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An evolutionary approach to the extraversion continuum

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Abstract

Heritable individual differences in personality have not been fully accounted for within the framework of evolutionary psychology. This paper argues that personality axes such as extraversion can usefully be seen as dimensions of trade-off of different fitness costs and benefits. It is hypothesized that increasing extraversion will be associated with increasing mating success, but at the cost of either increased physical risk or decreased parenting effort. In a sample of 545 British adults, extraversion was a strong predictor of lifetime number of sexual partners. Male extraverts were likely to have extra-pair matings, whilst female extraverts were likely to leave existing relationships for new ones. On the cost side, increasing extraversion increased the likelihood of hospitalization for accident or illness. There was no direct evidence of reduced parenting effort, but extravert women had an increased likelihood of exposing their children to stepparenting. The study demonstrates that extraversion has fitness costs as well as benefits. Population variation related in the trait is unlikely to be eliminated by selection due to its polygenic nature, likely spatiotemporal variability in the optimal value, and possible status- and frequency-dependent selection.

Keywords: Personality; Extraversion; Life history; Evolutionary psychology; Mating strategies

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1. Introduction

“Personality” describes within-individual, cross-situation consistency in broad classes of behavior. Personality characteristics, as assessed by self-report, are temporally stable, correlated with objective measures of behavior (see Matthews, Deary, & Whiteman, 2003, for a review), and predict important life outcomes such as health (Neeleman, Sytema, & Wadsworth, 2002), sexual behavior (Eysenck, 1976; Heaven, Fitzpatrick, Craig, Kelly, & Sebar, 2000), social networks (Swickert, Rosentreter, Hittner, & Mushrush, 2002), and marital adjustment (Kelly & Conley, 1987). Personality dimensions have a sizeable heritable component (Bouchard, 1994; Bouchard & Loehlin, 2001) and a proximate basis in genetic polymorphisms and associated neurobiology (Depue & Collins, 1999; Munafo et al., 2003). Why does this variation persist? Differences in social behavior, sexual behavior, health, and mating can affect reproductive success. Given the magnitude of such differences, personality variation may be subject to natural selection.

The effect of natural selection is generally to use up heritable variation in both continuous traits and single-gene characters, pushing one genotype to fixation. (Fisher, 1930; Maynard Smith, 1998). In evolutionary psychology, it has been assumed that the result will always be one optimal design and no variation. For example, Tooby and Cosmides (1992) argue that “Human genetic variation...is overwhelmingly sequestered into functionally superficial biochemical differences, leaving our complex functional design universal and species typical.” However, the discovery of prevalent polymorphism in systems such as that of the dopamine receptors and serotonin transporter, which are involved in mediating social behavior, suggests that not all variation between humans is functionally superficial (Cravchik & Goldman, 2000).

Personality variation is dimensional, which implies that it is underlain by continuous variation in the calibration of psychological mechanisms (Buss, 1991; Macdonald, 1995). Despite the eliminatory effect of natural selection, continuous traits in biological populations usually display significant heritable variation (Houle, 1992; Mousseau & Roff, 1987). Indeed, Lynch and Walsh (1998) point out that “almost every character in every species that has been studied intensively exhibits nonzero heritability.” This includes behavioral tendencies that can justly be called “personality” in numerous mammal, fish, and bird species (Gosling, 2001). There are several possible reasons for the maintenance of such diversity (for a fuller discussion, see Maynard Smith, 1998, Chapter 6).

First, mutation produces polymorphism just as selection removes it. The greater the number of genes affecting a trait, the greater the number of mutational targets in each generation, and so the greater the variation maintained by mutation–selection balance (Houle, 1992; Lande, 1975). Second, the optimal value of a trait may vary across different parts of the environment, or over time, in such a way that selection cannot track the optimum. In experimental populations of *Drosophila melanogaster*, for example, more additive genetic variance is retained if the food regime is made to fluctuate over time than if it is constant (MacKay, 1981). A recent study of the fitness consequences of aggression and boldness in the great tit *Parus major* showed that the optimal level of the trait for survival and reproduction varied from year to year according to environmental conditions (Dingemanse, Both, Drent, &

Tinbergen, 2004). Third, the fitness of a phenotype may be frequency or status dependent, which can also promote the retention of variation.

Individual variation can be seen as the trading off of one kind of benefit against another, in the context of limited overall time and energy. This is a premise of life history theory (Roff, 1992; Stearns, 1992). Such thinking has not yet been systematically applied to human personality psychology. The ultimate objective of individuals—to maximize reproductive success—can be decomposed into several subgoals, such as self-protection, feeding, mating, and parenting. Individual life history strategy is simply the compromise adopted between conflicting goals. Any continuous trait can be conceptualized as a dimension of life history trade-off, and, if personality represents continuous variation in the calibration of psychological mechanisms, then a life history framework can be used to make testable predictions about personality and fitness. First, there is likely to be stabilizing selection and, thus, detectably reduced fitness at the extremes of the distribution. Second, across the phenotypic range, there should be some measurable trade-off of different benefits.

This paper applies such a framework to extraversion. There are several descriptions of personality variation, using differing numbers of axes (e.g., Costa & McCrae, 1992; Eysenck & Eysenck, 1985), but there is consensus on the existence of a dimension of positive motivations, most often called extraversion. It has facets relating to sociability and facets relating to seeking stimulation and novelty in other domains (Costa & McCrae, 1992). Zuckerman's alternative framework (Zuckerman, Kuhlman, Joireman, Teta, & Kraft, 1993) separates these out into two independent axes. However, many studies have found the different components of extraversion to be sufficiently correlated to justify collapsing onto a single dimension, and Zuckerman's sensation-seeking scale correlates fairly strongly with Eysenck's extraversion measure (Eysenck & Zuckerman, 1978).

Depue and Collins (1999) argue that extraversion is a consequence of the strength of response to naturally rewarding stimuli, such as sex, food, or physical exhilaration. For the extravert, the salience of these rewards is greater than for the introvert, with the result that extraverts invest more time and energy on them (Barnes, Malamuth, & Check, 1984; Davis & Mogle, 1994; Eysenck, 1976; Swickert et al., 2002). The benefits of such activities are obvious. Indeed, natural selection has presumably made them rewarding precisely because they tend to be fitness enhancing. Thus, we predict that extraversion will be positively associated with some aspects of reproductive success (as suggested by Buss, 1991). In the mating domain, extraverts should be expected to create and take more mating opportunities. There is some previous evidence that this is the case (Barnes et al., 1984; Heaven et al., 2000).

As for costs, two sets of suggestions have been made. Buss (1991) points out that in their pursuit of fitness-relevant resources, extraverts may expose themselves to somatic risk. Evolution along the shy-bold continuum in other species is thought of as the trade-off of fitness-enhancing opportunities against the probability of survival (Wilson, Clark, Coleman, & Dearstyne, 1994). Risk could result from direct physical danger or stem from reduced energetic investment in somatic maintenance. Thus, the risk hypothesis would predict that some measures of physical well-being would be negatively associated with extraversion. The second set of predictions stems from the work of Trivers (1972). The allocation of time and resources to parenting must be traded off against resources invested into mating. In humans, this trade-off has most often been considered in the context of male–female differences, with males having greater incentive than females do to invest in mating effort, due to their larger variance in reproductive success (Buss, 1998). However, both males and females face the trade-off, and multiple strategies are available to both sexes (Gangestad & Simpson, 2000). Because extraversion is known to be associated with interest in mating and mate diversity (Eysenck, 1976; Heaven et al., 2000), it may be negatively correlated with interest in parenting. This hypothesis would predict some detectable reduction in care to offspring of extravert parents.

Our previous research on Zuckerman's sensation-seeking scale provides some evidence of the costs and benefits of that trait (Joinson & Nettle, submitted for publication). High scorers had increased numbers of sexual partners, but more accidents and addictions. The present study seeks to extend that work in two ways. First, it uses extraversion rather than sensation seeking. Although these two are related, they are not identical, and only the former is part of the five-factor model, which is the most widely accepted general model of personality. Second, we wish to examine more precisely the nature of mating strategies in relation to extraversion, and the different possible costs. To investigate these issues, we administered a questionnaire containing a personality inventory, questions about mating and reproduction, and more general questions about life outcomes, work, and health to 545 British adults. The participants were mature, with a wide range of ages, allowing questions about long-term reproductive strategy to be meaningful. The hypotheses to be tested were, in summary, that extraversion will be positively associated with matings and the attainment of other fitness-relevant resources; that extraversion will be associated with increasing risk of physical illness or injury; and that extraversion will be negatively associated with parenting effort and, hence, offspring well-being.

2. Methods

The study was carried out by setting up an anonymous website on which the questionnaire was completed. Internet data collection was felt appropriate due to its high level of perceived anonymity and ease of recruitment. Multiple submissions from the same IP address were deleted. All questions were encoded in such a way that nonresponses could be distinguished from the selection of the first response. The order of presentation of the personality inventory and the rest of the questionnaire was alternated. Although the website was publicly accessible, the participants were mainly drawn from two sources, a distance learning university with a diverse adult student body and viewers of a television psychology documentary where the study was advertised. The numbers of participants from these two sources were approximately equal. There were 545 participants overall (203 male, 342 female). The mean age was 39.51 years (S.D.=10.63, range 18–78).

The personality inventory employed was that of Buchanan (2001), which uses the short set of items from Goldberg's International Personality Item Pool (Goldberg, 1999b). Dimensions derived from this publicly accessible instrument correlate highly with Costa and McCrae's NEO-PI and have satisfactory reliability and factor structure (Goldberg, 1999a). The extraversion items yielded a mean score of 27.38 (S.D.=7.39), which is close to normative British data (Buchanan, 2001: mixed sex mean=28.93, S.D.=7.63). Mean female scores were marginally higher than that of the male, although the effect did not reach statistical significance [male 26.63, female 27.82; $t(529)=1.79$, $p=.07$]. Scores were uncorrelated with age ($r=-.01$, $df=526$, ns).

The other parts of the questionnaire covered basic demographics, work, socioeconomic status in adulthood and family of origin, siblings, health, marital and relationship history, children, and self-ratings on a number of five-point scales including interest in sex, desire to be famous, ambition, and competitiveness. Responding involved choosing from a drop-down list, selecting a check box, or typing in responses. Analyses are by correlation for variables properly conceived of as scales and ANOVA or *t* tests for dummy-coded categorical variables. Effect sizes are reported for all significant results. As much of the research in this area has focused on sex differences, analyses were conducted separately be sex as well as for the sample overall.

3. Results

Extraversion was positively correlated with a number of the self-rated dimensions, including interest in sex ($r=.21$, $df=524$, $p<.001$), ambition ($r=.31$, $df=528$, $p<.001$), competitiveness ($r=.28$, $df=526$, $p<.001$), enjoyment of travel ($r=.27$, $df=523$, $p<.001$), and desire to be famous ($r=.31$, $df=526$, $p<.001$). Extraversion and self-reported time spent in social activities were strongly correlated ($r=.45$, $df=525$, $p<.001$). All these correlations held essentially identically in the men and women considered separately as well as the whole sample (data not shown).

There was a pronounced linear relationship between extraversion and lifetime number of sexual partners [Fig. 1; $F(4,519)=9.96$, $p<.001$, $\eta^2=0.09$]. The relationship was significant and similar in the two sexes considered separately, but with a larger effect size in the women [men: $F(4,192)=3.42$, $p<.01$, $\eta^2=0.08$; women: $F(4,322)=7.58$, $p<.001$, $\eta^2=0.12$]. The number of sexual partners desired in the next 2 years was unrelated to extraversion [overall: $F(5,516)=0.47$, ns; men: $F(5,188)=1.33$, ns; women: $F(5,322)=0.37$, ns]. There was a significant association between extraversion and marital status in the overall sample [$F(4,517)=3.52$, $p<.01$, $\eta^2=0.03$]. Post hoc tests reveal that this was accounted for by those in their second or subsequent marriage or cohabitation having significantly higher extraversion scores than those single and never married or those in their first marriage. The pattern is the same in the two sexes considered separately, but it does not reach significance when they are split [men: $F(4,188)=2.03$, $p=.09$; women: $F(4,324)=2.14$, $p=.08$].

Participants stated whether they felt it was mainly themselves who ended their romantic relationships, mainly the other person, or the self and the other person equally. Respondents choosing these different categories differed in extraversion, with those feeling that they mainly ended their relationships having the highest, and those feeling it was mainly the other person and those who had had no relationship having the approximately equal lowest [$F(3,523)=4.71$, $p<.005$, $\eta^2=0.03$]. This pattern was observed in both sexes separately, but only significant in

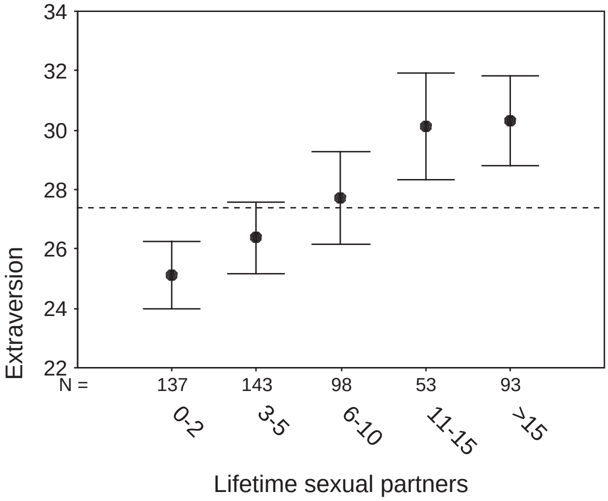

Fig. 1. Mean extraversion scores by lifetime number of sexual partners. The horizontal line represents the overall mean.

the women [$F(3,326)=4.43, p<.005, \eta^2=0.04$]. Participants also stated whether they had been unfaithful to a partner. There was a significant association with extraversion [Fig. 2; $F(3,522)=5.89$, $p<.001$, $\eta^2=0.03$], with mean extraversion increasing from those never unfaithful through to those who reported multiple instances. The shape of the relationship was the same in both sexes, but the effect size was larger and the result significant in the men [men: $F(3,192)=4.51, p<.005, \eta^2=0.07$; women: $F(3,326)=1.99, p=.11, \eta^2=0.02$].

There was no difference in extraversion between those who had children and those who did not [overall: $t(526)=1.42$, ns; men: $t(195)=0.68$, ns; women: $t(329)=0.33$, ns], nor a

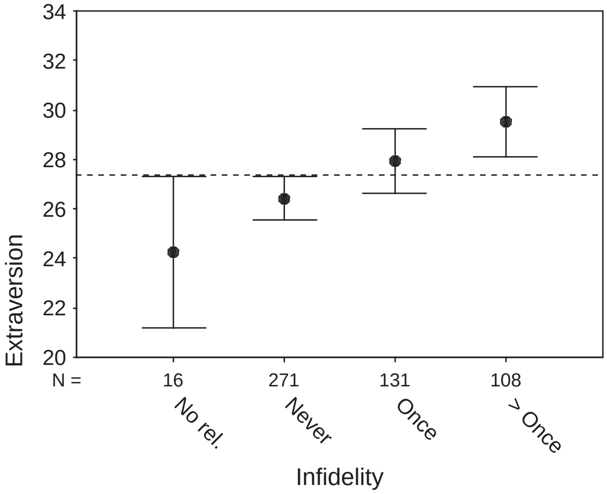

Fig. 2. Mean extraversion scores by whether the respondent has been unfaithful to a partner. The horizontal line represents the overall mean.

significant correlation between the number of children and extraversion (overall: r=.08, df=527, ns; men: r=.08, df=197, ns; women: r=.06, df=331, ns). However, amongst those who had children, those who had them by more than one partner were significantly higher in extraversion than were those who had them by one partner only [$t(279)=2.43$, $p<.05$, $d=0.30$; Fig. 3]. This pattern was significant in the women [$t(197)=2.44$, $p<.05$, $d=0.35$], but not the men [$t(80)=0.13$, ns], although the male numbers are low.

Extraversion scores were examined in relation to self-reported time spent with children (relatively little, intermediate, a lot), but there was no significant association [overall: $F(2,287)=2.92$, ns; men: $F(2,85)=0.7$, ns; women: $F(2,199)=2.10$, ns]. There was no significant association between extraversion and whether the children had had no minor or major health problems or accidents [$F(2,385)=0.39$, ns]. Breaking this analysis down by sex, the association was not significant for women [$F(2,200)=0.11$, ns], but was for men [$F(2,88)=4.53$, $p<.05$, $\eta^2=0.04$]. This was due to those (13) men whose children had had serious health problems being lower in extraversion than those (also 13 in number) whose children had had only minor health problems. The majority, whose children had had no health problems, were intermediate between the two other categories.

Finally, extraversion was examined in relation to the respondent's own health history. Those who had ever been hospitalized due to illness or accident were significantly higher on extraversion than those who had not [$t(525)=1.97$, $p<.05$, $d=0.17$]. This was significant only amongst the women, but the trend in the men was in the same direction [men: $t(194)=0.53$, ns; women: $t(329)=2.20$, $p<.05$, $d=0.24$]. Participants with four or more doctor visits in the last 2 years had slightly higher extraversion scores than did those with three or fewer, but the difference (which was due to a trend in the women but not the men) was not significant [overall: $t(525)=1.70$, $p=.09$; men: $t(195)=-0.15$, $p=.88$; women: $t(328)=1.76$, $p=.08$].

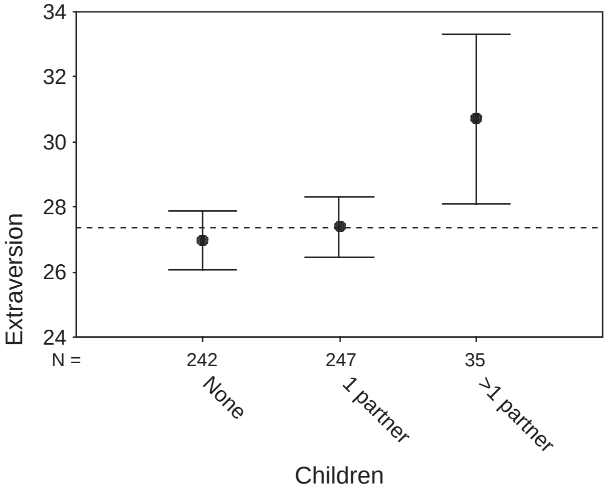

Fig. 3. Mean extraversion scores by respondent's reproductive history. The horizontal line represents the overall mean.

4. Discussion

The pattern of results confirms the findings of many previous studies. Compared to the introverts, extraverts spend more time in social activities, are more ambitious and competitive, enjoy traveling, and desire fame. The extravert's interest in sex is also confirmed, and this has effects across the life span which are relevant to reproductive success and, thus, to natural selection. The higher the extraversion score, the greater the number of lifetime mates. This was true for both men and women, but the pattern was achieved in different ways. Increasing extraversion in men was associated with increased frequency of extra-pair copulation. Highly extravert women had an increased likelihood of terminating relationships and ending up with children by more than one man. No effects were found on number of offspring, which is consistent with previous null findings in a developed world population (Eaves, Martin, Heath, Hewitt, & Neale, 1990). However, in a post demographic transition, contracepting population, differences in mating success do not necessarily translate into offspring numbers in the way that they would have done in an ancestral context (Pérusse, 1993). The study also demonstrates the link often suggested by evolutionary psychologists between status striving and mating effort because extraversion is a correlated package of ambition and interest in sexual variety.

Although the η^2 values are quite low, the effects observed are sufficiently strong to affect lifetime reproductive success. η^2 corresponds to the proportion of variation in the dependent variable accounted for by the independent variable. In this sample, there is abundant additional variation between individuals due to contingencies of their environment, age, and background, which lowers the personality-based η^2. However, the existence of environmental variation does not prevent selection from acting on genetic variation, since the personality effects are far from trivial. For example, the proportion of individuals having 10 or more sexual partners is 16.2% in the lowest quartile of extraversion and 43.8% in the highest quartile; 63.9% of men in the top quartile had had an extra-pair copulation, compared with only 30.6% in the bottom quartile. These are substantial behavioral differences, and thus, selective neutrality, which is one possible explanation for the maintenance of heritable variation (Buss & Greiling, 1999), seems unlikely.

Two possible costs of the extraverted strategy were investigated—reduced parenting effort and somatic risk. No direct evidence for reduced parenting effort was found here. However, in general terms, the mating behavior associated with extraversion must reduce such effort. Highly extravert men are more likely to be involved in extra-pair liaisons, which must involve time and resources. Highly extravert women, on the other hand, through their succession of partners, are likely to expose their children to stepparenting, which is a known risk factor for abuse, neglect, and harm to children (Daly & Wilson, 1985). Thus, in an ancestral environment, extraverts would be increasing the number of their offspring (men) or their genetic quality (women), but in all probability at a cost to infant survival and health.

Some evidence was found for somatic risks. Participants who had been hospitalized due to accident or illness had higher extraversion scores than did those who had not, and there was a trend towards more frequent doctor visits, although this did not reach statistical significance. Previous research on sensation seeking has revealed a positive association with accidents and physical violence (Joinson & Nettle, submitted for publication) and with traumatic injury (Field & O'Keefe, 2004). The component of extraversion bringing about the increased risk is presumably the sensation seeking rather than the affiliative one.

The study suffers from several limitations and should be considered as hypothesis generating. The lack of evidence of reduced postreproductive investment in offspring might be due to limitations of the simple self-report questions used. It might be fruitful to examine objective measures of parental investment, such as interbirth intervals, or objective child health records, in relation to parental extraversion. The exact causes of the greater hospitalization of extraverts should also be investigated in greater detail, perhaps using medical records, as has been done for neuroticism (Neeleman et al., 2002). Such effects have not been investigated in the extraversion literature, in part because the trait is linked to positive emotions (Costa & McCrae, 1980), and has thus been seen as beneficial rather than harmful. The evolutionary perspective, with its emphasis on the idea that all phenotypic decisions are trade-offs with costs as well as benefits, may thus prove a useful generator of new hypotheses.

With these limitations noted, the evidence presented here allows some preliminary generalizations about how selection might operate along the extraversion continuum. Increasing extraversion is associated with increasing desire to take risks, explore new environments, and compete for status. In tandem, it is associated with seeking varied mating opportunities, including extra-pair copulations (especially for men) and serial monogamy (for women). These strategies will respectively increase the number and genetic quality of offspring. Increasing extraversion thus increases fitness by promoting social dominance and mating success. However, high extraversion levels entail the risk of physical harm and, possibly, reduce investment in the protection of existing offspring. The dimension can therefore be conceived as a continuum along which different fitness costs and benefits are traded off. It is likely that optimal fitness is generally in the centre of the range and, thus, that extraversion is subject to stabilizing selection. Selection cannot remove heritable variation altogether, as the trait is probably affected by many mutational targets. Moreover, as the environment fluctuates, the optimal balance between risk and security may vary over short temporal or geographical scales. In addition, the payoffs to being an extravert could vary according to the majority strategy in the surrounding population, as is often the case with alternate reproductive strategies. Such processes as these would lead to the maintenance of a broad phenotypic spectrum in the population.

Heritable differences in exploratory behavior, affiliation, and surgency have been found in a number of species as well as our own. The evolutionary causes and consequences of such variation are beginning to be understood in other species. For example, bird studies have demonstrated not just that individual differences are heritable and related to behavior in the wild, but that they are systematically related to fitness, with different optima under different environmental conditions (Dingemanse et al., 2004; Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002). For humans, such a demonstration is necessarily more indirect, both for methodological reasons and because of the profound differences between the contemporary environment and that typical of our evolutionary history. Identifying the different environmental contexts that may select for different values of a trait will be particularly difficult in humans. Genetic data may occasionally be informative, as suggested by the finding that human populations with a history of migration have a greater frequency of long alleles of the DRD4 gene, which are related to sensation seeking, than sedentary populations do (Chen, Burton, Greenberger, & Dmitrieva, 1999). These difficulties aside, the present study suggests that, in humans, as in other species, personality differences can fruitfully be viewed as products of opposing evolutionary pressures.

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