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Review

Evolutionary theory and personality

Anthony A. Volk[1] and Alexandra Puchalski[2]

Personality is the result of a combination of environmental and genetic influences. Thus, there is a natural match between evolutionary theory and personality theory. However, the top-down application of evolutionary theory to personality has largely taken a back seat to bottom-up data driven approaches. We outline three hypotheses that can help inform the application of evolutionary theory to the study of personality: the importance of past environments in promoting current adaptations; the trade-offs associated with different trait levels that foster individual differences; and the adaptive calibration of individual personalities to specific environmental and genetic confluences. We offer examples of each of these in the hopes that they can help promote a greater integration of top-down evolutionary thinking in personality research.

Addresses
[1] Department of Child and Youth Studies, Brock University, Canada
[2] Department of Psychology, Brock University, Canada

Corresponding author: Volk, Anthony A. (tvolk@brocku.ca)

Modern personality research has been dominated by largely bottom-up lexical approaches that suggest important elements of personality are likely to have worked their way into languages and are thus detectable via reductive, factor-analytical analyses of adjectives [1]. These approaches, dominated by the Big Five (and to a lesser extent, the HEXACO), emphasize that the best model of personality is one that maximizes the amount of variance captured by the most parsimonious number of independent factors [2,3]. This bottom-up approach is largely atheoretical, including when applied to explorations of specific genes associated with personality e.g. Refs. [4–6]. While these bottom-up efforts have been fruitful, they largely overlook the complimentary approach of using top-down, theoretical approaches to personality.

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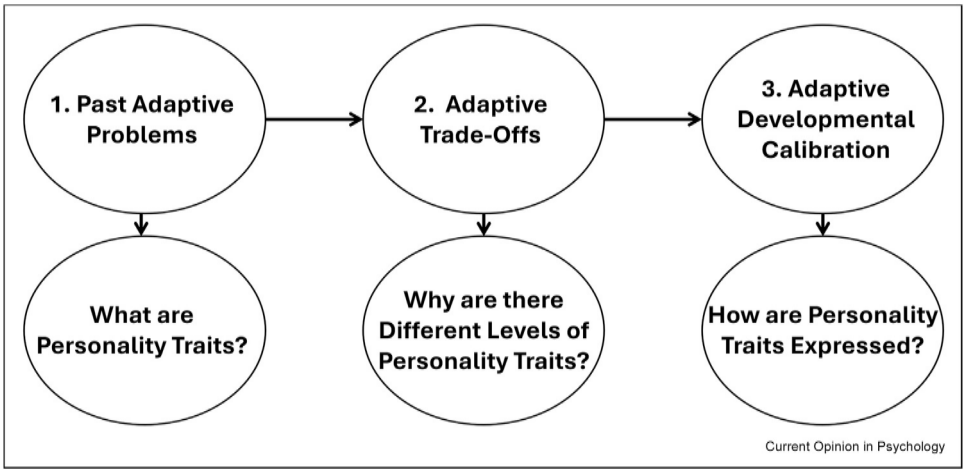
Given that approximately 40 % of variance in individual personality scores can be attributed to heritable influences [7–9], an understanding of personality requires an understanding of genes, and that in turn requires an understanding of evolutionary theory as genes are (on average) the product of evolutionary selection [10]. Evolutionary theory is one of the most durable and powerful theories in all of science, so personality theory may well benefit from being linked to such a strong theory [11]. It is surprising then, that most personality research has paid only cursory attention to evolutionary theory and that in turn, relatively little evolutionary psychology research has focused on personality [12]. Before we turn to our discussion of evolution and personality, we would first like to note that any subsequent use of agentic language for evolution is a linguistic facilitation rather than a reflection of actual biological volition or purpose.

Adaptationist perspective: a top-down approach

Biological theories of animal behavior have long recognized different patterns of behavior as adaptations to evolutionary problems [13,14]. One of the first modern evolutionary approaches to understanding personality argued that personality is an adaptive pattern of responding to different environmental demands [15]. Different demands require different solutions, hence not only the existence of different personality traits, but differing levels of those traits across individuals [15]. Central to this modern formulation of evolutionary personality research is the idea that personality exists not as a means in and of itself, but in service of broader survival and reproductive goals (e.g., parenting, mating, or somatic effort [16]).

Since this initial formulation, a number of different papers have been written to explain entire models of personality (e.g., Big Five [17]; HEXACO [18]) as well as specific personality traits (e.g., Agreeableness [19]; psychopathy [20]). Central to all of these modern evolutionary views of personality are three hypotheses: 1) humans faced reliable/consistent evolutionary pressures that could be addressed by patterns of behavior (i.e., personality); 2) these behavioral patterns typically involved trade-offs; and 3) these trade-offs are adaptively calibrated during development. As illustrated in Figure 1, these hypotheses causally follow each other, such that past pressures determine what adaptations are

Figure 1



Three hypotheses relating evolutionary theory to personality.

present (e.g., how many traits does personality have), trade-offs promote varying levels of these traits that can be normally (e.g., Big Five/HEXACO) or skewed (e.g., psychopathy) in their distribution, and adaptive developmental calibration controls the expression of these traits at the individual level (e.g., changes in personality over the lifespan). We will examine each of these hypotheses in turn.

Past adaptive problems- what does personality look like?

Evolution works in a forward direction, solving today's problems in tomorrow's generations [10]. Thus, to understand how modern genes influence personality, we need to know what pressures or problems our ancestors consistently faced in the past. While this can be challenging, there are some constants of past environments that we can be reasonably sure of, including: the need to survive, grow up, navigate human social systems, find a mate, and raise children into adults [15,21,22]. One can examine historical and hunter-gatherer data to gain information on past challenges and the individual differences they were associated with (e.g., mating and parenting strategies [23]). One can also make inferences about recent versus ancient patterns of behavior (e.g., the novel origins of psychopathy [24]; or the inculcation of different individual values in modern versus older cultures [25]). We know that in modern environments, larger personality differences emerge in more complex societies, suggesting that environmental complexity can serve as a factor for encouraging different behavioral/personality profiles [26]. Given that humans' environmental and cultural challenges have proliferated across our evolutionary history [27], it is likely that human personality has also evolved to become more complex [28].

Armed with the knowledge of past challenges and the theory that humans adapted their behavioral motivations to meet those challenges, one can then start to look for more specific expressions of general patterns of behavior [29–31]. That said, it should be noted that much work remains to be done in determining what were the specific reliable pressures that humans faced in past environments and, in particular, what were the specific behavioral solutions to those problems [29]. To date, there are no firm guidelines regarding just how many different adaptive problems personality has evolved to solve [19]. There may also exist different tiers of responsiveness, such that there are multiple personality traits involved in solving any single adaptive problem [18,32]. Thus, there remains significant work to be done on determining the number of recurring past adaptive problems and the number of behavioral solutions that evolved in response to those problems.

Adaptive trade-offs- why is there variation in personality?

The next hypothesis is that for many past challenges, there were multiple potential behavioral solutions to a particular problem, allowing for a range of personality types and levels to emerge [21,33]. For example, Lukaszewski and colleagues [19] make a convincing argument that trait anger (or HEXACO Agreeableness) is related to one's personal formidability, using the adaptive logic that stronger individuals can better afford the costs of reacting against others who threaten their resources and face better odds of success in any resulting conflict. In contrast, weaker individuals should be more willing to tolerate threats due to their higher costs of retaliating against, and lower odds of defeating, a more formidable opponent [19]. Researchers have

similarly argued that each of the Big Five traits represents a trade-off between opposing adaptive forces [17].

While there has been some support for Big Five trade-offs, there are problems with conceptualizations of Big Five Agreeableness [34] and, in particular, Neuroticism [17]. In contrast, the HEXACO outlines clear adaptive trade-offs for each of its traits [16,18,32,35]. The three traits that overlap with Big Five counterparts relate to the costs versus benefits of investing in: overall effort and planning (Conscientiousness), building and maintaining social relationships (Extraversion), and learning or trying new opportunities in the environment (Openness to Experience). The remaining three HEXACO traits relate to the two key biological processes that form underlie the capacity for extended and enduring social behavior: kin selection and reciprocal altruism [10]. Kin selection involves investing in related copies of one's genes and is associated with HEXACO Emotionality [18]. Reciprocal altruism is associated initiating cooperation or exploitation (Honesty-Humility) and forgiving versus punishing exploitation (Agreeableness [18]). These close ties with well-established biological theories of cooperation [10] afford the HEXACO better evolutionary theory validity than the Big Five (or other common trait models of personality [35]). This makes the HEXACO a prime example of how one can blend bottom-up statistical personality research with top-down evolutionary personality research.

Regardless of which model of personality is used, the belief is that a process known as balancing selection maintains the varying levels of personality traits in a population as a means of dealing with varying environments [36]. However, some questions have been raised about whether the relatively normal distribution of personality traits in populations is due to balancing selection or whether it is simply a by-product of random variation around a negatively-selected single adaptive level for each trait [37,38]. This would imply that much like cognitive variation (where selection largely aims for deleting harmful mutations and favoring higher intelligence [36]), there is relatively little evolutionary pressure on maintaining a range of personality trait values. While this challenge is worthy of further research and consideration, it is worth noting a few important caveats: the outcome of balancing selection can take millions of years to appear in genome-wide scans; it can easily overlap with cues of negative selection (i.e., selection against extreme effects); and it can operate at multiple selective peaks that mask its presence [39,40]. Moving beyond the issue of genetic selection for varying personality genes, a range of evolutionarily adaptive personality traits can emerge independent of negative or balancing selection via the third hypothesized process-the developmental route of adaptive calibration.

Adaptive developmental calibration- how does personality emerge?

Personality traits do not emerge fully formed at birth, but rather, are shaped by developmental processes that adaptively calibrate them to meet environmental demands [12,32,41–43]. For example, stronger individuals may be rewarded in their efforts to fight back against those who exploit them, leading them to develop a quicker temper or lower levels of forgiveness [19,44]. From a developmental perspective, personality is now believed to not be stable over the lifespan, but rather it shows predictable changes over the course of the lifespan [45]. While this is well known amongst animals [46], an evolutionary approach can elucidate how and why these personality changes match with major human life transitions (e.g., adolescence/early adulthood; adulthood; old age) in ways that promote adaptive outcomes for the different challenges typically experience at different points in the lifespan [47]. For example, adolescents and young adults scoring higher in selfish traits may be a means of prioritizing their own status as they leave their original nuclear family to start one of their own [47]. The reverse is true of older adults, whose more selfless traits may prioritize altruistic investment in kin and reducing group conflict instead of boosting their own status at ages when further reproduction is unlikely [47].

The principle of adaptive calibration can also explain the origins of non-clinical personality traits that result in societally maladaptive (i.e., antisocial) behavior. For example, environments that promote manipulating others may give rise to dark personality traits like psychopathy that reward such behavior [32]. Psychopaths lack many of the general deficits associated with criminality (e.g., low IQ, brain damage, birth problems [48]), are responsive to hostile developmental environments [49], are more likely to choose competitive versus cooperative majors [32], tend to avoid targeting kin [50], are proficient at recognizing vulnerability in others [51], are proficient at exploiting others [52], and achieve significant reproductive outputs [53]. All of these are hallmarks of adaptive developmental calibration that may reflect psychopathy's adaptiveness in specific environments that reward [55], rather than punish (e.g., the relative anonymity of modern society [24]), antisocial tendencies.

The process of calibration is regulated by gene × environment interactions that can either be passive (e.g., parents passing on a personality proclivity), evocative (e.g., a child's personality can evoke a response that increases or decreases that personality's expression), or active (e.g., a child can actively pursue environments that reward their personality traits [54]). Thus, calibration can be both a passive and an active response that involves the organism attempting to alter levels of personality traits to produce the greatest benefits at the least costs [32,36].

The end result is that personality differences that reflect adaptive solutions to the plurality of situations and environments that humans find themselves in Ref. [26].

Conclusions

Overall, there appear to be strong potential links between evolutionary and personality theories. These links, while acknowledged in both literature, remain underdeveloped [12]. Given that many different areas of psychological research are converging on the reality that human behavior is the product of both genes and environments [6], we argue that evolutionary and personality research are prime examples of this interaction and that when combined with each other, can offer a potent framework for explaining both normative [12,55] and clinical [56,57] patterns of human personality. We thus encourage researchers to consider all three evolutionary hypotheses outlined in Figure 1 as a means of incorporating one of science's most powerful top-down theories (evolution) into the design [e.g., 19, 29] and evaluation (e.g., Refs. [18,56] of personality research).

Author's contribution statement

Anthony Volk: Conceptualization, Writing - original draft, Writing - review & editing, Funding- PI. Alexandra Puchalski: Writing-review & editing.

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Declaration of competing interest

The authors declare no conflicts of interest.

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* of special interest
** of outstanding interest

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Further reading

10. ** This book is a synthesis of our modern understanding of evolutionary theory. The concepts it reviews are central to obtaining a modern understanding of evolutionary theory and should be considered required knowledge for anyone conducting evolutionary research.

11. * This article offers a good review of comparative approaches to personality across species using an evolutionary perspective.

12. * This article introduces a special issue on the topic of evolution and personality and lays the case for not just why personality theory would benefit from evolutionary theory, but for how evolutionary theories of human behavior would benefit from personality theory.

15. * Among the first modern attempts at understanding personality from an evolutionary perspective, this article outlines key conceptual and theoretical considerations associated with this interdisciplinary perspective.

18. ** This article outlines the theoretical costs and benefits of the HEXACO model of personality. It is an excellent example of trying to blend traditional lexical modelling of personality with evolutionary theory.

19. ** This article lays out a plausible format for linking personality and evolutionary theory. Inspired by Buss, 1991, it also contributes a novel and detailed review of how anger/HEXACO Agreeableness may have evolved as a conditional cost-benefit pattern of behavior.

29. ** This article outlines the evolutionary logic linking personality to evolved predispositions. In particular, it focuses on the evolution of motivational systems that could in turn lead to the expression of personality.

32. * This article offers a view of how Dark personality traits (as well as Light traits) may have evolved and developed through complimentary processes of tinkering and calibration. The basic principles laid out are applicable to other constellations of personality traits.

35. * This article compares and contrasts the evolutionary viability of different models of trait personality, including: single, dual, five, and six factor models.

36. ** This article summarizes the potential links between evolution, genetics, and personality. It is an excellent introduction to how these three areas of research can be linked with each other.

37. * This article questions the validity of the second hypotheses reviewed here- that there are adaptive variations in the levels of personality traits in response to different environmental pressures. It argues that personality variation is largely the random result of negative selection (i.e., removing faulty genes to preserve a single optimum level) rather than balancing selection (i.e., preserving a range of personality geneotypes because they are differentially adaptive in different contexts).

47. * This chapter elucidates an explanation for observed changes in HEXACO personality traits across three distinct phases of the human lifespan: adolescence and early adulthood, middle adulthood, and late adulthood/old age. It focuses on linking the observed personality traits in each phase of life with the unique adaptive problems faced at each phase.