Evolutionary Perspectives on Animal and Human Personality

JOSEPH H. MANSON and LYNN A. FAIRBANKS

Abstract

Among many nonhuman animals, individuals differ consistently in their response tendencies (e.g., shy vs bold) across multiple contexts. Researchers have tested evolutionary hypotheses accounting for these phenomena, and have also begun exploring evolutionary explanations for human personality variation. For evolutionary biologists, a trait's significance lies in its effects on *fitness*, that is, the lifetime reproductive success of individuals who bear the trait, including indirect effects through the reproductive success of genetic relatives. Recent evolutionary personality research has pursued several alternative theoretical lines of inquiry: *balancing selection* models explore whether optimal levels of personality traits vary across time, space, or trait frequency distribution; *mutation-selection balance* models propose that selection for a single optimum personality configuration is undermined by mutations at multiple genetic loci; and *facultative calibration models* hold that personality trait levels are adjusted, during individual development, to other characteristics that affect social bargaining power. A promising general approach links personality variation to variation in life history strategy, that is, the allocation of effort among the competing demands of growth, somatic maintenance, mate acquisition, and parental investment. Emerging areas of research include relationships between personality variation and biological fitness in humans and other primates; the extent to which personality trait levels are adjusted based on individual condition; the degree to which situational flexibility varies among individuals; and whether proposed structural models of personality, such as the human five-factor model (extraversion, neuroticism, agreeableness, conscientiousness, and openness to experience) are species-typical or are affected by variable ecological and social conditions.

INTRODUCTION

Traditional evolutionary approaches to animal behavior focused on optimal responses (within developmental and contextual constraints) to adaptive challenges such as predator encounters and contests over mates. Different responses by different individuals of the same age, sex, and circumstances were attributed to measurement error or to statistical "noise." In the past 15–20 years, inspired by pioneers such as Joan Stevenson-Hinde

Emerging Trends in the Social and Behavioral Sciences. Edited by Robert Scott and Stephen Kosslyn.
 ISBN 978-1-118-90077-2.

(Stevenson-Hinde & Zunz, 1978), D.S. Wilson (Wilson, Clark, Coleman, & Dearstyne, 1994), and Samuel Gosling (Gosling & John, 1999), researchers have confirmed and extended the intuitions of pet owners and zookeepers that (i) individual animals' responses are, to a substantial extent, consistent across situations and over long periods of time and (ii) individuals differ in these response tendencies. These two features (within-individual consistency and between-individual differences) serve as the defining features of *personality* for researchers of animal behavior. A closely related concept developed by Andrew Sih (Sih, Bell, Johnson, & Ziemba, 2004), the *behavioral syndrome*, emphasizes within-individual consistency across contexts—for example, an individual may show above-average aggressiveness toward predators, same-sexed rivals, and prospective mates.

The widespread observation of animal personality poses two theoretical puzzles. First, why has not natural selection equipped animals to respond in the fashion best suited to the present situation, rather than being constrained by a consistent response style that may lead to suboptimal choices? Second, given that some personality variation is a product of genetic variation among individuals, how does natural selection maintain this variation? In general, selection is expected to eliminate variation in traits relevant to biological fitness, that is, traits that affect an individual's ability to survive, reproduce, and pass its genes on to future generations. *Inclusive fitness* includes an individual's own reproduction as well as its effects on its relatives' reproduction, devalued by the proportion of genes shared with that relative. Research into the puzzles posed by animal personality has proceeded in parallel with a small but growing body of evolutionarily based research on human personality variation.

FOUNDATIONAL RESEARCH

Methods in the Study of Animal Personality

Two general methods have dominated research on nonhuman animal personality. *Standardized tests* expose animals to a situation designed to elicit variable responses. For example, temporarily captive songbirds are videotaped in a room containing artificial trees, and observers record how many trees are visited by each individual (Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002). Bighorn sheep are scored as more bold if they are more willing to enter a corral trap baited with salt, and as more docile if they struggle less during handling by humans (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000). Novel objects or conspecifics may be placed in captive animals' enclosures, and their reactions systematically coded.

The *rating method* uses questionnaires containing 20–60 adjectives (e.g., *active*, *popular*, and *irritable*) on which experienced observers (e.g., zookeepers and field assistants) rate each animal on a multipoint scale. Statistical techniques assess inter-rater reliability, and reduce the set of adjectives to a smaller number of general factors or dimensions of variation (Freeman & Gosling, 2010).

PROXIMATE AND DEVELOPMENTAL STUDIES OF ANIMAL PERSONALITY

A large body of research has used animal models of human psychiatric and behavioral disorders to focus on the proximate (e.g., physiological) and developmental mechanisms underlying personality variation. For example, adverse early experience, particularly separation from the mother, has been linked to emotional dysregulation and anxiety-related traits in nonhuman mammals (Levine, 2005). Genetic polymorphisms in neurochemical pathways have been shown to increase risk for antisocial behavior in humans and nonhuman animals, and these "risk" genes interact with adverse environments to increase vulnerability for behavioral disorders (Caspi & Moffitt, 2006; Soumi, 2011). Individual differences in personality traits have also been related to immune function and infectious disease susceptibility (Capitanio, 2011a). These and other studies provide valuable information about the proximate factors involved in personality variation, but they do not explain how "risk" genes for fitness-reducing personality traits persist in populations. For this, we turn to models from population biology.

Personality and Biological Fitness: Foundational Studies

Several different ideas have been proposed to explain how personality variation can be maintained in populations. Some researchers, beginning with Wilson *et al*. (1994) have drawn hypotheses from the concepts of *balancing selection* and *trade-offs*. The optimal level of a trait may vary geographically, between generations, over an individual's lifespan, between the sexes, or as a function of the existing distribution of trait levels in a population. As an example of the last phenomenon, *frequency-dependent selection*, if an animal population contains a mix of foragers (who harvest food from the environment) and scroungers (who parasitize the efforts of foragers), then scroungers are likely to have a higher net energy intake than foragers when scroungers are rare, but not when they are common (Barnard & Sibly, 1981).

Dingemanse, Both, and Drent (2004) have found that a songbird, the great tit, shows considerable variation in the speed with which individuals explore a novel environment. Fast explorers are also more risk-prone than slow explorers. A multiyear study in the wild showed that during years of food abundance and resultant high survival rates, fast-exploring adult males and slow-exploring adult females survived at the highest rates, whereas during years of scarcity, slow-exploring adult males and fast-exploring adult females prevailed. Researchers attributed the results to the sex-differentiated effects of resource availability on the intensity of within-sex competition. In both sexes, fast-exploring individuals outcompeted slow-exploring individuals for access to winter food. Only males defend territories, and male–male competition for these territories was greatest when many males survived a bountiful winter. Females were subordinate to males in competition for food, and were therefore at greater risk of death during winters of scarcity.

Similarly, complex relationships between personality and biological success have been found or suggested for other species. Réale and colleagues (Réale & Festa-Bianchet, 2003; Réale *et al*., 2000) have shown that bolder wild female bighorn sheep had higher fitness than shy females, and more docile females had higher fitness than less docile females. However, boldness and docility were negatively correlated, preventing natural selection from shaping an optimal level of both personality traits. Among male rhesus monkeys (Howell *et al*., 2007) and vervet monkeys (Fairbanks *et al*., 2004), more impulsive, risk-prone individuals are at greater risk of injury before reaching adulthood, but those who survive attain higher dominance rank following transfer to a new social group in late adolescence. This pattern suggests a trade-off between a higher risk of early death and a larger reproductive payoff for survivors later in life. A meta-analysis of data from 10 mammal species and 2 fish species revealed that bolder individuals, particularly males, experienced greater reproductive success but diminished survival prospects (Smith & Blumstein, 2008).

Researchers of human personality have proposed possible fitness trade-offs associated with personality variation, but relevant empirical studies remain rare. The most widely accepted, although still controversial, structural model of human personality posits five independently varying dimensions (five-factor model or FFM) (Costa & McCrae, 1995; Digman, 1990): extraversion (gregariousness, activity, positive emotions); neuroticism (negative affect, e.g., anxiety, anger, and depression) or its inverse emotional stability; agreeableness (altruism, trust, and straightforwardness); conscientiousness (order, self-discipline, and achievement striving) and openness to experience (including openness to ideas, feelings, aesthetics). Nettle (2005) found that among British adults, self-reported Extraversion was positively correlated with number of sexual partners, but also with the probability of experiencing hospitalization for accident or illness, suggesting a personality-mediated trade-off (at least in ancestral human environments) between production of offspring and individual survival. Relationships of human personality variation to fitness might encompass interactions among traits, as in some of the nonhuman animal systems. Among Australian women, the largest completed family sizes were found among those who were either high in extraversion and low in neuroticism or else low in extraversion and high in neuroticism (Eaves, Martin, Heath, Hewitt, & Neale, 1990).

CUTTING-EDGE RESEARCH

Evolutionary personality theory has recently begun to catch up with the rapid proliferation of empirical research. Several theorists have built on the basic idea that personality variation is tied to variation in *life history strategy*, that is, the allocation of effort among the competing demands of growth, somatic maintenance, mate acquisition and parental investment (Stearns, 1992). For example, Wolf *et al*. (2007) have developed an evolutionary model in which individuals may explore their environment thoroughly, trading off some near-term reproduction for longer-term increased access to higher-quality resources, or explore superficially, maximizing near-term reproduction at the expense of future resource gains. Over a wide range of starting conditions, a mix of stable personality configurations emerges, in which thorough environmental exploration is linked with risk aversion in both anti-predator and intraspecific aggressive contexts.

As an alternative to hypotheses that invoke balancing selection and trade-offs to propose that a wide range of personality types is adaptive, some researchers have attributed human personality variation to *mutation-selection balance*. In this view, natural selection favors a particular human personality configuration, to which a large number of genetic loci contribute, while mutations undermine this configuration. First developed by Miller to explain persistent variation in intelligence (Miller, 2000) and heritable mental illnesses (Keller & Miller, 2006), the mutation-selection balance theory has been more controversially applied to normal personality variation by Rushton, Bons, and Hur (2008). The hypothesized general factor of personality (GFP) is based on a proposed positive correlation among extraversion, agreeableness, conscientiousness, openness, and emotional stability. Figueredo *et al*. (2005) argue that behavioral propensities function best as coordinated sets of traits, and propose that people pursuing a slower life history (late onset of reproductive activity, high investment in a small number of children, etc.) are higher on the GFP. Another evolutionary approach, proposed originally by Tooby and Cosmides (1990) and developed further more recently by Lukaszewski and Roney (2011), proposes that human personality variation (e.g., in extraversion) is calibrated during development to individual characteristics (e.g., physical attractiveness and formidability) that affect social bargaining power.

Empirically, a recent study found that much of the heritable variation in traits resembling extraversion and emotional stability reflects the combined effects of many different low-frequency gene variants, as predicted by the mutation-selection balance hypothesis (Verweij *et al*., 2012). On the other hand, a study of traditional Senegalese villages found evidence for trade-offs and stabilizing selection in women's emotional stability: less stable women produced more children, but more stable women's children were healthier (Alvergne, Jokela, & Lummaa, 2010). The first large-scale published research on personality variation in a small-scale (hunter-horticulturalist) society (Gurven, von Rueden, Massenkoff, & Kaplan, 2013) found that a two-factor model (prosociality and industriousness) produced the best fit to the data, casting doubt on the universality of the FFM. Among men, reproductive success was positively correlated with Industriousness and with the FFM extraversion, conscientiousness, openness, and emotional stability dimensions, whereas among women, relationships between personality dimensions and fitness varied geographically (Gurven, von Rueden, Stieglitz, Kaplan, & Rodriguez, in press). Among the Senegalese studied by Alvergne *et al*. (2010) and among the recently settled former hunting-gathering Ache of eastern Paraguay (Bailey, Walker, Blomquist, Hill, & Hurtado, 2013), more extraverted men had higher reproductive success.

Recent studies of nonhuman animals have explored dimensions of personality variation beyond the boldness and aggressiveness continua that dominated earlier research. Among male great tits, competitive ability is negatively correlated with innovative problem-solving ability (analogous to human conscientiousness and/or openness) (Cole & Quinn, 2012). A model of the evolution of trust and trustworthiness suggests that social awareness (i.e., monitoring of third party interactions) and within-individual consistency in trustworthiness (a component of human Agreeableness) can coevolve, each trait selecting for increases in the other (McNamara, Stephens, Dall, & Houston, 2008).

KEY ISSUES FOR FUTURE RESEARCH

A number of key questions remain unresolved and will dominate evolutionary research into personality (both human and nonhuman) in the coming years:

1. To what extent is personality variation associated with variation in fitness? Models of balancing selection propose that, at least over wide spatial and/or temporal scales, different levels of personality traits have equal fitness. Alternatively, personality trait levels are expected to

correlate consistently with fitness (e.g., in humans, higher neuroticism with lower fitness) in models of mutation-selection balance or adaptively flexible personality in response to variable fitness-relevant states such as body size or parasite infection. Some personality configurations might represent a disadvantaged individual "making the best of a bad job," in which case low fitness is expected (although not as low as would occur if an individual in poor condition adopted a personality configuration appropriate to good condition).

2. A closely related question is the extent to which personality variation is *condition-dependent* (i.e., *state-dependent*). An alternative to state-dependent models regards personality variation as driven largely by variation in genotypes that affect psychological processes directly via neural and/or hormonal machinery (e.g., androgen receptors).
3. What are the relative impacts on personality variation of early developmental events that may cue life prospects (e.g., maternal condition during gestation and father absence during human childhood) versus adult health, social status, threats, and opportunities?
4. What is the relationship between variation in dimensions such as shy-bold, on the one hand, and individual variation in cross-situational plasticity (e.g., the capacity to vary one's level of boldness as a function of context)? A promising, recently developed model by Dingemanse, Kazem, Réale, and Wright (2010) integrates both forms of variation using the concept of *behavioral reaction norms*. Among other advantages, this concept facilitates the investigation of individual × environment interaction, that is, the nonrandom distribution of personality types across habitats.
5. How and why do different dimensions of personality variation covary in different species and in different human populations?

Pursuing these research questions in nonhuman animals will entail overcoming some formidable practical obstacles. Measuring lifetime fitness, as well as its components (time to sexual maturity, age-specific survival and fertility rates, offspring survival rates, etc.) in varied environments in long-lived nonhuman animals in the wild is a slow and expensive endeavor. However, personality measurement in wild populations promises to become easier through the use of (i) standardized situational tests on temporarily captive individuals and (ii) observer rating methods based on naturally occurring behavior. The latter have demonstrated sufficient reliability and validity in captive settings (e.g., Capitanio, 2011b) to justify their use in wild populations (e.g., Manson & Perry, 2013), and such research will become more common and fruitful. Some of the ecological variables (e.g., food abundance, predation risk, and parasite prevalence) proposed by modelers to affect personality variation are measurable using well-established methods, and new methods are currently being developed for noninvasive measurement of metabolic and hormonal variables in large mammals in the wild. Personality researchers studying captive or semi-free-ranging animals lack the opportunity to measure ecological variables or to collect generalizable data on fitness variation, but they have easier access to certain proxies for fitness (e.g., growth rates) than do researchers of wild animals.

In the evolutionary study of human personality, we foresee the growth of three particularly exciting research areas. First, measurement of personality variation and its association with fitness (or putatively fitness-linked characteristics such as growth rate or age at marriage) in a variety of small-scale, nonliterate societies will explore (i) the flexibility of personality structure itself and (ii) the ways that variable social, subsistence, and pathogen-prevalence conditions can favor different patterns of personality trait covariation. Multidimensional models, such as the FFM and the six-factor HEXACO model (Ashton & Lee, 2007), might turn out to apply only to the ultracomplex societies of recent history. Second, models of state-dependent personality variation (e.g., facultative calibration) will be tested in longitudinal and experimental studies that link changes in perceived individual circumstances (e.g., availability of social support and relative intelligence within a social milieu) to changes in personality traits and personality-like states. Third, sophisticated genetic methods such as genome-wide sequence analyses will continue to elucidate the genetic architecture of personality traits, affording tests of contrasting predictions from balancing selection and directional selection (e.g., mutation-selection balance) models of personality variation.

Finally, we expect progress in innovative personality measurement methods such as experimental implicit measures (e.g., attention to stimuli indicative of social threats or opportunities), naturalistic observation using techniques such as intermittent audio recording by portable devices (Mehl, Gosling, & Pennebaker, 2006), and economic games with real money at stake.

Cross-disciplinary collaboration and dialogue will be essential for further progress in the evolutionary study of personality (Nettle & Penke, 2010). Behavioral ecologists, both as theorists and as fieldworkers, are well equipped to develop and test models linking (i) costs and benefits associated with various forms of environmental variation, (ii) within-individual behavioral consistency and interindividual behavioral differences, and (iii) lifetime inclusive fitness. Personality psychologists draw on a long tradition of theoretical and statistical investigation of human personality structure, that is, the covariance of trait dimensions suggested by folk descriptions and by neurophysiological mechanisms. Comparative psychologists deploy ethological and experimental methods tailored to reveal reliable and valid dimensions of personality in particular species. Behavioral economists' methods engage individuals' motives (e.g., prosociality and risk aversion) in a controlled manner in the face of real costs and benefits. Neuroscientists' findings regarding the proximate (anatomical and physiological) underpinnings of personality variation will need to be integrated with theoretical accounts that focus on adaptive/functional explanations for personality variation. Behavioral geneticists bring increasingly powerful techniques capable of uncovering the signatures of past selection regimes.

Because these are early days in the evolutionary study of personality, we can only speculate tentatively on its implications for practical applications. We suspect that some personality configurations regarded by most contemporary Westerners as undesirable or even pathological (e.g., the highly conscientious, highly introverted person who is extremely reluctant to showcase her impressive accomplishments) will come to be seen as understandable, and perhaps best left alone, given an individual's other characteristics and social circumstances. Moreover, a wide range of personality variation, compared to pressure to adopt a particular configuration, may provide greater benefit to society as a whole.

REFERENCES

Alvergne, A., Jokela, M., & Lummaa, V. (2010). Personality and reproductive success in a high-fertility human population. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 11745–11750. doi:10.1073/pnas.1001752107

Ashton, M. C., & Lee, K. (2007). Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Personality and Social Psychology Review*, *11*, 150–166. doi:10.1177/1088868306294907

Bailey, D. H., Walker, R. S., Blomquist, G. E., Hill, K. R., & Hurtado, A. M. (2013). Heritability and fitness correlates of personality in the Ache, a natural-fertility population in Paraguay. *PLoS One*, *8*, e59325. doi:10.1371/journal.pone.0059325

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, *29*, 543–555. doi:10.1016/S0003-3472(81)80117-0

Capitanio, J. P. (2011a). Individual differences in emotionality: Social temperament and health. *American Journal of Primatology*, *73*, 507–515. doi:10.1002/ajp.20870

Capitanio, J. P. (2011b). Nonhuman primate personality and immunity: Mechanisms of health and disease. In A. Weiss, J. E. King & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 233–255). New York, NY: Springer.

Caspi, A., & Moffitt, T. E. (2006). Gene-environment interactions in psychiatry: joining forces with neuroscience. *Nature Reviews Neuroscience*, *7*, 583–590. doi:10.1038/nrn1925

Cole, E. F., & Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *279*, 1168–1175. doi:10.1098/rspb.2011.1539

Costa, P. T. J., & McCrae, R. R. (1995). Domains and facets: Hierarchical personality assessment using the revised NEO Personality Inventory. *Journal of Personality Assessment*, *64*, 21–50. doi:10.1207/s15327752jpa6401_2

Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology*, *41*, 417–440. doi:10.1146/annurev.ps.41.020190.002221

Dingemanse, N. J., Both, C., & Drent, P. J. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 847–852. doi:10.1098/rspb.2004.2680

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*, 929–938. doi:10.1006/anbe.2002.2006

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*, 81–89. doi:10.1016/j.tree.2009.07.013

Eaves, L. J., Martin, N. G., Heath, A. C., Hewitt, J. K., & Neale, M. C. (1990). Personality and reproductive fitness. *Behavior Genetics*, *20*, 563–568. doi:10.1007/BF01065872

Fairbanks, L. A., Jorgensen, M. J., Huff, A., Blau, K., Hung, Y.-Y., & Mann, J. J. (2004). Adolescent impulsivity predicts adult dominance attainment in male vervet monkeys. *American Journal of Primatology*, *64*, 1–17. doi:10.1002/ajp.20057

Figueredo, A. J., Vásquez, G., Brumbach, B. H., Sefcek, J. A., Kirsner, B. R., & Jacobs, W. J. (2005). The K-factor: Individual differences in life history strategy. *Personality and Individual Differences*, *39*, 1349–1360. doi:10.1016/j.paid.2005.06.009

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology*, *72*, 653–671. doi:10.1002/ajp.20833

Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, *8*, 69–75.

Gurven, M., von Rueden, C., Massenkoff, M., & Kaplan, H. (2013). How universal is the Big Five? Testing the Five Factor Model of personality variation among forager-farmers in the Bolivian Amazon. *Journal of Personality and Social Psychology*, *104*, 354–370. doi:10.1037/a0030841

Gurven, M., von Rueden, C., Stieglitz, J., Kaplan, H., & Rodriguez, D. E. (in press). The evolutionary fitness of personality traits in small-scale subsistence society. *Evolution and Human Behavior*. doi:10.1016/j.evolhumbehav.2013.09.002

Howell, S., Westergaard, G., Hoos, B., Chavanne, T. J., Shoaf, S. E., Cleveland, A., … Higley, J. D. (2007). Serotonergic influences on life-history outcomes in free-ranging male rhesus macaques. *American Journal of Primatology, 69*, 851–865. doi:10.1002/ajp.20369

Keller, M. C., & Miller, G. F. (2006). Resolving the paradox of common, harmful, heritable mental disorders: Which evolutionary genetic models work best? *Behavioral and Brain Sciences*, *29*, 385–452. doi:10.1017/S0140525X06229091

Levine, S. (2005). Developmental determinants of sensitivity and resistance to stress. *Psychoneuroendocrinology*, *30*, 939–946. doi:10.1016/j.psyneuen.2005.03.013

Lukaszewski, A. W., & Roney, J. R. (2011). The origins of extraversion: Joint effects of facultative calibration and genetic polymorphism. *Personality and Social Psychology Bulletin*, *37*, 409–421. doi:10.1177/0146167210397209

Manson, J. H., & Perry, S. (2013). Personality structure, sex differences, and temporal change and stability in wild white-faced capuchins (*Cebus capucinus*). *Journal of Comparative Psychology*, *127*, 299–311. doi:10.1037/a0031316

McNamara, J. M., Stephens, P. A., Dall, S. R. X., & Houston, A. I. (2008). Evolution of trust and trustworthiness: Social awareness favours personality differences. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *276*, 605–613. doi:10.1098/rspb.2008.1182

Mehl, M. R., Gosling, S. D., & Pennebaker, J. W. (2006). Personality in its natural habitat: Manifestations and implicit folk theories of personality in daily life. *Journal of Personality and Social Psychology*, *90*, 862–877. doi:10.1037/0022-3514.90.5.862

Miller, G. F. (2000). Sexual selection for indicators of intelligence. In G. Bock, J. Goode & K. Webb (Eds.), *The nature of intelligence*. New York, NY: John Wiley & Sons, Inc.

Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior*, *26*, 363–373. doi:10.1016/j.evolhumbehav.2004.12.00

Nettle, D., & Penke, L. (2010). Personality: Bridging the literatures from human psychology and behavioural ecology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *365*, 4043–4050. doi:10.1098/rstb.2010.0061

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*, 463–470. doi:10.1006/anbe.2003.2100

Réale, D., Gallant, B. Y., Leblanc, M., & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, *60*, 589–597. doi:10.1006/anbe.2000.1530

Rushton, J. P., Bons, T. A., & Hur, Y.-M. (2008). The genetics and evolution of the general factor of personality. *Journal of Research in Personality*, *42*, 1173–1185. doi:10.1016/j.jrp.2008.03.002

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, *79*, 241–277. doi:10.1086/422893

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*, 448–455. doi:10.1093/beheco/arm144

Soumi, S. J. (2011). Risk, resilience, and gene-environment interplay in primates. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, *289–297*.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford, England: Oxford University Press.

Stevenson-Hinde, J., & Zunz, M. (1978). Subjective assessment of individual rhesus monkeys. *Primates*, *19*, 473–482.

Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, *58*(1), 17–67. doi:10.1111/j.1467-6494.1990.tb00907.x

Verweij, K. J. H., Yang, J., Lahti, J., Veijola, J., Hintsanen, M., Pulkki-Råback, L., … Zietsch, B. P. (2012). Maintenance of genetic variation in human personality: Testing evolutionary models by estimating heritability due to common causal variants and investigating the effect of distant inbreeding. *Evolution*, *66*, 3238–3251. doi:10.1111/j.1558-5646.2012.01679.x

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, *9*, 442–446. doi:10.1016/0169-5347(94)90134-1

Wolf, M., Doorn, G. S., van Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*, 581–584. doi:10.1038/nature05835

JOSEPH H. MANSON SHORT BIOGRAPHY

Joseph H. Manson (http://www.sscnet.ucla.edu/anthro/faculty/jmanson/Home.html) is a Professor of Anthropology at the University of California, Los Angeles. He has published studies of female mate choice in free-ranging rhesus macaques and numerous topics, including personality structure, in wild white-faced capuchin monkeys. More recently, he has studied the interplay between a human personality trait, psychopathy, and face-to-face interaction and economic game-play decisions in small groups of previously unacquainted people. His current research uses audio sampling of individuals' daily lives to test hypotheses about personality variation drawn from life history theory.

LYNN A. FAIRBANKS SHORT BIOGRAPHY

Lynn A. Fairbanks (http://www.bec.ucla.edu/faculty.php?id=34) is an Emeritus Professor of Psychiatry and Biobehavioral Sciences at the University of California, Los Angeles. She has published numerous articles on individual differences in temperament and personality of vervet monkeys, focusing on the contributions of genetic, maternal, and contextual influences on variation in novelty seeking, impulsivity, sociability, and response to stressful life events. Her research on variation in maternal behavior illustrates the tradeoffs between maternal diet and condition, maternal investment, and offspring response and resilience in the development of behavioral differences. The eight-generation extended pedigree of the Vervet Research Colony has allowed identification of genetic influences and effects of gene–environment interactions on behavioral and physiological traits.

RELATED ESSAYS

Kin-Directed Behavior in Primates *(Anthropology)*, Carol M. Berman

Evolutionary Approaches to Understanding Children's Academic Achievement *(Psychology)*, David C. Geary and Daniel B. Berch

Genetics and Social Behavior *(Anthropology)*, Henry Harpending and Gregory Cochran

An Evolutionary Perspective on Developmental Plasticity *(Psychology)*, Sarah Hartman and Jay Belsky

Grandmothers and the Evolution of Human Sociality *(Anthropology)*, Kristen Hawkes and James Coxworth

Childhood *(Anthropology)*, Karen L. Kramer

Cooperative Breeding and Human Evolution *(Anthropology)*, Karen L. Kramer

Mechanisms of Fear Reducation *(Psychology)*, Cynthia L. Lancaster and Marie-H. Monfils

A Bio-Social-Cultural Approach to Early Cognitive Development: Entering the Community of Minds *(Psychology)*, Katherine Nelson

Gestural Communication in Nonhuman Species *(Anthropology)*, Simone Pika

Vocal Communication in Primates *(Anthropology)*, Katie E. Slocombe

Primate Allomaternal Care *(Anthropology)*, Stacey Tecot and Andrea Baden