Miller, 2007). It is noteworthy, therefore, that it increasingly appears they may have been correct all along.

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