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Beyond birth order: The biological logic of personality variation among siblings

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Abstract: Notwithstanding their relatedness, siblings vary as much as strangers with respect to personality traits. Attempting to explain this paradox across many publications, Frank J. Sulloway invokes evolutionary theory, specifically emphasizing Malthusian competition and referencing the concept of *adaptive radiation*, which produced beak variation among Darwinian finches as they spread across the Galapagos Archipelago. However, Sulloway understands birth order and other familial dynamics to create personality variation among siblings, using evolutionary concepts only as illustrative comparisons. The present paper argues that Sulloway mistook a literal truth for an analogy. Sibling personality variation does not mirror a process of evolution, it is a process of evolution. Substituting the macroevolutionary process of *adaptive radiation* for the microevolutionary process of *adaptive diversification*, and emphasizing the perpetuation of genetic material above the survival of the organism, sibling personality variation is herein explained as a hedge against lineage extinction. Unable either to predict environmental challenges or create pluripotent offspring, parents diversify their brood and thereby diversify their risk. As discussed, sibling personality variation as an ontogenetic process of adaptation remains relevant, but only in so far as it augments a primary genetic process of evolution.

ABOUT THE AUTHOR

Steven C. Hertler is a licensed examining psychologist with a research program centering on personality disorders generally, and obsessive personality specifically, which uses behavioral genetics, evolutionary biology, and behavioral ecology to alternatively explain classic character types. While much of his research has concentrated on personality, additional writings have explored life history evolution, comparative psychology, cross-cultural psychology, and climate as it affects evolved behavior and human nature.

PUBLIC INTEREST STATEMENT

Across many traits, siblings are more alike than different. For instance, among brothers and sisters, height, intelligence, and coloration, correlate, whereas personality contrasts. As per standing theories, in an attempt to limit competition, siblings develop traits exactly opposite one another. With different personalities, they occupy different niches. This explanation is intuitive, but it has limited empirical support. In addition, sibling personality variation is substantially genetic and found among a variety of animals. The present paper argues that environmental factors like birth order, only accentuate preexisting genetically inherited differences between siblings on personality traits. Genetic variation among offspring across personality traits is an evolved hedge against lineage extinction. Genetic material more reliably passes from parent to offspring because of the behavioral variation that personality imparts. Personality traits impose costs and provide benefits at each level and so having offspring with different personalities diversifies risk. In contrast homogeneity within offspring personality would be akin to putting all eggs in one basket.

Subjects: Social Sciences; Behavioral Sciences; Development Studies

Keywords: personality; siblings; Sulloway; birth order; evolution; adaptive radiation; adaptive diversification

1. Introduction

Though they share half their complement of genetic material, the personalities of siblings vary as much as the personalities of strangers (Dunn & Plomin, 1991; Hoffman, 1991; Lalumière, Quinsey, & Craig, 1996). That is an intriguing fact. Jane Austen's contrast between a sensible *Eleanor* and a sensitive *Maryanne* is not fictional. Expertly described and widely acknowledged though it is, sibling personality variation is difficult to explain. Frank J. Sulloway has dedicated much of his career to precisely that line of inquiry. His research, described across countless papers and several books, explains sibling personality variation through a combination of psychoanalytic and evolutionary insights, bolstered by historical anecdotes and steady logic.

Sulloway, acting in part the heir to Adler, emphasizes birth order; though he does so in a more sophisticated manner, as he sees birth order as an important proxy for age, physical size, and status. Pointedly treated in his book chapter, *Birth Order, Sibling Competition, and Human Behavior*, Sulloway (2001) finds the ultimate origins of sibling personality variation in the competition for resources, specifically parental resources. In this way, Sulloway's reasoning is Malthusian,¹ if not Darwinian. He recognizes that resources are scarce, noting that this was all the more true prior to modernity, and remained acutely so for those living in premodern conditions. Darwinian natural selection then overwhelms Hamiltonian inclusive fitness,² rendering siblings rivals for the scarce resources of attention, nutrition, time, and instruction that parents must inevitably divide among their offspring. In demonstrating the point, nature is rummaged, and easily yields examples of siblicide. For instance, birds and their nest mates, instead of expressing fraternal solicitousness, often oust their competition from the nest, in spite of their genetic relatedness. More than this, Sulloway finds examples among seals, and plants, and other animals, showing sibling competition to be a rule rather than an exception (Sulloway, 2011). Here is an important reorientation away from Freudian, and toward Darwinian dynamics. As Sulloway notes: "In Darwinian theory, sexual desires have nothing to do with these conflicts. Rather, siblings compete to optimize parental investment and hence to get out of childhood alive." Sulloway understands this "biological propensity to engage in sibling rivalry," to be "one of the ultimate causes of personality development."

Sulloway connects personality variation and sibling rivalry by way of niche differentiation, or niche splitting. As per this theory, personalities vary adaptively to maximize resource extraction from parents. A first born child, for a time, is an only child, and consequently will often take a straightforward route to resource extraction by "seeking the favor of their parents." Accordingly, "firstborns tend to be conscientious, parent-identified, and respectful of authority." Those born afterward find this niche already exploited and so less often attempt to occupy it. As a result, they "seek out an unoccupied family niche" generally becoming "more exploratory, unconventional, and tolerant of risk." The second born, finding the first born occupying one niche, rather than competing straightforwardly via the same personality strategy to occupy that same niche, assumes some alternative personality strategy to maximally exploit an alternative niche. In this way, "sibling competition promotes mutual differentiation in order to avoid direct conflicts." The process of niche differentiation by way of personality variation emerges passively through differences in parental investment, dominance hierarchies among siblings, and the constraints of birth order. However, it also emerges actively through the processes of *niche picking* and *deidentification*, both of which are autonomous bids to diverge (Sulloway, 2011, p. 95).

When explaining sibling personality variation in this fashion, Sulloway (2001) invokes the evolutionary process of *adaptive radiation*, speciation wrought by adaptation to divergent niches (Schluter, 2000). More specifically, adaptive radiation often occurs when a single species emigrates from a uniform homeland, to occupy a variegated array of divergent environmental niches, which elicit

evolved change on a single, or small number of variables (Travisano, 2009) sufficient for speciation (Brakefield & Zwaan, 2011; Schluter, 2000). In the most celebrated case of adaptive radiation, the species was an ancestral finch, the homeland was South America, the variegated environment was the Galapagos Archipelago, the evolved trait was beak size and shape, and the speciation event was divergence into approximately 14 Darwinian finches (Sato et al., 2001; Sulloway, 1995, 1996, 2001, 2007a, 2011). Sulloway's enduring interest in adaptive radiation (Galligan et al., 2012; Kleindorfer et al., 2014; Kleindorfer, Chapman, Winkler, & Sulloway, 2006; Kleindorfer, Sulloway, & O'Connor, 2009; O'Connor, Sulloway, Robertson, & Kleindorfer, 2010; Sulloway, 1982, 1984; Sulloway & Kleindorfer, 2013), like his meticulous study of Darwin's notebooks and correspondence (Sulloway, 1982, 1983, 1984), derives from parallels with human personalities as they diverge strategically toward the exploitation of divergent niches. These parallels are perhaps most fully and explicitly explored by Sulloway (2011) in his paper, *Why Siblings are like Darwin's Finches: Birth Order, Sibling Competition, and Adaptive Divergence within the Family*.

Notwithstanding its evolutionary trappings, this is not an evolutionary theory. This fact is explicitly mentioned, as when Sulloway states, "this is a Darwinian story, albeit one with a predominantly environmental twist" (Sulloway, 2001, p. 70). He finds siblings only "hardwired to compete for parental favor, but the particular strategies that they adopt within their own family are determined by the specific niche in which they have grown up" (Sulloway, 1999, p. 202). By this, he means that human personality variation is only an ontogenetic version of the phylogenetic³ change exhibited in adaptive radiation. As he explains, "... humans accomplish through learning what Darwin's finches and other species have achieved through organic evolution ..." In sum, human personalities diverge in response to a Malthusian threat to survival, but that divergence, though metaphorically analogous to adaptive radiation, is produced developmentally.

2. Purpose of the present paper

The present paper argues that Sulloway mistook a literal truth for an analogy. Sibling personality variation does not mirror a process of evolution, it is a process of evolution.

To demonstrate that point, the present paper will engage in deconstruction, reconstruction, and defense, by way of the following structure: (1) it will critique Sulloway's theory on the bases of empirical evidence, developmental trends, comparative psychology, and heritability estimates; (2) it will briefly describe an evolutionary understanding of personality variation, as driven by *adaptive diversification*,⁴ the microevolutionary⁵ analog of adaptive radiation; (3) it will then explicitly explain the evolutionary rationale behind sibling variation, which transcends the need to ease competition among offspring through diversification, and relates most directly to the imperative of avoiding lineage extinction;⁶ (4) lastly, comparative evidence of bet-hedging as a method of avoiding lineage extinction will be provided for plants and animals. As discussed, sibling personality variation as an ontogenetic process of adaptation remains relevant, but only in so far as it augments a primary genetic process of evolution.

3. Birth order and its record of empirical support

Sulloway's theory, like its Adlerian predecessor (Adler, 1956; Eckstein & Kaufman, 2012; Shulman & Mosak, 1977) and decades of many intervening variants (Beer & Horn, 2000; Bleske-Rechek & Kelley, 2014; Curtis & Cowell, 1993; Eckstein et al., 2010; Ernst & Angst, 1983, 2012; Ha & Tam, 2011; Howarth, 1980; Hudson, 1990; Marini & Kurtz, 2011; McArthur, 1956; Sampson, 1962; Very & Prull, 1970; Watkins, 1984), labors under an empirical record that can be interpreted as weakly supportive (Bouchard, 1993; Michalski & Shackelford, 2002; Rowe, 1990; Schooler, 1972). Certainly, many studies uphold theoretical claims (Eckstein & Kaufman, 2012; Healey & Ellis, 2007; Nyman, 1995; Very & Prull, 1970). For instance, Saroglou and Fiasse (2003) found birth order effects for rebelliousness, religiosity, conscientiousness, and agreeableness. Jealousy (Buunk, 1997), extraversion (Dixon, Reyes, Leppert, & Pappas, 2008), anxiety, pride, tolerance (Howarth, 1980), leadership (Smith & Goodchilds, 1963), dominance, conformity (Phillips, Bedeian, Mossholder, & Touliatos, 1988), and cooperation (Howarth, 1982) are among the other traits which have been associated with birth

order. In contrast, building upon the assertions of classical papers like *As the Twig Is Bent: The Myth of Child-Rearing Influences on Personality Development* (Rowe, 1990), are recent authoritative studies showing “definitive evidence that birth order has little or no substantive relation to personality trait development” (Damian & Roberts, 2015). “By combining large datasets from three national panels,” Rohrer, Egloff, and Schmukle (2015) “found no birth-order effects on extraversion, emotional stability, agreeableness, conscientiousness, or imagination.” Thus, they conclude, “this finding contradicts lay beliefs and prominent scientific theories alike and indicates that the development of personality is less determined by the role within the family of origin than previously thought.” Also writing for the *Proceedings of the National Academy of Sciences* in the same year, Damian and Roberts, in an article entitled, *Settling the Debate on Birth Order and Personality*, find birth order “has null effects on personality across the board.”

Birth order effects have a rich literature that resists condensation.⁷ It is difficult to reconcile the contrasting results described above without descending into that literature. Some argue that as methodological techniques improved, the empirical record eroded. Others argue that issues of methodology and interpretation obscure the association. There is dissent concerning whether birth order effects should be direct or indirect, mediated or moderated, weak or strong. For instance, Karabenick (1971), discussed sampling problems. Dunkel, Harbke, and Papini (2009) expressed concerns about mismatch between theory and method which might potentiate type II errors stemming from the developmental and longitudinal nature of birth order effects. In attempting to controvert assertions that conflicting results cancel one another out, and thereby equate to evidence of null assumptions, Sulloway (2011) invokes the confounds of social class and family size. Additionally, in his able apologia, Sulloway (2000, 2001) maintains that a correlation of .10 is meaningful because it is statistically significant, even as detractors cite its correspondingly small effect size. As Sulloway (2001, p. 60) states, “when we are able to document such seemingly modest effects in large controlled studies, we generally ought to point to them with pride and to affirm that they are not so small after all.” Though these points are well taken, and serve to show that the familial dynamics may have some effect, that effect is not likely to be large; and certainly it is not likely to be large enough to support the assertion that these familial effects are the main driver of sibling personality variation (Jefferson, Herbst, & McCrae, 1998; Rodgers, 2000; Rosenberg, 2000; Stagner & Katzoff, 1936; Townsend, 2000).

3.1. Developmental trajectories

Then there is the issue of development. Some personality traits are, to an extent, *heterotypic*, meaning they manifest differently in type and strength across development (Donnellan & Robins, 2009, p. 193). This too is acknowledged. Sulloway (2011, pp. 101–102) interprets the longitudinal studies indicating progressive exaggeration of sibling personality trait differences to be evidence of deidentification⁸ in operation. This certainly is plausible because one would expect the developmental processes purportedly causal of personality variation to accrete with stalagmite slowness, shaped as they are by years of vying interaction. Neuroticism, and to a lesser extent openness to experience, seem to follow a trend line supportive of Sulloway in that these traits are manifest early in development, and decrease steadily over the life course. However, personality traits often show marked developmental arcs, as does conscientiousness, a trait that increases across the lifespan, declining in late life (Donnellan & Robins, 2009, p. 196; Table 12.1). Conscientiousness is then not fully manifest until adulthood when its effects to mitigate sib-ship competition would become moot. Additionally, sib-ship competition does not then explain why conscientiousness, as it is needlessly strong during adulthood, would thereafter decline in later life. Sexual selection is an alternative explanation which better fits such a developmental arc. In this view, conscientiousness augments as one progress toward reproductive age, and is sustained through reproductive maturity, waning only in the post-reproductive years. Thus, it would follow a similar arc as testosterone. Supportive of this view, conscientiousness promotes status and wealth, which parlay into reproductive success (Vall et al., 2015). Furthermore, conscientiousness is ranked extremely high on measures of mate preference, both among dating couples and newlyweds (Botwin, Buss, & Shackelford, 1997; Figueredo, Sefcek, & Jones, 2006). Like conscientiousness, agreeableness and extraversion follow similar developmental trend lines, building toward adulthood and waning with senescence (Donnellan & Robins, 2009).

3.2. Perspectives from comparative psychology

Identification or disidentification⁹ with authority (Sulloway, 1996), cognitively driven preconscious gravitation toward unexploited niches (Sulloway, 2001), and the complexities of *deidentification* from extant siblings (Sulloway, 2007a, 2007b) can conceivably generate observed personality variation for several reasons, all relating to artifacts of human development, with its slow *pace of life* and prolonged *life history*.¹⁰ Humans advance from a helpless *altricial*¹¹ state to reproductive maturity over a protracted period. Most obviously, this grants time within which sibling competition can shape the development of personality. More than this, slow maturation rates are incongruously paired with short inter-birth intervals. In contrast to humans, for instance, the chimpanzee reaches maturity much earlier, but has longer inter-birth intervals (Hertler, 2015a). These life history particularities allow many human offspring to simultaneously coexist in a state of immaturity, all of which are competing for nutrition, enculturation, proximity, protection, and attention. Lastly, humans are highly encephalized,¹² rendering cognitively driven processes of sibling differentiation plausible on yet another level.

The extreme slowness of human life histories (Ellis, 1987, 1988; Figueredo, Vásquez, Brumbach, & Schneider, 2007), however, only appears to be a necessary precondition to personality variation when personality variation is conceived to be postnatally manufactured in the manner specified by Sulloway. Indeed, personality variation is generated across a range of life histories, and seems neither to require solicitous parental care, nor an opportunity for siblings to compete for that care. Illustrative of this point is the study of intraspecific behavioral variation within animal populations, increasingly described as animal personality (Briffa & Weiss, 2010; Cavigelli, 2005; Gosling, 2001; Watters & Powell, 2012), which is well documented among many bird species, like the graffinch, grackle, and great tit (Dingemanse, Kazem, Réale, & Wright, 2010). Likewise, personality variation is evident among mammals such as vervet monkeys (Dingemanse et al., 2010), lion-tailed macaques (Rouff, Sussman, & Strube, 2005) gorillas, (Eckardt et al., 2015), chimpanzees (King & Figueredo, 1997), as well as horses (Mills, 1998), Asian Elephants (Barrett, 2015), captive dolphins (Kuczaj, Stan, Highfill, & Byerly, 2012), domestic dogs (Gislason & Call, 1982), and cats (Gartner, Powell, & Weiss, 2014). Mammalian personality variation remains evident in African striped mice (Joshi & Pillay, 2016) golden hamsters, eastern chipmunks (Dingemanse et al., 2010), and other rodents (Dosmann, Brooks, & Mateo, 2015; Le Cœur et al., 2015), all of which have conspicuously short life histories among the mammalian class. Still, even though these animals do not show the extreme life histories characteristic of humans, they do show parental care and simultaneous dependents competing for that care. Thus, one may argue that these conditions, though less pronounced, remain sufficient for the generation of personality variation through rudimentary forms of the familial environmental mechanisms described by Sulloway. And in fact, some theoretical theses (Reddon, 2012) and empirical evidence (Guenther & Trillmich, 2015) does suggest just that.

Notwithstanding, implausibility is stretched to incredulity when one continues to observe personality variation expressed within populations of fruit flies and crickets (Mather & Logue, 2013), dung beetles and bees (Wolf, van Doorn, Leimar, & Weissing, 2013), stickleback fish, rainbow trout, wolf spiders, hermit crabs, damselfish (Dingemanse et al., 2010), snails (Carere & Maestripieri, 2013), octopi (Gosling & Mehta, 2013), cockroaches (Mather & Logue, 2013; Mishra, Logue, Abiola, & Cade, 2011) and guppies (Berdal, 2015). As in certain species of cockroach (Nalepa & Bell, 1997), some among these afore-listed animals do evidence extensive postnatal parental care. Nevertheless, even when strongly present, the nature of the parental care provided in some of these instances precludes sibling competition. The octopus for instance, oxygenates her young with tentacle flapping and jets of water, monitors and rejects spoiled egg festoons, provides protection from predators, and in many other respects acts the part of a solicitous parent (Sarvesan, 1969). Still, essentially all these maternal behaviors are performed while offspring are sequestered in egg sacks and therefore have no personality-related ability to compete with one another for parental resources. As with octopi, parental care in crustacea (Tallamy, 2000, 2001), fish (Goodwin, Balshine-Earn, & Reynolds, 1998) and insects (Tallamy, 1984) is often (Gilbert & Manica, 2010) expressed as provisioning (Zeh & Smith, 1985) or guarding, just prior to, and during the egg stage (Knouft, Page, & Plewa, 2003). On

the basis of this comparative evidence, it appears personality variation can exist, not only in the absence of slow life histories with their protracted juvenile states and overlapping dependencies, but also in the absence of parental care and the ability to compete for parental care. Animal personality is evident across phyla, order, and family.¹³ Some studies (Mueller et al., 2013) suggest that, like the *hox gene*¹⁴ regulating body plan across species, genetic regions that regulate personality variation are conserved. Of final note, though some have called for further exploration of postnatal dynamics (Guenther & Trillmich, 2015), animal personality variation *en masse* is described as a function of evolutionary ecological factors (Kight, David, & Dall, 2013), parasitism (Barber & Dingemanse, 2010), natural selection and sexual selection in competition for food, sex and safety (Dosmann & Mateo, 2014) throughout the lifespan.

3.3. Behavioral genetics and the role of familial influence

Lastly, and most importantly, Sulloway's theory is not supported by behavioral genetics data. Consult the first law of behavioral genetics (Turkheimer, 2000), seminal twin studies (Dworkin, Burke, Maher, & Gottesman, 1976; Floderus-Myrhed, Pedersen, & Rasmuson, 1980; Tellegen et al., 1988), authoritative texts (DeYoung & Gray, 2009; Plomin & Caspi, 1990), current empirical research (Dochtermann, Schwab, & Sih, 2015), reviews (Bleidorn, Kandler, & Caspi, 2014; Bouchard, 2004; Loehlin, 1992; Turkheimer, Pettersson, & Horn, 2014) or meta-analyses (Polderman et al., 2015; Vukasović & Bratko, 2015), all of which will concur in attributing a large share of personality variation to genetic influence. Actual estimates may vary by source and method used for investigation, or by trait and type under investigation; yet, through this moderate noise, one finds that approximately half of observed personality variation is genetic in origin. More than this, environmental influence, what one may regard as the other half in a static division, is disproportionately related to extra-familial environmental influence. By common estimate, extra-familial effects are on the order of seven times as influential as familial environmental effects (Sulloway, 2007a). Replicated in later works (Sulloway, 2007a, 2007b, 2011), Sulloway (2001, p. 45) acknowledges this in the following passage: "From studies of twins raised together and apart, behavioral geneticists have concluded that only about 5% of the variance in individual personality traits is attributable to the shared environment—that is, growing up in the same family ..."

This would seem to contradict a theory of sibling personality variation based precisely on those shared environmental factors that seem so ineffectual. Sulloway recognizes and addresses this contradiction by suggesting that the "family is not a single environment, but rather a collection of microenvironments." Sulloway continues, explaining that "the main reason why the shared family environment does not have a substantial impact on personality is that very little of the family experience is actually shared" (Sulloway, 2011). He takes the family as a "collection of microenvironments" because siblings within the same house can experience the same thing differently, and are treated differently by parents because of their birth order, age, and the dynamics of their older siblings. This is an able defense of familial influence that might temper straightforward interpretations of behavioral genetics data (Beer, Arnold, & Loehlin, 1998; Eysenck, 1990; Goldsmith, Buss, & Lemery, 1997). At the same time as this may caution against reflexively concluding that the "*shared environment* of a stable home and a consistent pattern of childrearing exert little influence in shaping the temperament of the child" (Dumont, 2010, pp. 123–124), it does not establish the familial environment as a dominant, or even a coequal, determinant. Extra-familial factors are clearly more influential. More than this, genetic determinants, straightforwardly acknowledged, lay claim to the largest share of the variance in personality, as expressed between siblings and at large.

4. Adaptive radiation and adaptive diversification

A dearth of empirical support for birth order effects aside, it should be emphasized that the above-cited literature on personality formation supports a biological alternative: developmental arcs suggest sexual selection; comparative psychological data suggest generalized evolutionary relevance; and behavioral genetics data suggest strong inborn variation. Ironically, that *biological alternative* may well be the process of adaptive radiation used metaphorically by Sulloway.

Drawing upon previous works on the evolution of personality (Buss & Hawley, 2011; Figueredo et al., 2011; Penke, Denissen, & Miller, 2007), Hertler (2015b) advanced a variant of adaptive radiation as a literal explanation of personality variation. As therein explained (Hertler, 2015b), adaptive radiation is a *macroevolutionary* process with a *microevolutionary* analog. Where competition drives a process of *adaptive radiation* resulting in speciation, competition also drives a process of *adaptive diversification* resulting in variation. Adaptive radiation and adaptive diversification are different only in degree, otherwise they are very much the same process. The impetus behind adaptive radiation is as Sulloway states, both in that competition is emphasized, and in that diversification into alternate niches adaptively functions to ease that competition. Such competition can drive variation within a species producing morphs, wherein stably expressed morphological and behavioral variation is generated within one species of the same sex, population, location, and generation. As previously described (Hertler, 2015b), it is through the process of adaptive diversification that sympatric¹⁵ interbreeding populations maintain *jack* and *Chinook* salmon (Geary, 2003; Kenrick, Maner, Butner, Li, & Becker, 2002) and analogous morphological variation among bluegill sunfish (Buss & Greiling, 1999), small marine isopods (Gross, 1996), cichlid scale-eating fish (Stearns & Hoekstra, 2005), arctic char (Cachel (2006), damselflies (Sherrat & Wilkinson, 2009), dragonflies (Sinervo & Calsbeek, 2010), guppies (Olendorf et al., 2006), crossbills (Benkman, 1996), and Gouldian finches (Pryke, Astheimer, Buttemer, & Griffith, 2007). In cases where adaptive diversification operates less strongly, it creates less marked variation, which remains temperamental and behavioral, as is the case generally for animal and human personality. Whether morphological or behavioral, the within species diversity generated by adaptive diversification allows entry into alternative niches, all of which eventually become stably saturated (Hertler, 2015b).

4.1. Brood variation and bet-hedging

While the process of adaptive diversification was treated at length (Hertler, 2015b), the rationale behind sibling personality variation, which Sulloway emphasizes, was not pointedly addressed. A very different explanation of sibling variation follows from a literal evolutionary explanation. Where Sulloway has taken a person-centered approach to explaining diversity, emphasizing its benefits for an individual making facultative adaptive shifts during development, the present view takes a gene-centered approach to explaining diversity, emphasizing genetic benefits of maintaining heritable diversity within the lineage across time.

We all extend from an unbroken ancestral succession stretching back more than 100,000 years to the divergence of our species, and indeed far beyond it (Buss, 2007). In the case of every extant human, that chain persisted unbroken. Not enjoyment, happiness, or even survival (Stearns & Hoekstra, 2005), but the persistence of that lineage¹⁶ through time is the ultimate goal for which humans were designed (Dawkins, 2006). The bodies that we inhabit, inclusive of the skin that can experience such pleasure and pain to the brain that generates consciousness, are only properly understood as vehicles for the replication of a genetic heritage. Once the imperative to avoid lineage extinction is properly understood via the gene-centric view of Dawkins, personality variation among siblings can be better recognized as a function of that imperative.

Personality-based variation among siblings is a compromise produced of vying constraints. First, there is variation in the spatial, social, and temporal (Dingemanse, Both, Drent, & Tinbergen, 2004) environment (Hertler, 2015b; Penke et al., 2007; Penke & Jokela, 2016), such that it is impossible to predict what demands one's brood will face. At the same time, it is impossible, because of evolutionary constraints (Carere & Maestripietri, 2013; Wolf et al., 2013), to create pluripotent offspring capable of flexibly adapting to all eventualities through unending *phenotypic plasticity*.¹⁷ It is within this context that "genetic diversification of offspring represents a bet-hedging strategy that evolved as an adaptation to unpredictable environmental contingencies ... when environmental cues that might otherwise selectively trigger developmentally plastic changes are of limited reliability or validity" (Wolf & Figueredo, 2011). In consequence of the inevitability of unpredictability, and the impossibility of pluripotency, we have personality. Personality is a temperamental stance taken amidst a range of potential options (Reale, Reader, Sol, McDougall, & Dingemanse, 2007). It is a stable

*reaction norm*¹⁸ that confines behavioral expression within certain limits (Schuett, Tregenza, & Dall, 2010). As on a roulette table, one wager can only straddle a small number of color or number options, one personality can only express a small swath of potential behavioral variation. As with the roulette wheel, the outcome of whose spin cannot be predicted, the environmental stressors faced by one's offspring cannot be predicted. With these shared constraints, the gambler acts the part of the parent in hedging his bets. Thus, the gambler places bets at various points across the board, and the parent generates within-brood personality variation. Risks are thereby diversified; all is not wagered on one eventuality; losses are less likely to be total. "No matter how the environment turns out" as Wolf and Weissing (2010) state, some "are well adapted to the local conditions." In sum, *if one can't predict the demands faced by offspring, and at the same time can't make pluripotent offspring, brood variation is the best possible hedge against lineage extinction.*

4.2. Bet-hedging to avoid lineage extinction in plants and animals

Theory (Capinera, 1979; Cohen, 1966; Crean & Marshall, 2009; Koops, 2003) observation (Berg & Redbo-torstensson, 1998; Lips, 2001) and experimentation (Beaumont, Gallie, Kost, Ferguson, & Rainey, 2009; Crean & Marshall, 2009) suggest that, as financiers diversify investments (Choueifat & Coignard, 2008; Hertler, 2015b; Peters, 2011), organisms hedge their bets.¹⁹ Bet-hedging is a logical adaptation to unpredictable environmental (Einum & Fleming, 2004) and fluctuating temporal (Wilbur & Rudolf, 2006) selective pressures (Erich, Ringler, Hödl, & Ringler, 2015; Simons, 2009) that encourages competitive fecundity though geometric growth (Crean & Marshall, 2009), and discourages lineage extinction through strategic diversity. Evidence of bet-hedging is particularly prominent among semelparous animals and plants with annual lifecycles (Childs, Metcalf, & Rees, 2010; Shemesh & Novoplansky, 2013) living in exacting ecologies (Philippi, 1993). Facing climatic harshness, and with only one chance to propagate genetic information, it is not surprising that bet-hedging has been established among many species of desert annuals (Nilsson, Tuomi, & Astrom, 1996; Simons & Johnston, 2006; Venable, 2007), such as those in the genus *Heterotheca*. These plants, in coping with the unpredictability of water availability, produce slow and fast maturing seeds and thus "spread risk in time" with the effect that the "first type of seed allows rapid growth in a permissive habitat" when conditions are favorable, and "the second type of seed provides insurance against extended draught" when conditions are unfavorable (Stearns & Hoekstra, 2005, pp. 218–219). As among desert plants, such diversified bet-hedging is extensively documented in egg development (Gialdi, 2011) in relation to number (Rees, Jessica, Metcalf, & Childs, 2010), hatching time (Furness, Lee, & Reznick, 2015; Laaksonen, 2004), moisture dependence (García-Roger, Serra, & Carmona, 2014), and temperature dependence (Saiah & Perrin, 1990).

Not only insulating against lineage extinction, but minimizing variance across reproductive cycles and encouraging geometric growth (Philippi & Seger, 1989), the process of bet-hedging is in no wise confined to iconic examples, or expressed only in precise conditions. To gain some sense of scope, the ubiquity of bet-hedging becomes evident when viewing the number and phylogenetic range of organisms (Simons, 2011) across which it is present (Crean & Marshall, 2009). For instance, bet-hedging is established in species of yeast (Levy, Ziv, & Siegal, 2012), birds (Amundsen & Slagsvold, 1998; Boyce, 1988), turtles (Rollinson & Brooks, 2007), frogs (Dziminski & Alford, 2005; Thumm & Mahony, 2002), and toads (Thumm & Mahony, 2005). Bet-hedging is likewise found among parasitic trematodes (Poulin & Hamilton, 2000), nematodes (van Dijk & Morgan, 2010), fish lice (Hakalahti, Häkkinen, & Valtonen, 2004), protozoa (Philippi & Seger, 1989), viruses (Stumpf, Laidlaw, & Jansen, 2002), and bacteria (Veening, Smits, & Kuipers, 2008). In turn, sea slugs (Krug, 2009), plankton (Weinkauff, Moller, Koch, & Kucera, 2014), shrimp (Simovich & Hathaway, 1997), and many species of fish (Einum & Fleming, 2002; Furness et al., 2015; Morrongiello, Bond, Crook, & Wong, 2012; Shama, 2015; Sogard, Berkeley, & Fisher, 2008) begin to establish the ubiquity of bet-hedging among aquatic animals. Further still, bet-hedging has been increasingly demonstrated among insects: stinkbugs (Kudo, 2001), crickets (Bradford & Roff, 1993), weevils (Menu & Desouhant, 2002), fruit flies (Kain, Zhang, Klein, Samuel, & de Bivort, 2014), butterflies (Thomas, Elmes, & Wardlaw, 1998), moths (Tanmaru, Ruohomäki, & Saloniemi, 1999), bees (Danforth, 1999), lace bugs (Philippi & Seger, 1989), and spiders (Watson, 1991).

Developmental diapause,²⁰ parental investment,²¹ dispersal²² and brood size²³ are among the many variables across which bets can be hedged; suffice it to say, however, that behavioral patterns analogous to personality are among these. Bet-hedging is discussed in the context of life history theory, which subsumes human personality traits within its expansive set of traits (Chisholm, 1999; Figueredo & Wolf, 2009; Roff, 2002; Wolf & Figueredo, 2011). Wolf and Weissing (2010) have accordingly discussed bet-hedging and personality in parallel. More pointedly, it was found that Reale, Dingemanse, Kazem, and Wright (2010), in the middle of their article entitled *Evolutionary and Ecological Approaches to the Study of Personality*, surmise that “bet-hedging should favour personalities because they might buffer fitness variances against environmental unpredictability.” Ever more consistent with the present thesis, Réale et al. parenthetically state, in the middle of the sentence just quoted, that bet-hedging of this type comes “in the form of maternal effects to vary offspring state.” Unfortunately, Réale et al.’s supposition is not pursued as the exclusive focus of any article, as judged from a review of the 160 subsequent citations of their work.²⁴ Notwithstanding, it is thus not unreasonable to make one further extension and suggest that the personality variation among human siblings, so long observed and wondered about, is the product of a bet-hedging strategy.

5. Discussion

Adaptive radiation, Darwinian finches, and Malthusian competition paired with evidence of siblicide, and bolstered by instances of comparative psychology, are expertly interwoven by Sulloway in explaining personality variation between siblings. Personality psychology is indebted to such an ardent attempt to escape a Lockean orbit and break with Freudian script. For all this, Sulloway is unable to defy Kuhn (1962), remaining, as he does, within the received paradigm notwithstanding the aforementioned evolutionary accoutrements. There remains the pre-Darwinian exemption of humans from the animal kingdom, and the substitution of environmental learning for organic evolution. Restrictions in mechanism, scope and aim are evident. With respect to mechanism, personality variation is undoubtedly augmented environmentally, but is fundamentally generated genetically. With respect to scope, personality variation eases competition within the family in adaptive ways, but this is part of a superior necessity to ease competition amidst the population at large. With respect to aim, personality variation undoubtedly aids in survival of individuals, but is principally needed to promote the propagation of lineages. Though Sulloway, bridges the social and biological sciences, bringing competition and niche differentiation to the fore, these concepts are biological realities capable of explaining personality variation among siblings only when literally applied within a gene-centric neo-Darwinian framework.

The personalities of siblings vary biologically in consequence of a bet-hedging strategy, as do the personalities of many organisms. While the primacy of biological variation should not be lost in the interest of balance, birth order, and other environmental factors have continuing relevance. Clearly there are gene–environment interactions that coalesce to produce observed personality variation between siblings. In this particular, personality is like many traits. Biological inheritance constrains the expression of a trait within a certain range of values, and environmental factors operate within that range to produce a single value. For example, a person may then have a genetic disposition to grow to between 65 and 72 inches, with nutrition determining adult height. Much more so than with height, with respect to personality, genetic and environmental variance is not statically apportioned, but instead synergistically combines. As reviewed previously (Hertler, 2015b), *genotype-specific habitat selection*, *experience producing drives*, *gene–environment correlations*, and *reactive heritability* (Block, 1995; Keller, 2010; Krueger, South, Johnson, & Iacono, 2008; Penke, 2011; Rozanov, 2012; Scheiner, 2006) are terminological elaborations on this synergistic theme. Each term denotes a complex interplay between heritable dispositions and environmental influences, continuing a process of strategic differentiation between siblings. Environmental factors accentuate or attenuate heritable personality variation even as they do not initially create it. In making this point, the present position exposes personality variation as an evolved hedge against lineage extinction without either denying causal influence to environmental factors or minimizing the above-described synergistic interaction effects.

5.1. Limitations and future research

Notwithstanding citations of Sulloway, in his history of personality psychology written in 2010, Dumont regarded sibling personality variation as an unexplained phenomenon. The present thesis provides an explanation—one consistent with developmental patterns, comparative data, behavioral genetics research, and evolutionary personality theory. However, in continuing to transition from proposition to proof, the thesis herein provided will have to go beyond exposition and evidence of bet-hedging among plants and animals, to explore human mating patterns. As such, a limitation of this review, and a focus for future reviews, will be to explore mating, looking for evidence that humans mate strategically so as to promote personality variation in offspring. If personality variation among offspring does serve the bet-hedging function of minimizing the risk of lineage extinction, mating in respect to personality should parallel mating with respect to *immune loci*,²⁵ such that it should be *dissortative*,²⁶ with complementarity being sought over similarity. Nevertheless, mature, variegated, and complex as it is, the data-set on human mating should not be expected to confirm or disconfirm the present thesis unless approached with an understanding of the genetic transmission of personality traits and styles, life history evolution, population density effects, and the advantages and disadvantages of sexual reproduction.

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Notes

1. *Malthusian* is the adjectival use of the surname *Malthus*, as in Thomas Robert Malthus, the eighteenth century divine and demographer. Malthus is best known for juxtaposing arithmetic increases in resources with geometric increases in human population. From this mismatch, dire consequences were predicted.
2. *Inclusive fitness* is also known as kin selection. It is a powerful theory within evolutionary biology attributed to W. D. Hamilton, which relates to the altruism that is an outgrowth of genetic relatedness. Altruism was difficult to explain evolutionarily. Inclusive fitness explained altruism among kin by emphasizing that the genetic material residing within the individual, is also distributed among the individual's kin. If an individual survives, so does 100% of his genetics. But if that individual sacrifices his life to save the lives of three brothers, his body dies, but 150% of his genetic material survives in the persons of his three brothers. As such an altruistic disposition can evolve.
3. *Ontogenetic* and *phylogenetic* are a pair of terms, respectively, denoting the development of the individual organism and the evolutionary development of the species.
4. *Adaptive diversification* will be treated at greater length as it is contrasted with adaptive radiation and discussed as an explanation of personality variation. Suffice it to say at present, adaptive diversification is when evolution selects for a range of types instead of a species specific optimum.
5. *Microevolution* is contrasted with *macroevolution*. In microevolution, evolutionary changes occur within a population causing diversity and differences. Nevertheless, change is not sufficient for speciation, such that all members of the population remain within the same species. Macroevolution occurs when evolutionary changes are sufficiently pronounced to cause speciation. Macroevolutionary changes occur in sexually reproducing species when population members can no longer interbreed, or do not longer attempt to do so.
6. *Lineage* is the genetic line of a family. It is one's ancestry.
7. The richness of birth order literature can be gleaned through the 3,950 retrieved results obtained on a google scholar search conducted on 30 December 2016 for the words *birth order* within the title.
8. *Deidentification* is the process of differentiation that siblings undergo during development. They actively diverge from one another, becoming contrasts with different traits and abilities.
9. *Disidentification* is similar to *deidentification*. In the literature, disidentification seems to be the larger process, of which deidentification is an instance. Deidentification is most often used to denote disidentification that is specific to the sibling relationship. Both involve conscious and unconscious divergence between people. A son who never touches alcohol because his father was an alcoholic, is practicing disidentification; he is becoming the opposite of the example set for him. In contrast, identification is imitative. Staying with the same example, it would entail following in the father's footsteps and becoming an alcoholic as well. In the literature, disidentification seems to be the larger process, of which deidentification is an instance.
10. Related to personality through overlapping traits like conscientiousness, *life history evolution* explains developmental timing, longevity, and maturation rates among other core biological, social, and cultural variables. For an introduction see Stearns (1992). *The evolution of life histories* (Vol. 249). Oxford: Oxford University Press.
11. Altricial contrasts with precocial. These are ends of a continuum relevant to the state of independence of a new born or hatched organism. On one side are altricial young that, like the human baby, cannot do much for themselves and would starve for want of parental intervention and attention. On the other side is precocial young that, like the Australian Brushturkey, can move, defend and feed for themselves immediately upon hatching.
12. *Encephalized* refers to the brain size; but brain size as relative to body size. One can calculate a cephalic

- index or an encephalization quotient that provides a ratio between brain and body.
13. *Phylum, order, and family* are classifications within the Linnaean taxonomy, which separates all life into the following classifications: domain, kingdom, phylum, class, order, family, genus, and species.
 14. The *hox gene* is a portion of the genome regulating body plan, such as segmenting. It is deeply conserved over evolutionary time. This means that the same genetic regions regulate body plans in humans as in tigers and flies. The number of *hox* genes varies by organism, as does the number of segments and general body plan, but across a great range of life, it is the *hox* gene region that regulates body plan.
 15. *Sympatric* refers to having a shared locale. Sometimes speciation or divergence, as described above, results from geographic isolation. Two populations passively drift from one another because they are not interbreeding or otherwise are actively goaded by different ecologically imparted evolutionary pressures to become increasingly different. By including the word *sympatric*, it is to denote that this process of divergence through adaptive diversification is taking place within a single locale. These population members are *not* diverging and diversifying because they are drifting or subject to different selection pressures from the overarching environment. To the extent that different environments (environmental heterogeneity) is responsible for adaptive diversification, it is not due to large-scale changes in climate, but due to certain proportions of the population being driven into various micro-niches within the social environment.
 16. This refers to the ancestral lineage, meaning familial descent from parents to offspring or a group with common descent. This should not be confused with the survival of the species at large.
 17. *Phenotypic plasticity* refers to the ability to alter one's phenotype without changes to the underlying genotype. Certain fish species undergo transformations of sex referred to as sequential hermaphroditism. For instance, the female sex becomes the male sex. The sex change occurs through hormonal changes interacting with environmental cues. This is an extreme example of morphic or bodily phenotypic plasticity. On the other hand, there is behaviorally based phenotypic plasticity. Related to human personality, one personality and set of genetics is phenotypically plastic to the extent to which it allows a wide range of behavior. People of course can make facultative changes that override temperamental inclinations; they can act differently in different situations. Someone with an anxious temperament can make a conscious effort to take risks, for instance. Nevertheless, personality by definition is a brake on phenotypic plasticity.
 18. A *reaction norm* helps explain the interaction between personality traits and situational demands. It is an elegant solution to the classic state-trait debate that took place between social psychologists and personality psychologists. The social psychologists emphasized the power of the situation to drive behavior irrespective of individual differences. The personality psychologists emphasized fixed trait dispositions that would drive consistent behavior irrespective of situational differences. The reaction norm reconciles these views by describing traits as imparting, not behavior, but thresholds for behavior. Situations are then important in their relation to the fixed threshold. Consider a passive person and an aggressive person. Both may lash out and physically attack someone. However, the passive person may need to be provoked in an extreme way; perhaps by being hit or spit upon. The aggressive person, in contrast may resort to similar physical violence from being bumped into or insulted.
 19. As reviewed by Hopper, Rosenheim, Prout, and Oppenheim (2003) *bet-hedging* can occur within and between generations, can be *phenotypically or genotypically* expressed, and can be of the *conservative or diversified* variety. Suffice to state, it is intergenerational, genotypic, diversified *bet-hedging* presently applied to an understanding of sibling personality variation.
 20. *Developmental diapause* consists of a stage of biological cessation; a type of suspended animation. A kangaroo oocyte can stop growing by avoiding implantation while its older sibling is still suckling, sometimes waiting hundreds of days before accessing maternal resources. Alternatively, there are many seeds and ferns and other plants that can stop growing or reproducing while conditions are unfavorable.
 21. *Parental investment* denotes the degree of direct and indirect resources that are expended on rearing a juvenile offspring to a state of maturity.
 22. *Dispersal* relates to movement away from the parent plant or animal. Dispersal is advantageous to the extent that it limits competition between parent and offspring. Relevant to the present discussion, it can also limit competition between siblings. If one sibling disperses, by for instance joining the armed forces, it leaves the other free to exploit local resources, including family resources.
 23. *Brood size* or *clutch size* is a measure of how many offspring are produced. Brood size is sometimes used in connection with lifetime reproductive fitness and sometimes in connection with offspring produced in a given breeding season or birthing.
 24. Searching exclusively within these 160 citations, only 19 retrievals were made for the word *sibling*. Even among these, sibling, did not appear in any title. Additionally, reading through the titles of these and the other 141 citing articles, it was not apparent that the explanation of personality variation as *bet-hedging* was, in any instance, the topic of pursuit.
 25. *Immune loci* relate to regions of the genome with immense variation. Immune profiles vary by blood type or *human leukocyte antigen variation* or *major histocompatibility complex*. Immune loci, and immunological differences generally, are relevant to the extent that they are the best example of actively maintained diversity. They also illustrate the necessity for *bet-hedging*. An immunologically heterogeneous brood subject to a wave of illness is more likely to have surviving members than an immunologically homogenous brood.
 26. *Disassortative* contrasts with *assortative*. *Disassortative* denotes active mismatch or heterogeneous coupling; whereas *assortative* denotes active matching or homogenous coupling. When applied to mating, the former will maximize brood diversity and the latter will minimize it.
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