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Authors' Response

Evolution, Genes, and Inter-disciplinary Personality Research

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Abstract

Most commentaries welcomed an evolutionary genetic approach to personality, but several raised concerns about our integrative model. In response, we clarify the scientific status of evolutionary genetic theory and explain the plausibility and value of our evolutionary genetic model of personality, despite some shortcomings with the currently available theories and data. We also have a closer look at mate choice for personality traits, point to promising ways to assess evolutionarily relevant environmental factors and defend higher-order personality domains and the g-factor as the best units for evolutionary genetic analyses. Finally, we discuss which extensions of and alternatives to our model appear most fruitful, and end with a call for more inter-disciplinary personality research grounded in evolutionary theory. Copyright © 2007 John Wiley & Sons, Ltd.

We were gratefully impressed to learn that our target paper received 22 commentaries, coming from disciplines as diverse as traditional personality psychology (**Funder**, **Matthews**, **McCrae**), molecular behaviour genetics (**Bates**, **Lee**, **Strobel**), quantitative behaviour genetics (**Jang**, **Johnson**, **Livesley**, **South and Krueger**, **Rebollo and Boomsma**), evolutionary behavioural ecology (**Dingemanse**, **Réale**, **Sih and Bell**, **van Oers**) and evolutionary psychology (**Campbell**, **Euler**, **Figueredo and Gladden**, **Gangestad**, **Keller**, **Saad**, **Troisi**). This shows the scientific community's high level of interest in understanding heritable personality differences within an evolutionary framework. The volume of commentary is also a testament to the inter-disciplinary challenge such an endeavour entails. We would like to thank all commentators for their thoughtful remarks and constructive criticism.

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The overarching goal of our paper was to provide a theoretical introduction to evolutionary genetics for personality psychologists. Therefore, we found it especially pleasing that most commentators appeared open to an evolutionary genetic approach to personality, or even applauded it. We take this as an affirmation that our most central message—that personality psychology can benefit from an evolutionary approach grounded in evolutionary genetics—is already widely acceptable, if not fully accepted.

Our second major goal was to try to infer the mechanisms that maintain genetic variation in personality differences, given the predictions from different evolutionary genetic models, and the phenotypic and genetic evidence available from personality psychology. Most commentaries focused on specific assumptions, conclusions or details of our resulting evolutionary genetic model of personality. As **Keller** states, such healthy discussion is crucial in strengthening the relatively young scientific movement of evolutionary behavioural genetics. Of course, our evolutionary model of personality is only one possible reading of the current state of evolutionary genetic theory and the empirical research on human personality. It should be regarded as an initial working model that should be challenged, refined and extended.

In this response to commentaries, we will first reply to objections to the theoretical reasoning and use of empirical evidence in our target paper, and then discuss more general issues—the optimal levels at which we should study the evolutionary genetics of personality, how our model should be extended in the future and which alternatives could be explored further. Because so many researchers from diverse backgrounds made comments that were often quite specific, space limitations did not permit us to reply in detail to every point. However, we tried to address the key recurring themes in this rejoinder, and hope that such debate leads multidisciplinary research on the evolutionary genetics of personality to flourish in the future.

EVOLUTIONARY GENETICS AS A THEORETICAL FRAMEWORK FOR PERSONALITY PSYCHOLOGY

Funder and **McCrae** applauded our approach as being a healthy departure from the early days of 'evolutionary' accounts of personality that could not be refuted by empirical evidence. In contrast, **Bates** criticised our attempt as using 'armchair' evolutionary theorising instead of hard empirical 'field work' to settle the evolutionary history of traits. We think this 'data-first' bias, shared by **Bates** and many other personality researchers, is an understandable reaction to the peculiar history of personality psychology, but is now inhibiting progressive research. Before the trait approach integrated factor-analytic, cross-cultural and behaviour genetic studies of personality structure, personality psychology was a mess—a hodgepodge of Freud, Rogers, Maslow and other 'classic figures' who were long on theory and short on data. Frustration with this history (in which theory has more often retarded research than advanced it) has inoculated many personality psychologists against anything that sounds like theory. Here, we simply point out that evolutionary genetic theory has quite a different status than Maslow's hierarchy of needs, or any other traditional 'personality theory'. Evolutionary genetic theory is the dominant formal way that biologists use to think about the effects of selection, mutation, drift and migration on the genetic structures of traits and populations. It is the mathematical heart of biology, and is rooted in 140 years of progressive research. Well-established evolutionary genetic theories do not share the same limitations of traditional 'personality theories'. In any case,

DOI: 10.1002/per

we repeatedly descended from theory's armchair to compare evolutionary genetic predictions against the current state of empirical knowledge on human personality differences.

CAN WE ALREADY TELL SOMETHING USEFUL ABOUT THE EVOLUTIONARY GENETICS OF PERSONALITY?

To infer evolutionary histories and selective regimes from personality data is indeed a big step, dependent on the quality of both available data and theoretical models. **McCrae** asks if we really know enough to take this step, and **Keller** reminds us to be careful and critical before claiming firm conclusions. Evolutionary genetics, while well-established and intimately intertwined with quantitative genetics in evolutionary biology (**Gangestad**), is a rather new area for most psychologists and behaviour geneticists, who have only just begun to recognise its potential. We would hate to derail such a development through premature conclusions. It is also true that most theoretical models still provide at best ordinal predictions about trait characteristics for realistic evolutionary conditions (**Euler**), and that the relevant empirical data are still incomplete, though maybe not as indecisive as suggested by **Bates**, **McCrae** and **Keller** (a point to which we will return below). Therefore, the model we proposed is not the only possible one, and it should not be understood as conclusive. However, as the Table 1 in our target paper shows, even though the theoretical predictions for individual characteristics of traits shaped by certain evolutionary mechanisms are sometimes vague, the *pattern* of predictions that emerges across various characteristics clearly discriminates between them. Similarly, even though the quality of available empirical evidence for the individual characteristics varies widely, it was the overall pattern of data that struck us and led us to propose the model that general intelligence is under mutation-selection balance, whereas personality traits are under balancing selection.

Before we discuss how decisive the different predictions and lines of evidence really are, we would like to address the usefulness of an 'inconclusive' evolutionary genetic personality model. After all, **Keller** called for an exceptionally high standard of evidence at the current stage. We agree that it is likely too early to draw a *conclusive* model, but we see the merits of proposing a sufficiently *plausible* model to help generate new hypotheses, guide empirical research, and inform theories about personality in general (see **Funder** and **Matthews**). The important point is that a plausible model should be explicitly labelled as such and should not blind researchers to alternatives. Nor should it constrain empirical endeavours, which could lead to scientific myopia. Contrary to **Bates**' reading of our target paper, we did not call for a theory-driven moratorium on any particular kind of research, even including molecular genetic studies on the genetic bases of general intelligence (*g*). Instead, we explicitly stated that such studies should be done to test the predictions of our model, though they might benefit from being more theoretically informed.

CAN WE ALREADY MAKE INFERENCES FROM GENETIC ARCHITECTURES?

Keller questioned our use of genetic architecture information to infer mechanisms of genetic variance maintenance. This criticism has a theoretical and an empirical aspect that

DOI: 10.1002/per

are somewhat mixed up in his commentary. On theoretical grounds, we have to agree with **Keller** and also with **Figueredo and Gladden** that it is hard at the moment to discriminate between mutation-selection balance and balancing selection based on the relative contribution of non-additive genetic variance (V_{NA}) to the total genetic variance of a trait (i.e. the coefficient D_α). We acknowledged the inconclusiveness of the current literature, but were less explicit about it later on (especially in Table 1, where we simply stated the prediction we regard as most likely). As **Keller** rightly stated, the prediction that the proportion of V_{NA} will be medium for traits under mutation-selection balance and large for traits under balancing selection might be considered as the weakest in Table 1.

However, we do not follow **Keller**'s sudden dismissal of the prediction that V_{NA} will be higher in traits under selection (including mutation-selection balance and balancing selection) than in neutral traits. The argument here is that selection tends to deplete additive genetic variance (V_A), while V_{NA} is largely robust against selection. (On a side note, **Lee** is right that this is an extrapolation from Fisher's fundamental theorem, but a widespread one that is correct under many conditions, e.g. Roff, 1997.) Nor does **Keller** provide a theoretical counter-argument. Instead, he points to the rather independent issue of *empirical* difficulties with the establishment of V_{NA} estimates, a topic on which we totally agree. In humans, most inferences about genetic architectures come from twin studies (e.g. **Livesley**), where the traditional design confounds V_A and V_{NA}, and V_{NA} can only be estimated when shared environmental influences are neglected. In line with Keller and Coventry (2005), we think that studies with large extended twin-family designs would provide the best solution.

Furthermore, **Keller** noted that the unknown scale properties of most personality questionnaires and ability tests render rather uncertain even the existing estimates of genetic variance components from more powerful designs. As support, he cited a recent study by Lykken (2006) in which a scale transformation eliminated the V_{NA} component of skin conductance level, a psychophysiological measure of arousal. However, Lykken (2006) argues that this correction actually served as a statistical control for all kinds of confounding factors beyond arousal that influence skin conductance (e.g. individual differences in the density and reactivity of sweat glands). In such cases where the scale transformation decreases the complexity of the measured construct, a reduction in V_{NA} is what should be expected. This does not undermine the general validity of the untransformed score or the scale of the applied measure; it just shows that the untransformed score reflects a construct that is influenced by several interacting heritable components (Lykken, 2006). In our model, such a transformation would correspond to a statistical control of all but one of the interacting endophenotypic personality mechanisms. If a transformation like that becomes ever possible for personality traits, we would also predict a decline of V_{NA}. We agree with **Keller** (see also **Bates**) that the development of new personality measures with improved scale properties (esp. ratio scales) is highly desirable, but we put more trust in the V_{NA} estimates from extended twin-family designs than **Keller** does. While these results might not help us very much to discriminate between different forms of selection on personality differences (mutation-selection balance vs. balancing selection), they do suggest that selective neutrality of personality, as favoured by **Campbell**, is unlikely.

While it is hardly possible to distinguish between mutation-selection balance and balancing selection based on just V_{NA} estimates, data on inbreeding depression can be more decisive. This is because polygenetic traits under mutation-selection balance should always show inbreeding depression, while only traits under balancing selection through

DOI: 10.1002/per

overdominance will (**Keller**), and overdominance is actually rare and evolutionarily unstable. In this case, the problem is on the empirical side: Experimental inbreeding studies are only possible in non-human animals, and strong natural experiments (e.g. children from cousin marriages) are rare. Fortunately, this kind of inbreeding data exist for intelligence (supporting mutation-selection balance), but is lacking completely for personality traits. In a noteworthy first attempt to fill this gap, **Rebollo and Boomsma** reinterpreted Camperio Ciani et al.'s (2007) study, and also reported their own data, on personality differences between parents and their children who mated with a spouse from a geographically close or distant region. Both studies together suggest that those who mate within the same regions (which may reflect stronger inbreeding effects) have children who are lower on sensation seeking (esp. excitement seeking) and openness to experience, while results are unclear for extraversion and there was no effect for neuroticism, agreeableness, conscientiousness, anxiety or anger. The problem with these results is that they are very indirect and allow for various alternative interpretations. It is especially striking that effects were found exclusively for traits (i.e. sensation seeking and openness to experience) that can be directly associated with migration tendencies and active niche selection. This is most obvious in the worldwide distribution of DRD4 polymorphisms, which suggests that carriers of the allele that has been associated with high sensation seeking are more likely to migrate (Chen, Burton, Greenberger, & Dmitrieva, 1999). It is also striking that **Rebollo and Boomsma** found the sensation seeking difference already in the parent generation, even though we know nothing about the geographical mating habits of their parents. As these authors themselves state, migration might be a plausible alternative explanation for these particular results. What we need next are studies of inbreeding effects on personality traits with stronger designs (some suggestions are given by Mingroni, 2004).

Similar conclusions can be drawn for the other aspects of genetic architecture we discussed: while the theoretical models are specific enough to make predictions that distinguish at least one of the major evolutionary mechanisms for the maintenance of genetic variance from the other two, most empirical evidence on the number of genetic loci, the number of polymorphic loci and the average effect size of loci is still rather indirect. Again, the overall pattern of results allows us to evaluate which mechanism is the most plausible for a given trait, but better data is needed to substantiate these conclusions.

IS MATE CHOICE SIMILAR FOR INTELLIGENCE AND PERSONALITY TRAITS?

On the phenotypic level, evolutionary genetic theory suggests that traits under mutation-selection balance, but not traits under balancing selection or selectively neutral traits, should be sexually attractive in a general, species-typical way. The logic here is that choosing sexual partners based on reliable indicators of low mutation load will endow potential offspring with 'good genes'. In our target paper, we argued that studies on human mate choice support general mate preferences and assortative mating for intelligence, but not for personality traits. **McCrae** doubts this claim. He remarks that studies on self-reported mate preferences often find strong preferences for personal attributes such as 'honest', 'considerate' and 'affectionate', which can be ascribed to the

DOI: 10.1002/per

agreeableness domain. However, aside from the problem that self-reported preferences often do not reflect actual mate choices (Penke, Todd, Lenton & Fasolo, in press), it is important to distinguish between sexual attraction *per se* and pragmatic preferences for long-term mates. Long-term relationships are, ideally, cooperative relationships, so people prefer honest and trustworthy partners for long-term mating relationships, just as in other social relationships (Cottrell, Neuberg, & Li, 2007). The likely reason for this, however, is not sexual attraction *per se*, but the pragmatic avoidance of exploitation, distress, inconvenience and inefficient coordination (called 'relationship load' by Buss, 2006). This becomes obvious in studies where preferences are assessed across different mating contexts and relationship durations (e.g. Kenrick, Groth, Trost, & Sadalla, 1993). These studies show that the preference for agreeableness-related attributes vanishes when a mate is chosen for a sexual affair or a one-night-stand, where not much cooperation is necessary. Furthermore, it is unclear whether the long-term preference for warmth and trustworthiness really reflects the ideal of an agreeable mate personality (i.e. a trait of an individual), or the ideal of a secure attachment relationship (i.e. a dyadic trait) (Penke et al., in press). At least from an evolutionary theoretical perspective, people should seek a long-term partner who is faithful and supportive within the context of the relationship, but people should be less concerned their partner's behaviour towards, for example, alternative mates, rivals or out-group members. Exceptions might be traits like benevolence, generosity, heroic virtues and magnanimity. These agreeable characteristics seem to be sexually attractive in short-term and long-term mates, but apparently because they are reliable indicators of good condition and low mutation load (Griskevicius, Tybur, Sundie, Cialdini, Miller, & Kenrick, in press; Miller, 2007). However, the important point here is that high agreeableness *per se* is not sexually attractive, but some specific forms of agreeableness are generally attractive if they can only be displayed by individuals in good condition. Similarly, only people with high intelligence will be able to convert a high openness to experience into sexually attractive degrees of creativity (Haselton & Miller, 2006; Miller, 2000a). These personality traits are not always sexually attractive in themselves, but can be attractive under certain circumstances, when they advertise good condition and genetic fitness.

McCrae also noted that some degree of assortative mating has sometimes been shown for conscientiousness and openness to experience, but other studies (e.g. Watson, Klohnen, Casillas, Nus Simms, Haig, & Berry, 2004) failed to show assortative mating on these traits. We are not aware of a meta-analysis of the large human assortative mating literature, but the general picture is that assortative mating for intelligence is a well-established phenomenon, while findings are rather weak and inconsistent for individual personality traits.

Finally, **McCrae** mentions that assortative mating can result from social homogamy (i.e. choosing a mate from within one's self-selected social environment, such as college, job or neighbourhood), not just from direct assortment on perceived traits within competitive mating markets. More sophisticated research designs are able to disentangle these two alternatives, and they reveal that direct preferences exist independent of social homogamy, especially for intelligence (e.g. Reynolds, Baker, & Pedersen, 2000; Watson et al., 2004).

Overall, we think it is fair to say that intelligence is very often directly preferred in mate choice, while the evidence does not support such a general conclusion for personality traits.

DOI: 10.1002/per

IS PERSONALITY EVOLUTIONARILY RELEVANT AT ALL?

The most important kind of evidence to distinguish between selective neutrality and any selection-based account for heritable personality differences (including mutation-selection balance and balancing selection) is the empirical link between personality and fitness. Only if personality differences have behavioural consequences that influence fitness, can we posit that some form of selection acts directly on personality. Fitness is ideally operationalised as the relative long-term (multi-generational) reproductive success of genotypes in populations, but phenotypic selection studies have established more practical operationalisations of fitness, such as measured reproductive success over a single lifespan or even shorter periods such as breeding seasons (**Réale**). Since the necessary data are not hard to gather for human personality, it is both surprising and unfortunate that human phenotypic selection studies are extremely rare. More of these studies are desperately needed to inform an evolutionary genetic approach to personality (**Dingemanse**, **Réale**, **van Oers**).

But does this mean that we have to fall back to the most 'parsimonious' baseline model of selective neutrality, as suggested by **Campbell**? We do not think so. As calculated by Keller and Miller (2006), the correlation between a truly neutral trait and fitness must not be greater than $\pm .0055$ (i.e. the square root of the maximal .003% fitness difference under which genetic drift is a more important factor than selection, given typical ancestral human population sizes). This effect size is greatly exceeded in the few studies that directly link personality differences to general reproductive fitness in humans (e.g. Eaves et al., 1990) and other animals (see Dingemanse & Réale, 2004), and in the much more numerous studies that link personality differences to specific components of human fitness (such as survival, social status, mating success and reproductive strategies; see our target paper for references). Even if it turned out that genetic drift had been somewhat stronger throughout our evolutionary history than assumed in Keller and Miller's calculation (**Réale**), which would allow somewhat greater effect sizes for neutral traits, and even though the effect sizes for single fitness components should be interpreted with caution because of evolutionary trade-offs (**Réale**), it seems highly unlikely that all of the well-documented behavioural consequences of personality differences are invisible to selection.

Finally, note that the selective non-neutrality of personality differences contradicts not only Tooby and Cosmides' (1990) neutrality account for the maintenance of genetic variance in personality, but also their pathogen-defence hypothesis (**Campbell**, **Livesley**). This hypothesis assumes that the *behavioural* consequences of personality differences are so invisible to selection that their genetic foundations can vary freely, such that the organism's proteome is more distinctive, unpredictable and harder for pathogens to exploit. Even if all personality-related polymorphisms (such as DRD4 or 5-HTTLPR) had pleiotropic effects at the level of organismic biochemistry that are relevant to anti-pathogen defence, any such anti-pathogen effects would need to be larger than the behavioural fitness payoffs of personality differences, in order for the pathogen-defence model to be applicable. The same logic must hold for any similar hypotheses that regard heritable personality differences as by-products of other adaptations (**Keller**). We would also like to add that, despite the ingenuity and prominence of the Tooby and Cosmides (1990) paper, we are not aware of studies that have directly tested the pathogen-defence model. So far, we regard our model as a more plausible alternative.

DOI: 10.1002/per

ENVIRONMENTAL CHALLENGES FOR AN EVOLUTIONARY PERSONALITY PSYCHOLOGY

Our model suggests that future phenotypic selection studies should pay special attention to the way that human personality traits interact with specific environments. If spatio-temporal environmental heterogeneity is responsible for maintaining genetic variance in personality traits, then the correlation between a trait and fitness should reverse across some environments. Thus, certain environmental variables should act as statistical moderators of the relationships between personality traits and measures of survival, reproductive success and/or kin success. A methodological implication is that we need more precise, valid and evolutionarily informed ways of categorising and measuring the environmental factors that interact with personality traits to yield adaptive or maladaptive behaviour (**Funder, Matthews, Saad**). Characterising environmental structure at a useful level of description is a rather old problem that psychologists recognised long ago (see Meehl, 1978), but still struggle to solve (for a notable attempt see Holmes, 2002).

While we cannot offer a panacea, we suggest that an evolutionary framework for personality, richly informed by mid-level adaptationist theories (e.g. concerning kin selection, multi-level selection, reciprocity, sexually antagonistic coevolution, parent-offspring conflict and life-history theory) might help to isolate relevant environmental features. This is because environments can vary in many ways (**Johnson**), but not all of them are equally relevant for understanding the fitness payoffs of particular traits. A useful exploratory heuristic might be to consider 'Which variable environmental factors create different adaptive problems that are solved better or worse by individuals with certain personalities?' For example, big cities with high population densities and anonymous interactions might give Machiavellian cheaters more chances to exploit others than small villages would, in which reputations spread faster through gossip; thus, cities may offer higher fitness payoffs for disagreeable individuals than small villages do. Living in big cities might also imply frequent changes in people's social networks, which lead to persistent uncertainty about one's social status and mate value, and about the pool of available mates, friends and allies. Neurotic fears of social rejection might be as maladaptive in this context as an indiscriminate tendency to strive for the alpha rank all the time. Harsh and dangerous physical environments likely make social cooperation and mutual support necessary, as do intergroup conflicts over limited resources, so both may favour agreeableness and neuroticism. More generally, the differences in styles of social interaction that are at the core of many personality traits suggest that we should pay special attention to social-environmental factors that may mediate and modulate relationships between personality traits and fitness payoffs. Such a research program is already exemplified by work on sociosexuality as a personality trait with different mating payoffs in different environments (Gangestad & Simpson, 2000).

Saad emphasised the four different roles that environmental factors play in an evolutionary genetic approach to personality. So far, this section only discussed environmental niches, which provide selection pressures. Two of Saad's other environmental roles, the ontogenetic environment of personality development and the current real-time situational context of personality functioning, are combined in our reaction norm model as the 'environment' that interacts with the genotype to evoke a behavioural response. These two different functions of the environment as (1) the source of selection pressures and (2) one of the interacting factors in reaction norms (which correspond to the two 'Environment' boxes in Figure 3 of the target paper) appear to be

DOI: 10.1002/per

mixed up in one of **Funder**'s remarks: The ontogenetic and real-time environmental factors that evoke personality differences (an interaction effect) might or might not be the same across different environmental niches that select for or against these differences (a main effect). In future evolutionary genetic studies of personality, it should be helpful to distinguish more carefully between the environmental factors that shape a phenotypic personality trait and the environmental factors that make this trait have certain fitness cost and benefits.

The fourth role of the environment that **Saad** acknowledges is the ancestral EEA. Contrary to the commentaries by **Livesley** and **Bates**, the more evolutionarily remote and ancient forms of this environment play a negligible role within an evolutionary genetic perspective on current heritable variation in human personality. Understanding the remote Pleistocene EEA is very useful to explain non-heritable conditional strategies and universal sex differences (**Troisi**, **Saad**), as in mainstream adaptationistic evolutionary psychology. However, genetic variation in contemporary human populations depends on much more recent selection pressures over the last few hundred generations, within the Holocene. Thus, an evolutionary personality psychology may end up paying much more attention to the environment-specific payoffs for personality traits during recent (e.g. Neolithic) prehistory, and even within historically documented civilisations. For example, the divisions of labour and diverse social roles that emerge within complex hierarchical societies may have permitted a much wider range of personality traits to flourish than would have been possible under small-scale, egalitarian, hunter-gatherer conditions in the Pleistocene.

AT WHICH LEVEL SHOULD WE STUDY PERSONALITY TRAITS FROM AN EVOLUTIONARY PERSPECTIVE?

We have apparently reached one of those intriguing points in the history of science when there is a mutual recognition between two fields that they have been working on the same problems in slightly different but complementary ways. In this case, the two fields are evolutionary behavioural ecology (the study of variation in animal behaviour) and personality psychology (the study of variation in human behaviour) (**van Oers**). Such times of mutual recognition are always accompanied by initial confusions over terminologies, assumptions, methods and objectives, before the two fields can take full advantage of each other's insights and findings. Evolutionary ecologists, who usually study animals that cannot report their thoughts or feelings, naturally must focus on observed behaviours, and their correlations, contingencies and fitness consequences across environments. Since personality psychologists have restricted their studies to a very talkative mammal, they usually prefer to ask their subjects to verbally report their thoughts and feelings, and to look for latent personality constructs that can explain patterns across these self-reports (**Réale**). In terms of the watershed model, evolutionary ecologists usually start their analyses more 'downstream' than personality psychologists (**Euler**)—by observing emitted strategic behaviour rather than by recording verbal responses about intended or remembered behaviour.

Evolutionary ecologists usually have a solid training in evolutionary genetics, and they know that selection does not operate on a single trait at a time, but affects all traits that are genetically intercorrelated at once. That is why one objective of animal personality studies is to find behavioural tendencies that are genetically correlated (the 'character state perspective', **Dingemanse**, **Sih and Bell**), to understand how patterns of genetic variance

DOI: 10.1002/per

and covariance in behavioural propensities fit into the genetic variance–covariance matrix (the '**G** matrix') that describes all phenotypic traits, whether morphological, physiological or behavioural. The higher goal is to identify fairly independent dimensions in the **G** matrix, since these dimensions could also evolve fairly independent of each other. Consequently, these dimensions would constitute the most suitable units of analysis for evolutionary genetic studies (Mezey & Houle, 2003).

Personality psychologists are very familiar with looking for independent dimensions in variance–covariance matrixes, using methods such as factor analysis. However, they started doing so many decades before evolutionary ecologists did, and tended to use phenotypic correlations among cognitive tests, or among self- or peer-ratings on personality-descriptive adjectives or questionnaire items, rather than among field observations of actual behaviour. This search culminated in the discovery of independent, latent phenotypic dimensions in humans, of which the *g*-factor and the FFM of Personality reached the highest consensus. Most interestingly, these dimensions replicate fairly well on the genetic level (e.g. Plomin & Spinath, 2004; Yamagata et al., 2006), suggesting that research on human personality has already come close to characterising the genetically correlated dimensions that evolutionary ecologists are still seeking in other species. What is now called the 'character state perspective' in evolutionary ecology is so fundamental to personality psychology that we simply took it for granted in our target paper. Resolving such terminological and methodological confusions might be the most important first step for inter-disciplinary personality research.

When **Livesley** and **McCrae** suggested instead that lower-order, interdependent personality facets may be the best level of analysis for an evolutionary genetics of personality, they may have confused the heritable individual differences relevant to personality research with the species-typical, domain-specific adaptations studied by adaptationistic mainstream evolutionary psychology. A hallmark of adaptations is their complex functional design, which would break down when too much genetic variation is introduced. As a consequence, most heritable individual differences cannot be adaptations (Tooby & Cosmides, 1990) and they cannot be analysed using traditional standards of adaptationism. Rather, they are dimensions of genetic variation that are tolerated within systems of interacting adaptations. For example, humans are likely endowed with adaptations to regulate attachment relationships (**Troisi**), to discover signs of social rejection (Leary & Baumeister, 2000) and to monitor environmental dangers (Nettle, 2006). All these systems are under strong stabilising selection to function effectively (which maintains their complex adaptive design), but they are still all influenced by individual differences along a heritable dimension called neuroticism. This dimension of personality variation is not at the same level of description as the adaptations themselves, and is maintained by different selective forces—according to our model, by balancing selection given environmental heterogeneity—rather than stabilising selection for raw functional efficiency.

The lower-level facets of broad personality dimensions show substantial genetic intercorrelations (Yamagata et al., 2006) and will thus show correlated responses to selection. This makes them unlikely to be the most useful units of analysis in studying the evolutionary genetics of personality traits. That being said, we are open to ongoing debate concerning which and how many personality factors best represent independent dimensions of variation in the behavioural aspects of the human **G** matrix. We concentrated on the dimensions of the FFM, mainly because of their clarity and familiarity, and the rich literature on them. **South and Krueger** as well as **Figueredo and Gladden** suggested that there may be even higher levels of abstraction than the FFM, as

DOI: 10.1002/per

suggested by the evidence of modest phenotypic (Markon et al., 2005) and genetic intercorrelations between the FFM domains (**Johnson**). One problem with such jumping to a higher level of abstraction is that some genetic correlations may be different from zero at a statistical level of significance, but not at an evolutionary level of significance (cp. **Jang**): these genetic correlations may be caused by environmental factors through gene-environment interactions (GEIs), making them environment- and population-dependent. In the target paper, we adopted van Oers et al.'s (2005) argument that genetic correlations due to structural pleiotropy (i.e. shared mechanisms on the endophenotypic level) should not change signs across environments, whereas those due to GEIs should change signs across environments. **Johnson** noted that this criterion might fail to distinguish between types of genetic correlations because people select, create and evoke their own environments, leading to gene-environment correlations (r_{GE}s). The effects of GEIs and r_{GE}s can easily be confused in empirical results and are difficult to separate (but see Johnson, 2007). **Johnson** argues that r_{GE}s are problematic because they could lead to a homogenisation of the populations in certain environments with regard to the traits under study (if its result is that every niche harbours only individuals with exactly those personality trait levels that fit best to the niche's demands). In this case, the genetic correlations could indeed be attenuated by reduced trait variance—possibly down to zero, given perfect r_{GE}s. However, we do not see how the variance reduction within environments that could be caused by r_{GE}s can lead to artificial *sign changes* in genetic correlations across environments. But even if the discriminatory power of the criterion offered by van Oers et al. (2005) is limited in certain cases, we do not follow **Johnson**'s conclusion that this (possible) methodological issue with the detection of structural pleiotropies implies that they are rare in nature.

More critical is **Dingemanse**'s remark that the **G** matrix is not static and might differ between environments and populations as a result of local selection pressures. Genetic correlations that freely evolve between populations are likely not constrained by structural pleiotropy, but may be the result of selection for limited plasticity. While this does not make them less interesting from an evolutionary genetic perspective, some of our arguments would indeed be invalidated (see **Dingemanse**). We think that the key data to distinguish between structural pleiotropy and selected limits on plasticity would come from cross-cultural studies. If the factorial structure of the behavioural aspects of the **G** matrix replicate across populations around the world, it is unlikely to reflect recent, local selection pressures. Initial data suggest that the FFM shows good replication of genetic factorial structure across three populations from three continents (Yamagata et al., 2006). This and other studies also suggest that the structure of the behavioural aspects of the **G** matrix reflects fairly accurately the phenotypic structure of the FFM personality dimensions, which allows us, according to the protocol suggested by Roff (1997, p. 100), to use phenotypic structures as a surrogate for genotypic structures. Phenotypic data is available for a larger sample of cultures, and again they suggest that the FFM structure replicates rather well across populations (McCrae & Allik, 2002). While more cross-cultural (and within-culture cross-environmental) comparisons of **G** matrices would be desirable (preferably with designs that are able to differentiate between additive and non-additive genetic variance), these results suggest that the structure of the FFM is caused by structural pleiotropy across behavioural propensities within each of its main dimensions. It remains to be seen, however, if other genetic factor solutions replicate better across cultures, or if the FFM dimensions (and the *g*-factor, for which a similar logic holds) already are the best level to study the evolutionary genetics of personality.

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EXTENSIONS OF OUR EVOLUTIONARY GENETIC MODEL OF PERSONALITY

Evolutionary genetics is a rich and complex field, and offers much more to personality psychology than we could cover in our target paper. Since evolutionary genetics is novel ground to most personality psychologists, we chose to focus rather simply on the major evolutionary mechanisms that can maintain genetic variation in traits. Also, we tried to rely on theoretical arguments and models that are already well-established and relatively uncontroversial in evolutionary genetics. So, for example, we did not discuss the new but sketchy literature on the maintenance of genetic variance in reaction norms (**Sih and Bell**), where the current conclusions depend on the specific assumptions of complex models and are sometimes contradictory (see de Jong & Gavrilets, 2000 vs. Zhang, 2006). Also, we could only make parenthetical references to some other topics, such as niche picking (a form of active r_{GE}). In the future, our model should be extended by including, among others, a more explicit account of r_{GE}s (**Jang, Johnson, Sih and Bell**), reactive heritability beyond condition-dependency (**Gangestad**), indirect selection in social groups (**Sih and Bell**) and models of genetic variance maintenance in reaction norms (**Sih and Bell**). It should also be contextualised within the broader frameworks of evolutionary game theory (**Sih and Bell**) and life-history theory (**Gangestad**). We regard these extensions as generally compatible with our model, but more theoretical and empirical work is needed to see how exactly they would affect our conclusions about the origins and nature of genetic variation in personality. **Dingemanse** reminded us that our model and any future extensions should ideally be tested in formal mathematical models, not just as verbal descriptions. Furthermore, statistical models are needed that allow us to test these relationships against empirical data. First steps in this direction have already been made (**South and Krueger**, **Johnson**; Wolf et al., 1998), but there clearly is plenty of work that still needs to be done.

In itself, an evolutionary genetic model of personality cannot offer a complete theory of personality. It can provide an ultimate perspective on why heritable personality differences exist, how they change over evolutionary time and environments and which fitness effects they may have. This makes it an important building block of any comprehensive personality theory. In the end, however, any evolutionary genetic model of personality should be complemented by more proximate theories (such as **Matthew**'s) concerning the phenotypic structure, underlying mechanisms and lifespan development of personality traits. However, as **Funder** correctly noted, our evolutionary genetic model of personality is more compatible with some proximate personality theories than with others, and those theories that contradict it will have to provide alternative accounts for the existence of genetic variance in personality. In the following, we will compare our model to some alternatives suggested in the commentaries.

ALTERNATIVES TO OUR EVOLUTIONARY GENETIC MODEL OF PERSONALITY

Recent selective sweeps

Mutation-selection balance models assume that within any given population, for any given trait, there is an abstract, idealised, mutation-free genotype that would show optimal

DOI: 10.1002/per

adaptation to the population's environmental demands and selection pressures. Applied to the case of human intelligence, mutation-selection balance models suggest that the highest possible *g* level can be attained only when all genes that influence cognitive functioning are free of harmful mutations. **Lee** called this a 'Platonic ideal'. Both **Bates** and **Lee** pointed to studies suggesting that human general intelligence has been subject to recent selective sweeps and in the midst of a genetic transition (Evans, Vallender, & Lahn, 2006; Wang et al., 2006; see also Williamson et al., 2007). We agree that the hypothetical optimal genotype for optimal intelligence is an oversimplification, and might be better conceptualised as a 'moving target'. Most mutations in protein-coding and regulatory regions of the genome are harmful, but beneficial mutations are more likely to occur when environments change. Given all the changes that have been occurring in the human ecology during the last 20 000 years, (including larger social groups and mating markets, novel habitats, agriculture and literacy), it is very likely that some *g*-related mutations have become beneficial and are currently on their way to fixation. These newly favoured polymorphisms might exist at any current prevalence level, and might have large phenotypic effects, so molecular genetic studies might be better able to identify them.

Beneficial mutations that are on the rise probably contribute to the genetic variance of *g*, but so does a load of many, rare, small-effect harmful mutations. This is not only a widespread empirical conclusion (Plomin, Kennedy, & Craig, 2006), but also a necessary implication if *g* has a large mutational target size. (**Bates** notes that several thousand rare polymorphisms with strong effects on general intelligence have been identified, but these evolutionary transient, harmful mutations usually cause severe mental retardations, not individual differences in the normal range; see Plomin & Spinath, 2004.) In our view, only a conceptualisation of *g* as a downstream trait that represents the functional integrity of large parts of the brain and the genome can explain why there are positive-manifold genetic correlations between different cognitive abilities, why *g* is linked to general phenotypic condition and why *g* is sexually attractive. It can also explain why trauma often reduces, but never raises, *g* (**Keller**; Keller & Miller, 2006). We do not see how these findings can be reconciled with recent selective sweeps as the only explanation for the heritability of *g*. In an effort to refute our mutation-selection balance account, Bates referred to unpublished evidence of a zero genetic correlation between *g* and fluctuating asymmetry. While we cannot evaluate this study, such a result would challenge only one possible mediator between mutation load and cognitive ability (the construct of 'developmental stability'), not the general claim that *g* is under mutation-selection balance. Contrary to **Bates** and **Lee**, we doubt that recent selective sweeps alone can explain most of the genetic variance in *g*, but we believe that such sweeps, in conjunction with mutation-selection balance, may be important, with their relative contributions to be determined by future empirical research.

Cognitive reaction norms

While the *g*-factor of intelligence seems to have a direct link to many components of fitness, **Strobel** noted that individual differences in certain lower-order cognitive processes show phenotypic and genetic relations to personality traits—which, in our balancing-selection model, should have net fitness neutrality when averaged across all relevant environments. He suggests that such lower-level traits that combine cognitive and personality characteristics may constitute a third category of traits to consider in extending our model. We do not think that such a fundamental modification is necessary. Our two

DOI: 10.1002/per

trait categories are basically defined by the selective mechanisms that maintain their genetic variance, not by their apparent psychological nature (i.e. 'cold' and cognitive vs. 'hot' and temperamental). If the lower-order cognitive processes discussed by **Strobel** are indeed under balancing selection and structurally linked to personality traits, they clearly fall in the 'reaction norm' category of our model and are likely best conceptualised as facets of certain personality traits. However, since they are usually assessed by cognitive tests that load on the *g*-factor, it might be advisable to control for *g* (which we suggest captures mutation load variance) when their genetic underpinnings and their associations with personality traits are studied.

Gene-environment correlations

It is hardly debatable that humans have been perfecting ways to modify their own environments for thousands of years. Due to technical and cultural innovations, modern humans seldom face unmodified natural ecologies; rather we confront complex built environments and social institutions that have been shaped as our 'extended phenotypes'. Consequently, r_{GE}s might be more important for humans than for any other species. **Jang** and **Johnson** argued that modern humans are so adept at creating, selecting and evoking their own ideal environmental niches that almost no genetic variance in personality is lost to selection now. We agree that modern selection-minimising environments might be one reason why 'maladaptive' genetic variants, like those leading to mental illnesses, are sometimes preserved in the population (**Jang**). However, we doubt that r_{GE}s can fully explain genetic variance in the normal range of personality. The reason is that mere survival is not the only adaptive problem—fitness also depends on success in social competition for resources, status and mates. In modern societies, few will die because they are ill or incompetent, but many will fail to maximise the quantity and quality of their sexual partners and offspring (e.g. Keller & Miller, 2006). As we argued in our target paper, it is likely that personality differences have their strongest effect on fitness in the social domain (see also **Matthews**). As long as diverging interests exist in social groups, no single individual will have full control over his or her social environment (**Sih and Bell**; Penke et al., in press). Some will do better than others, partly due to luck, but primarily due to individual differences in general fitness and variation in the fit between people's personalities and their (socio-)environmental niches. Thus, r_{GE}s may alter or attenuate the selection pressures on personality differences, but they are unlikely to eliminate them. Note also that if r_{GE}s indeed neutralised all selection pressures, personality differences would be under neutral selection, which is, as we argue in our target paper and above, inconsistent with empirical evidence. Accordingly, r_{GE}s alone cannot maintain genetic variance.

Antagonistic pleiotropy

Sih and Bell remark that antagonistic pleiotropy is still discussed as a viable mechanism for maintaining genetic variance, for example by Roff (2002). While it is true that the final word has not been said about this mechanism (especially when trade-offs between more than two traits are involved), even Roff, in a recent review (Roff & Fairbairn, 2007), regards antagonistic pleiotropy alone as very unlikely to explain persistent genetic variance. However, even if some genetic variance in some personality traits is maintained by antagonistic pleiotropy, it would not alter our model dramatically. All it would imply is that environmental heterogeneity is not necessary in these particular cases.

DOI: 10.1002/per

Continua of evolutionary stable strategies

Keller lists MacDonald's (1995) hypothesis of weak stabilising selection on personality traits (which allows for continua of evolutionary stable strategies) as a viable explanation for genetic variation in personality. However, stabilising selection, even if weak, can only erode, but never maintain, genetic variation (Roff, 2002). The same is true for the related mechanism of correlational selection (**Sih and Bell**; Roff & Fairbairn, 2007). In both cases, either personality traits must be selectively neutral, or the mutational target size of personality traits must be sufficiently large that enough mutational variance is reintroduced (see **Gangestad**), or some form of balancing selection must occur. This brings us back to the three main mechanisms we discussed.

The *K*-factor

The *r*-*K* continuum describes differences in life-history strategies between species. Each species has evolved a complex functional design that allows for its specific strategy of growth, mating and parenting. For example, many finely coordinated adaptations in a rat's phenotype interact to let it mature fast, reproduce early and often, develop a small brain, refrain from extensive parental investment, die early, etc., and these systems of adaptations are different from those in an elephant or human. Such an *r*-*K* continuum might apply not just to explain between-species differences in life-history adaptations, but to explain within-species differences in behavioural strategies and personality differences. **Figueredo and Gladden** suggested that the human **G** matrix might be characterised by just one principal dimension—the '*K*-factor'—corresponding to individual differences in life-history strategies and their associated personality traits. Our concerns with this suggestion are mostly theoretical.

We do not see how such an all-encompassing genetic dimension can be maintained by frequency-dependent selection or any other form of balancing selection. Selection cannot change the whole adaptive design of a species back and forth at the level of all genetic loci that influence life-history traits, since this would inevitably break up the complex functional coordination of the life-history strategy (Tooby & Cosmides, 1990). Instead, balancing selection can only maintain a small set of polymorphisms that act as 'switches' between different life-history or behavioural strategies (Kopp & Hermisson, 2006; Turelli & Barton, 2004). These polymorphisms must, through cascading effects in genomic regulatory systems, affect all adaptations involved in the strategy. One—and possibly the only—example for such a potent genetic switch in humans is the SRY gene that guides the sexual differentiation of males and females (Tooby & Cosmides, 1990). In the case of the *K*-factor, a similar master genomic regulatory switch would have to be identified (and we suspect it already would have been discovered if it existed, given the intensity of gene-hunting for loci with major behavioural effects). Such a master regulatory switch might, for example, affect a range of behavioural traits by regulating testosterone levels and receptor sensitivities during brain development and functioning, since testosterone affects a wide range of sexual, competitive, aggressive and parental behaviours (Ellison, 2001). However, testosterone-related polymorphisms alone cannot explain all the other traits subsumed in the *K*-factor, including general intelligence and the dimensions of the FFM. As long as there is no evidence for more potent genetic switches that affect all these traits, we regard *K*-factor theory as slightly over-ambitious in trying to explain human individual differences. Alternatively, **Gangestad** offers some more detailed considerations on the

DOI: 10.1002/per

evolutionary genetics of life-history strategies, including reactive strategy adjustment to one's own mutation load (i.e. condition-dependency). We encourage future studies to proceed in the directions he suggests.

CONCLUSION

Our target article introduces a way to study personality from an evolutionary perspective, based on evolutionary genetics. Thereby, it supplements adaptationistic evolutionary psychology with a toolbox for the study of individual differences, and it supplements behaviour genetics and personality psychology with a theoretical framework to understand heritable personality differences. We reviewed three theoretical models for the maintenance of genetic variance in heritable traits, and assessed the available empirical evidence to draw conclusions about the plausibility of each model as it might apply to human personality. While some aspects of the evidence remain weak, the overall pattern of results suggests that balancing selection is more plausible than its alternatives as an explanation for most heritable personality traits, as is mutation-selection balance for general intelligence. It remains to be seen whether our model can integrate future theoretical innovations and empirical findings. We are open to alternatives, extensions, modifications and most importantly empirical studies with more refined methods that test the predictions of our model.

Clearly, the development of a comprehensive evolutionary personality psychology is a big challenge that is still to be met. Many of the challenges and opportunities in this endeavour lie in its inter-disciplinary nature: neither psychologists nor biologists will be able to solve this problem on their own (**van Oers**). The commentaries are encouraging because they suggest that both sides are willing to learn from each other. If basic communicative issues (terminologies, etc.) can be resolved, we see many opportunities for fruitful inter-disciplinary cooperation, and maybe we can even come a little bit closer to the utopian ideal of consilience (**Euler**).

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