Evolutionary Biology and Personality Psychology

Toward a Conception of Human Nature and

Individual Differences

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ABSTRACT: Although personality psychology subsumes the study of both individual differences and species-typical characteristics, the field has not yet resolved several key concerns: (a) what are the most important species-typical characteristics; (b) what are the most important ways in which individuals differ; and (c) how can species-typical characteristics and individual differences be reconciled within a general theory of personality. Evolutionary biology provides one set of criteria for identifying these characteristics and for designating relative importance among them. Genotypic universality, automaticity, and adaptation are examined as potential criteria for identifying important species-typical characteristics. Heritability, inclusive fitness, sexual selection, and assortative mating are evaluated as criteria for designating important individual differences. Suggestions are made for resolving some of the conceptual and operational difficulties entailed by implementing these criteria. It is argued that, although substantial problems remain, evolutionary biology can provide one means for identifying relations between individual differences and species-typical characteristics.

Evolutionary biology and personality psychology, broadly conceived, share several common concerns. Both fields seek to identify enduring organismic characteristics and to locate their origins and functional significance in environments. Both fields deal with past and present adaptation. And both grant a central role to individual variation, which is the focus of most personality research and the *sine qua non* of evolution. These shared concerns suggest intriguing potential connections. This article attempts to offer directions for an integrative effort, while identifying some of the difficulties of this endeavor.

The first section of the article identifies several key issues in personality psychology, with particular attention given to the separation between approaches emphasizing species-typical tendencies and those focusing on systematic variation around those tendencies. The second section identifies themes in evolutionary biology that parallel those in personality

psychology, typological and population approaches, and highlights some of the alternative aims, assumptions, methods, and limitations of each. The third section outlines three major directions for linking evolutionary biology and personality psychology. The final section attempts to identify some of the most promising programs for future research.

Some Key Concerns in Personality Psychology

Although disagreement exists about the defining issues in personality psychology, the following questions address one set of the field's prominent concerns:

1. What are the major enduring commonalities among people in action, motivation, and cognition? This question subsumes study of the origins of the major commonalities, their stability and change over time, their relations to each other, their functional significance, and their consequences. One major current concern is to establish criteria for considering something species typical or part of human nature.[1]

2. What are the important enduring ways in which individuals differ in action, motivation, and cognition? This question embraces study of the origins of major individual differences, their development (stability and change) over time, the relations among them, and their consequences. A major task in personality psychology is to establish criteria for identifying the most important ways in which individuals differ (Allport, 1937; Buss & Craik, in press; Cattell, 1946; Goldberg, 1972; Wiggins, 1979).

[1] The term *human nature* is used here without reference to content and without commitment to particular units such as motivational states, cognitive processes, or classes of acts.

3. How can the relations between the major commonalities and the major individual differences be conceptualized and understood? Subsumed by this question are the following subquestions. How do findings of individual variation limit or importantly qualify statements about the major commonalities? How do species-typical patterns constrain the manifested range of individual differences? How can theory and research on the major commonalities and individual differences be integrated to form a coherent understanding of our species?

In the past five decades, a separation has developed in the field of personality psychology between theory and research. Most personality theories focus on describing human nature, on identifying, in Maddi's (1980) terms, the "core tendencies" or "core characteristics" of the species. Psychoanalytic theory, for example, posits universality of energizing force and of psychic apparatus, as well as invariance of stage sequence. Dimensions of individual difference can be derived from such theories. For example, variation can be attributed to differences in the speed of transition through the universal stages or to differences in the current level attained. But these individual differences are subsidiary to common attributes. Species-typical characteristics have usually taken precedence over individual differences in personality theories.

In contrast, most current personality research focuses on individual differences: describing, explaining, and identifying covariation between the ways in which individuals differ. Indeed, many current personality psychologists define the field solely by reference to this issue: "Personality is that branch of psychology which is concerned with providing a systematic account of the ways in which individuals differ from one another" (Wiggins, 1979, pp. 395; Wiggins, Renner, Clore, & Rose, 1971). This focus seems to exclude from study the key issue of species-typical characteristics that forms the core of most personality theories.

In sum, although the prominent concerns in personality psychology involve individual differences and common human characteristics, the field has proposed few criteria for identifying the most important individual differences, the important species-typical characteristics, and the relations between these sets of attributes (but see Cattell, 1946; Eysenck, 1967; Goldberg, 1972; Gough, 1968; Norman, 1963; Wiggins, 1979). Evolutionary biology provides one framework for investigating these issues.

Typological and Population Approaches in Evolutionary Biology

It is an oversimplification to speak of evolutionary biology as though it were a single, monolithic, consensually agreed upon set of ideas (Mayr, 1982). Major differences surround key issues such as the unit and level of selection (e.g., gene, individual, or group; see, e.g., Alexander, 1979; Dawkins, 1976; Williams, 1966), the amount of genetic variation within species (e.g., Wilson, 1978), and the explanatory status of evolutionary theory (e.g., Searle, 1978). At least two major themes may be identified, each with separate aims, assumptions, methods, and limitations.

The first, here called "typological thinking" (adapted from Mayr, 1963), has as its aims discovering basic species-typical characteristics, discovering the adaptive significance of species traits, monitoring the genetic basis of species behavior, and predicting species-typical responses from evolutionary postulates.[2] Applied to *Homo sapiens,* this set of concerns reduces to attempts to uncover the "pan-human psyche," the "traits of human nature" (Wilson, 1978, p. 34), the "human biogram" (Tiger & Fox, 1971), or the "universal human ethogram" (Fuller, 1983, p. 460). An assumption (sometimes implicit) of typological thinking is that within-species variation is relatively small, a deviation from the species archetype, and subsidiary in importance to the major topography of species traits.

Among recent evolutionary approaches, sociobiology has tended to emphasize species-typical traits (as has ethology). Genetic variability within species is recognized, but does not occupy a central role in such approaches. According to Wilson (1978), "either possibility—complete cultural determination versus shared cultural and genetic determination of variability within species—is compatible with the more general sociobiological views of human nature" (p. 43). Indeed, even though genetic heterogeneity within populations is required by evolutionary models of sociobiology (Fuller, 1978, 1983), "sociobiology has tended to downgrade [within-species] differences and to stress the *universals of human nature* that have been shaped by similar selective forces everywhere" (Fuller, 1983, p. 470; emphasis added).

Comparative phylogenetic analysis is one of the major methods of typological thinking (Wilson, 1975).[3] Species comparisons highlight the similarities of our species with others, generating, for example, general mammalian traits (e.g., group living) or general primate traits (e.g., hierarchical social arrangement), as well as the unique features of each species. Correlating variations in ecological niches with variations in the traits of species that occupy

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[2] It may be more accurate to speak of "evolutionary approaches with typological (species-typical) emphasis," rather than "typological approaches." The latter is used here for expositional clarity.
[3] Other methods include those of behavioral ecology and laboratory-based experiments.

Table 1
A Comparison of Typological and Population Approaches

	Typological	Population
Aims	To discover "human nature" To discover the adaptive significance of species traits To monitor the genetic basis of species behavior	To discover variation among species members To monitor the genetic basis of observed variation To discover the reasons for which variants are selected
Assumptions about variation	Variation is small and subsidiary in importance to species-typical characteristics	Variation is real and consequential
Primary methods	Comparative phylogenetic analysis	Quantitative and population genetics
Limitations	Variability of traits limits utility of postulating species-typical attributes Defined so broadly that any outcome of quantitative genetic research is compatible	Findings limited to extant population variation and to environments within which population is studied Will not discover species traits

these niches provides one method for inferring the adaptive significance of species traits (see Lewontin, 1978, and Williams, 1966, for detailed discussions of adaptation).

In sum, typological thinking takes the species as the focal unit and through comparative phylogenetic analysis seeks to identify the major traits of each species and the adaptive significance of each of those traits. Although within-species genetic variation is sometimes recognized, it is typically viewed as subsidiary in importance.

In contrast, "population thinking" (adapted from Mayr, 1963) has as its aims discovering variation among conspecifics, monitoring the genetic basis of observed variation, and discovering the forces by which variation itself increases or decreases, as well as the forces causing some variants to increase or decrease in frequency in the population. Quantitative genetics is a primary method of population thinking, and it focuses on partitioning phenotypic variation into genetic and environmental sources and identifying the interactions and correlations among these causes of variation.

Both typological and population approaches in evolutionary biology carry limitations due to their primary focus. Population approaches are limited in that the methods of quantitative genetics will not discover species-typical traits. Leggedness, for example, would have a heritability near zero because variations from two-leggedness are due mostly to environmental sources (e.g., accidents), rather than to genetic sources (Loehlin & Nichols, 1976). Findings are also limited to extant population variation and to the environments within which the population is studied. Heritability can vary as a function of the range of environments. And increases in trait dispersion (e.g., one genetic consequence of assortative mating) may increase heritability estimates. Heritability estimates cannot be viewed as eternally fixed; instead, they reflect the dispersion within the population within the existing range of environments at a given period of time.

Typological approaches, in contrast, are limited in that observed variability of traits within species limits the utility of postulating species-typical characteristics.[4] Measures of central tendency lose individual predictability and descriptive utility as dispersion about them increases. Because typological approaches emphasize species universals, phenotypic variation traceable to genotypic variation is often ignored or viewed as tangential to the typological enterprise. Thus, the field of quantitative genetics tends to be viewed as independent when it could be integral to more typologically oriented approaches (see, e.g., Fuller, 1983; Thiessen, 1979). Table 1 summarizes the broader aims, assumptions, methods, and limitations of typological and population thinking as they are conceived here.

These two themes of evolutionary biology can be closely aligned with the questions identified earlier as major concerns of personality psychology (cf.

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[4] This limitation applies primarily to presumptively "obligate" traits (genes producing the same phenotype under all environmental conditions commonly encountered) rather than to "facultative" traits (genes producing different phenotypes in different environments). See also the section on directions for rapprochement.

Campbell, 1975; Cunningham, 1981; Dickstein, 1979; Freedman, 1971, 1979; Hoffman, 1981; Hogan, 1983; Kenrick, Dantchik, & MacFarlane, 1983; Rushton, 1984; Van den Berghe & Barash, 1977). Typological approaches may aid conceptualization of, and research on, the major commonalities of our species (i.e., human nature). Population approaches, on the other hand, may be used to identify the important individual differences and their implications. It is probably no coincidence that sociobiologists, rather than behavior geneticists, have speculated about the implications of their (often) typological approach for conceptualizing human nature (see, e.g., Barash, 1977; Symons, 1979; Wilson, 1978). Behavior geneticists, on the other hand, tend to avoid discussion of human nature, restricting study primarily to variation within species. It has been argued, for example, that behavior genetics can designate importance among individual differences within our species by identifying the traits with the highest heritabilities (see, e.g., Eysenck, 1967, 1981).

But the application of typological approaches to discussions of human nature and the use of behavior genetics to identify the important ways in which individuals differ logically follow from prior conceptual issues that must be resolved or at least made explicit if these applications are to be successful. Indeed, the absence of defining criteria for "human nature" in articles and books carrying this phrase in their titles may reflect the implicit standing of these issues in the application of principles of evolutionary biology to personality psychology.

Three major issues are considered here: (a) What criteria can be established for considering something "part of human nature," or an important species-typical commonality? (b) What criteria can be established for considering something an important way in which individuals differ? (c) How can typological and population approaches be reconciled within a general theory of personality?

Some Directions for Rapprochement

Establishing Criteria for Determining Important Species-Typical Characteristics

Explicit criteria must be established for considering something part of human nature, or an important species-typical characteristic. Inclusion criteria for deciding whether or not a feature is part of human nature have not generally been made explicit. Until such criteria are established, theorizing and research on human nature remain at the level of favorite lists and constructs of convenience. It is impossible at this early stage to provide an exhaustive list of potential criteria. Several candidates, some of which have been implicit in current formulations, can be critically examined.

Universality. Perhaps the most common implicit criterion for designating an attribute part of human nature concerns its prevalence or universality. This criterion assumes that manifested ubiquity reflects (or correlates with) featural importance. Features found across cultures, races, and populations are assumed to be more part of human nature than those features that are unique to certain subgroups or individuals. Attributes of limited generality are not considered to reflect human nature.

The level of analysis to which the universality criterion applies must first be specified. Questions such as "Is aggression part of human nature?" can be posed at the phenotypic or genotypic level. These levels of analysis are often conflated in efforts to specify the traits of human nature. If posed phenotypically, the appropriate index would be whether or not each species member displays aggression. If posed genotypically, however, universalities of aggression displayed by each species member would not be required, although other conditions would have to be met (see below). In contrast to the phenotypic and genotypic levels, questions such as "Do all human groups develop dominance hierarchies?" are posed at the level of social structure. Therefore, universalities across groups, rather than across individuals, would be required. However formulated, the universality criterion calls for some form of pan-species invariance at a particular level of analysis.

Within-species variability, therefore, poses a major problem for the universality criterion. Phenotypically, the greater the manifested dispersion within species, the more statements of universality must be qualified. Similarly, at the level of social structure, variability among groups empirically undermines statements of universality. Problems at the genotypic level are even more pronounced because they involve limitations imposed by current methodologies as well as by empirical findings.

The universality criterion at the genetic level incurs problems when the methods for establishing the genetic basis for a trait are examined. The field of behavioral genetics has developed methods for apportioning phenotypic variation into genetic and environmental sources (Falconer, 1960; Fuller & Thompson, 1978; McClearn & DeFries, 1973; Plomin, DeFries, & McClearn, 1980). That is, observed differences between people are traced to heritable and nonheritable differences. These genetic methods cannot be applied to discerning the major commonalities because, by definition, commonalities are attributes for which little individual variation exists.

In addition to these methodological difficulties, which can be overcome in principle, empirical findings from the field of behavior genetics pose a second

problem for postulating universality at the genetic level. Empirically, most personality traits such as dominance, aggression, and extraversion appear to show moderate heritability (e.g., Fuller & Thompson, 1978; Loehlin & Nichols, 1976). That is, phenotypic differences are traced partly to genetic differences within our species, rather than to varying environmental conditions that differentially potentiate a universal genetic substrate. Findings of genetic variability compromise the invocation of a universal "human biogram" and throw into question whether aggression (or any other trait) is a "trait of human nature" rather than just a feature in the behavioral repertoires of a subset of individuals.

Spontaneity, automaticity, and intractability. A second potential criterion by which attributes can be evaluated for potential inclusion as part of human nature is whether they are produced spontaneously, with little or no environmental impetus or incentive. The tendency of pigs to revert spontaneously to rooting behavior in spite of training and reinforcement schedules to the contrary, for example, would constitute evidence that rooting is part of pig nature (Breland & Breland, 1961, 1966). Similarly, if dominance hierarchies spontaneously emerge in groups of adults and children, where no particular instructions or external requirements were presented, this would fulfill the spontaneity criterion, and such structures would be included as potential candidates for being part of human nature. In Skinner's (1938) terms, these behaviors are operants, emitted spontaneously when no strong environmental forces reign.

A related criterion, one that builds in an environmental contingency in its specification, is automaticity—the extent to which a behavior or attribute is reflexively displayed in response to a given environmental elicitor. The knee-jerk and moro reflexes would be examples of respondent attributes. Attachment (Bowlby, 1969), emotional expression (Darwin, 1872/1965; Plutchik, 1980), and fixed action patterns (e.g., Tinbergen, 1951) might be additional examples. The spontaneity and automaticity criteria both invoke innate, unconditioned, and relatively difficult to modify features of behavior, with the two differing only in the role played by the specific, efficient, antecedent cause. Features of behavior that are spontaneously emitted and automatic are presumed to be more a part of the "human biogram" than those features requiring extensive training or conditioning.

The automaticity criterion encounters difficulties in that well-learned responses can become quite automatic in the ease or rapidity with which they are elicited. Yet their origins lie with previous learning history rather than being intrinsic to the species. Similarly, what appears to be spontaneously emitted also may depend upon prior learning schedules,

which may vary from individual to individual, culture to culture, and even generation to generation. There is no guarantee that spontaneity derives from an intrinsic species nature and not from particular reinforcement schedules, although there may be conditions (e.g., smiling behavior in congenitally blind persons) that may permit reasonable inferences.[5]

A criterion related to spontaneity and automaticity is intractability—the idea that species attributes that are difficult to alter are more part of human nature than more ephemeral features, or those easily altered by environmental forces. The criterion of intractability has the advantage that its operationalization is straightforward, entailing assessment of the effectiveness of imposed contingencies. Its drawback is that limitations or gaps in knowledge could preclude change, easily observed once effective environmental contingencies are discovered.

Adaptation. A third criterion embedded in evolutionary biology involves adaptation. Species features that solve ecological problems and enable organisms to function well (survive, reproduce) in their niches can be viewed as more important or intrinsic to our "human biogram" than features lacking adaptive functions. Implicit in this criterion is a defensible means for partitioning the behavioral stream into functionally significant units (e.g., acts or classes of acts). In addition, some reasonable categorization of niches is required for calibrating organismic behavioral units with corresponding environmental units so that functional significance can be identified.

Assuming these requirements can be met, the concept of adaptation carries two additional problems (Lewontin, 1978; Williams, 1966). First, the concept implies a preexisting environment that poses a problem to which adaptation is the solution. The concept appears to bypass the role of the organism in creating the niche. Niches may be created specifically to correspond to preexisting organismic attributes (Buss, 1981, 1984a, 1984b, in press; Plomin, DeFries, & Loehlin, 1977; Scarr & McCartney, 1983). It makes little sense to postulate adaptive functions for ecological problems when the ecology itself is forged by the organism.

In addition, species traits are often involved in a variety of functions. It is particularly difficult to designate the specific problem solved by a given trait, or to infer the selective pressures that may have been operating previously to create the trait. A plausible function can be invented for any characteristic. But such post hoc arguments, however per-

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[5] Even this smiling behavior, however, could arise through operant conditioning.

suasive, do not provide clear criteria for ordering species traits by importance (but see Alexander, 1979, for a set of hypotheses and predictions; see Glickman, in press, for a more general historical treatment in the context of comparative psychology).

In summary, attributes under consideration for inclusion as part of human nature can be evaluated against certain biological criteria. Each of these criteria possesses problems. Some are conceptual (e.g., at what level of analysis should the universality criterion be invoked?). Others are empirical or operational (e.g., findings of genetic variation; undeveloped methods for discerning genetic commonalities within species). And still others remain problematic, even after conceptual clarification and operationalization, due to untested premises (e.g., assumptions about environmental effects). Additional and related criteria could have been discussed (e.g., speed of learning, developmental invariance), and should be examined in the future. The more limited aims of this section, however, are to highlight several criteria that are currently implicit in existing conceptions of human nature, to point to problems and limitations in their application, and to underscore the requirement that explicit criteria must be established for considering something part of our "human biogram" if evolutionary biology is to be effectively linked with personality psychology.

Establishing Criteria for Identifying Important Individual Differences

A second major task for integrating evolutionary biology with personality psychology concerns identifying the important individual differences from among the hundreds or thousands that are available or imaginable.[6] Criteria can be instated to order individual differences by importance and priority. Differences in ear-wiggling ability must be distinguished from variations in dominance or in access to sexual partners—individual differences with demonstrated evolutionary consequences. From the standpoint of evolutionary biology, four criteria may be employed to designate importance: heritability, inclusive fitness, sexual selection, and assortative mating.

Heritability. Heritability may be offered as one criterion for ordering individual difference variables from most to least important. Differences among individuals that are traceable to genetic differences can be considered important because they provide the variation necessary for evolution. "These individual differences are of the highest importance for us, for they are often inherited . . . and they thus afford materials for natural selection to act on and

accumulate" (Darwin, 1859, pp. 59–60). Estimates of heritability can be derived from family studies, twin studies, and adoption studies, and convergence among these methods can be examined empirically. Heritability is particularly attractive as a criterion because it provides a direct link between evolutionary biology and personality psychology.

Several considerations, however, may seriously qualify the standing of heritability as a criterion for importance. The first is the argument marshaled by Thiessen (1972), in which individual differences showing high heritability are viewed as "genetic junk." Attributes may show great variability precisely because of their *unimportance* in evolutionary history. Variability may be low for traits that have been subjected to severe selection pressure and are therefore ubiquitous among species members (see also Falconer, 1960). Nonetheless, whatever the prior evolutionary standing of heritable differences, such differences do provide "materials for natural selection to act on and accumulate" and may acquire importance for that reason.

A second problem is more pragmatic. The resolution of behavior genetic studies has not been sufficiently articulated to establish differential heritability, at least within the personality realm (see, e.g., Loehlin, 1978; Loehlin & Nichols, 1976). If moderate heritability can be shown for *all* personality traits, then the heritability criterion cannot be employed to order dispositions by importance. Optimism has been expressed, however, that differential heritability must exist (e.g., Loehlin, 1978), and there are preliminary indications that can be discovered empirically (Carey, Goldsmith, Tellegan, & Gottesman, 1978; Loehlin, 1982; Zonderman, 1982).

A third qualification of the heritability criterion is that estimates are inextricably linked to the existing population distributions and to the particular range of environments during the time period within which estimates are made. Thus, two major factors could alter the ordering of dispositions by heritability magnitudes: (a) changes in the range and type of environments and (b) changes in population distributions on dispositions.

Changes in environment could be of the form of increasing uniformity (e.g., due to increases in common influences such as television and other media), which might amplify heritability estimates of some traits. Alternatively, compensatory environments and "coercion toward the biosocial norm" (Cattell, 1973) could decrease heritability on those attributes toward which provisions and coercion are directed. Magnitude orderings of dispositions by heritability can and probably do change as a function of altered environments.

Heritability estimates can also change as a function of changes in population distributions. One

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[6] This problem is logically related to discovering important equivalence classes in behavior (see, e.g., Herrnstein, 1977).

such change may be brought about by assortative mating (Eckland, 1968; Jensen, 1978; Vandenberg, 1972), which can increase phenotypic and genotypic variance and hence heritability. Differential assortative mating for some traits and not for others could produce shifts in the ordering of traits using the heritability criterion. Thus, changes in population distributions—both genotypic and phenotypic—can alter heritability estimates.

In linking evolutionary biology with personality psychology, heritability provides one criterion by which dimensions of individual difference may be ordered by importance. Care must be taken, however, not to infer previous evolutionary adaptation solely from findings of heritability.[7] In addition, present heritability ordering should not be viewed as fixed. Heritability estimates can change with alterations in environments and population distributions. Finally, application of the heritability criterion awaits sufficiently precise demonstrations of differential heritability.

Inclusive fitness. Individual difference variables may be ordered by their correlation with genetic perpetuation or inclusive fitness (Hamilton, 1964). The most direct method for operationalizing inclusive fitness would be to derive indices of genetic perpetuation that include offspring of biological relatives as well as an individual's own offspring. The degree to which different traits covary with subsequent gene representation would rank these traits by importance.

Traits showing significant heritabilities that are correlated with measures of inclusive fitness take on intrinsic importance within evolutionary biology because they are the traits for which frequencies can be expected to increase (positive correlation) or decrease (negative correlation) in succeeding generations. Such traits become part of the complex selection process that forms the core of evolutionary biology. They acquire additional importance for personality psychology because such changes could produce alterations in the mean frequencies of manifested acts that are encompassed by these traits.

Assessing trait–fitness linkages is a never-ending process, however, because changes in culture, environment, and even trait distributions are likely to alter such correlations. One speculative example is that the current trend toward increased longevity may have an impact on trait–fitness correlations. Although increases in longevity may have little effect on direct production of offspring, longer life spans may increase the opportunities to facilitate the genetic perpetuation of distant kin, such as great grandchildren and grandnieces. This implies a shift in the ratio of inclusive to individual fitness opportunities that could tilt selection in favor of traits that are correlated with altruism, such as generosity or empathy (Hoffman, 1981).

In addition to continuous evaluation of changes in trait–fitness associations, care must be taken not to erroneously infer trait–fitness covariation solely from evidence of heritability (see footnote 7). Finally, the concept of inclusive fitness must be adequately operationalized before it can be effectively employed for the conceptual functions it could serve.

Sexual selection. Darwin initially proposed the concept of sexual selection to account for attributes such as the plumage of peacocks that he believed could not be explained by the process of natural selection (Darwin, 1871). Sexual selection subsumed two related processes: intrasexual selection, or competition between members of one sex for access to members of the opposite sex, and intersexual (epigamic) selection, the differential choice of mating partners possessing preferred characteristics. Although sexual selection operates through differential reproduction of individuals and is now recognized as being subsumed by natural selection or inclusive fitness (cf. Campbell, 1972; Trivers, 1972), the processes defined by sexual selection can be important proximate mechanisms through which differential gene representation is achieved.

By identifying individual differences central to mate choice and competition, the study of sexual selection provides a third basis for designating importance among individual differences. Potential partners with preferred attributes will be more frequently chosen for mating; those relatively deficient in these qualities will tend to be excluded and therefore will be less represented in subsequent generations. Species-typical preferences exist to the extent that consensus occurs among species members about the valued attributes in potential mates (e.g., intelligence, cooperativeness). Traits can therefore be ordered on the degree to which they are consensually valued, and are thus intrinsic to mate choice. As with the heritability and inclusive fitness criteria, however, preferred mate characteristics may be time- and culture-bound. The extent to which characteristics central to sexual selection transcend cultures and eras remains unanswered empirically (cf. Bateson, 1983; Campbell, 1972), but poses an intriguing research agenda (Buss & Barnes, 1984).

Assortative mating.[8] A fourth criterion that may be employed for identifying the most important individual differences involves patterns of nonrandom

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[7] It is possible, however, that certain patterns of heritability may permit inferences about directional selection. Findings of low heritability in the narrow sense (additive genetic variance) combined with high heritability in the broad sense (due to genetic dominance) are theoretically consistent with directional selection for a trait in evolution (Fisher, 1930; Jensen, 1983).

[8] Although assortative mating is discussed here in the context of individual variation, it has also been examined as a species-typical trait (Fox, 1979; Thiessen & Gregg, 1980).

mating. Assortative mating, the coupling of individuals based on resemblance on one or more traits, is currently the most striking deviation from random mating, or panmixia.[9] In the past several decades, moderate levels of assortment have been documented for cognitive and intellectual abilities (e.g., Johnson et al., 1980; Price & Vandenberg, 1980; Watkins & Meredith, 1981; Zonderman, Vandenberg, Spuhler, & Fain, 1977), and low but consistently positive levels of assortment have been observed for personality and interest variables (e.g., Buss, 1984a, 1984b; Jensen, 1978; Vandenberg, 1972; Price & Vandenberg, 1980).

Within the context of evolutionary biology, the importance of assortative mating for identifying important traits lies with the profound genetic consequences that follow from assortment. For example, assortative mating can increase the variability of a trait in the next generation, can create correlations among traits that were initially uncorrelated (e.g., between physical beauty and IQ), and can increase correlations among certain biological relatives (e.g., between parents and offspring) on those traits for which assortment occurs. Because of these wide-ranging genetic and social consequences, assortative mating can be used as a fourth criterion for ordering individual difference traits by importance.

The primary problem with assortative mating as a criterion is that differential assortative mating (i.e., greater assortment for some traits than for others) has not yet been demonstrated, at least within the personality domain. Failure to find differential assortment may be due to inadequacies of the measuring instruments. Built-in covariation among traits due to item overlap can preclude the discovery of differential assortment that might be present. Alternatively, low but consistently positive levels of assortment may be the rule in the personality domain, with little or no differential assortment occurring.

Although differential assortative mating provides a potential criterion for identifying the most important within-species differences, application of this criterion must await reliable demonstrations of differential assortment. Even when more precise assessment becomes available, this criterion will be limited by the fact that the traits on which assortment occurs may change from generation to generation. Continuous population monitoring will be necessary to prevent outmoded generalizations.

In sum, four criteria have been proposed by which important individual differences may be identified and ordered: heritability, inclusive fitness, sexual selection, and assortative mating. All provide direct links between evolutionary biology and personality psychology. Other criteria could be invoked for identifying and ordering dispositions by impor-

tance, such as covariation with access to resources (cf. Buss & Craik, in press). Although difficulties qualify these criteria, each provides a starting point. Once important human commonalities and individual differences have been identified, the further step of specifying the relations between them must be taken.

Specifying Relations Between Human Commonalities and Individual Differences

The relations between important species-typical characteristics and important individual differences should be identified and their implications understood.

Perhaps the largest division in modern psychology concerns what Cronbach (1957) has called "the two disciplines of scientific psychology." Cronbach framed the division as a contrast between correlational and experimental psychology, but these terms may be too closely tied to particular methods. Another way to conceptualize this division is to ask whether general laws are sought (common to most or all species members) or whether individual variation is the primary focus of study. In spite of Cronbach's (1957) incisive statement of the problem and its reiteration nearly two decades later (Cronbach, 1975; see also Underwood, 1975; Vale & Vale, 1969), little progress has been made in bringing these two disciplines into closer alignment. Linking evolutionary biology and personality psychology may foster this integration.

In examining the relations between species traits and within-species differences, it is necessary (a) to separate the different conceptual levels of analysis across which relations can be identified and (b) to separate the descriptive properties that are applicable to each level. Three levels of analysis are particularly relevant for considering the relations between species traits and individual differences: genotypic structure, phenotypic structure, and social (group) structure.

When species-typical characteristics and within-species dispersion are examined at different levels of analysis, questions about their causal connections become salient.[10] Within this hierarchy, causal relations are commonly viewed as extending primarily

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[9] Other deviations from panmixia include selective mating, polygamy, inbreeding, and outbreeding.

[10] It is possible, of course, to examine the relations between different attributes occurring at the same level. Interactions of alleles at a single locus on the homologous chromosome (dominance) and of alleles at different loci (epistasis) are types of relations at the genetic level. Similarly, individual differences in height can causally affect individual differences in dominance, both at the phenotypic level. This section, in contrast, is concerned with causal relations between dispersion and species typicality, and it is at different levels of analysis that these relations are most apparent.

from lower to higher levels. Species-typical genotypic structures, for example, can affect phenotypic dispersion through interaction with features of the environment. Phenotypic dispersion, in turn, can create species-typical emergents at a higher level. But species-typical emergents such as social hierarchies can also feed back causally to the lower levels, both genotypic and phenotypic. Examples of these relations between levels are given below:

1. Genotypic species-typical traits can produce phenotypic individual differences. One type of connection occurs when species-typical traits cause observed dispersion through their interaction with features of the environment. For example, nepotism (altruism toward kin) may be a genotypic species-typical characteristic, yet enduring phenotypic differences in altruistic behavior are predictable from the number and genetic closeness of conspecifics in proximity. Sherman (1980) found that individual differences in alarm calling when faced with a potential predator (an altruistic act because it calls attention to and endangers the alarm-caller) are predictable among female ground squirrels from the number of genetic kin in the immediate surroundings. Thus, nepotism may be a genotypic species-typical characteristic, with phenotypic differences caused by the interaction of this proclivity with environmental features. Evolutionary biology is useful in identifying these relations because it highlights the important environmental variables, such as number of kin in proximity, that are likely to interact with species proclivities, such as nepotism, to produce individual variations.

2. Phenotypic individual differences can cause emergent social characteristics that are species-typical. A second type of connection occurs when individual differences create a species-typical emergent. Because resources are often finite and individuals differ in their ability to attain them, the formation of status hierarchies based on access to resources may be a species characteristic that inevitably emerges in human groups (Hogan, 1983; Lopreato, 1984). Thus, the existence of individual differences in attributes such as intelligence, dominance, and cooperativeness may invariably lead to the formation of hierarchies. Evolutionary biology is useful in identifying these relations because it calls attention to those individual differences that may be linked to survival (e.g., intelligence) and to gene representation (e.g., dominance)—individual differences likely to form the basis for the hierarchy. Thus, individual differences can causally produce emergent species-typical characteristics.

3. Common species structures can produce an increase (or decrease) in genotypic and phenotypic variation. More subtle causal connections occur when emergent group structures affect genotypic and phenotypic variation. One function that hierarchies serve, for example, is to govern who mates with whom. Empirically, strong marital assortment occurs for socioeconomic status. As a consequence, assortative mating will also occur for those attributes (e.g., intelligence, dominance) that tend to covary with status. Assortative mating increases genotypic variance on those attributes for which assortment occurs, producing greater frequencies of individuals at the tails of the distribution (Crow & Kimura, 1970; Jensen, 1978; Vandenberg, 1972). Thus, a social hierarchy, because it is linked with assortative mating, can causally affect the amount of genotypic (and phenotypic) variation occurring in subsequent generations—an increase in the dispersion that was in part responsible for the construction of the hierarchy to begin with. At the same time, genetic dispersion may be partly responsible for the creation of the hierarchy. In sum, the causal and reciprocal connections between species-typical and individual difference characteristics can extend across all three levels of analysis.

4. Individual differences can be unrelated to species-typical traits. In many cases, species traits and within-species dispersion may be unrelated to each other. Separate levels of analysis are often useful precisely because they provide insights not available through, or connected with, alternative levels. There need not be ubiquitous connections between levels of analysis. And where there are connections, they need not occur between species-typical and individual difference characteristics. The descriptive task entailed by analysis of both types of attributes requires identifying the absence, as well as the presence, of these connections.

Discussion

The field of personality psychology is centrally concerned with the traits that characterize our species as well as with the major ways in which individuals characteristically differ. Although most current personality research focuses upon individual differences, personality theories almost invariably postulate core human characteristics. Within such theories, individual differences typically take on derivative and subsidiary roles. These themes are also seen in evolutionary biology, where attempts to discover the "human biogram," the "pan-species psyche," or the "traits of human nature" form disciplines separate from biological approaches, such as quantitative behavior genetics, that focus more centrally on variation within species.

It has been argued that certain conceptual and operational inadequacies must be addressed before integration is possible. Methodologically, research instruments must be coordinated with the central

questions posed by evolutionary biology. Explicit conceptual criteria should be instated for considering a given feature, attribute, or pattern as a species trait. Criteria for determining the most important ways in which individuals differ also must be established. Perhaps most important, conceptual frameworks should be developed within which important individual differences can be integrated with species-typical characteristics. Evolutionary biology provides one framework for addressing these issues.

This article has attempted to highlight the features of evolutionary biology most relevant to the concerns of personality psychology. To examine the species-typical questions posed by evolutionary biology, methods could be developed that do not derive meaning solely from comparisons with other individuals (or with other attributes within individuals), as do nearly all current methods within personality psychology. Inclusion criteria for considering a given feature a species trait (e.g., genotypic universality, adaptation) should be critically examined. Criteria implicit within existing conceptions can be made explicit and operationalized so that potential candidates for inclusion are examined empirically. In the individual difference domain, four preliminary criteria—heritability, inclusive fitness, assortative mating, and sexual selection—can be operationalized currently and warrant further attention. Because problems exist with each of these criteria, it may be asked what this analysis has achieved. Given the numerous difficulties, what are the most promising future directions?

The field of personality psychology currently seems fragmented. The study of isolated traits without explicit rationale remains the norm, not the exception (Goldberg, 1981; Wiggins, 1979). Linkage with evolutionary biology provides one set of criteria, albeit incomplete, for identifying traits and for establishing relative importance among them. This does not undermine the importance of nonbiological criteria (see Buss & Craik, in press, for an extended discussion of alternative criteria). But it is likely that traits linked with biological processes such as assortative mating, sexual selection, and inclusive fitness may be precisely those that fulfill other important criteria such as those of psychological, social, and sociological importance.

This potential link between biological and social science phenomena suggests that importance itself may be identified by the range of impact within and across disciplines. Mate selection, for example, acquires importance because it is a social and cultural process based partly on biological principles that have genetic consequences and sociological implications (Buss, 1984a, 1984b). Traits linked with criteria anchored in evolutionary biology acquire importance partly through their range of impact across different disciplines and across different levels of analysis.

In addition to identifying a set of criteria for importance, this analysis points to some of the research efforts needed to utilize them. In the domain of individual differences, for example, research could examine preferences in mate selection, differential assortative mating, and differential heritability. Loehlin (1982) has provided a promising lead for discovering differential heritability by finding that the factors of extraversion and neuroticism have higher heritabilities than do factors orthogonal to these traits, such as stereotyped masculine interests, intolerance of ambiguity, and persistence.

By illustrating some ways in which typological and population approaches can be linked, this analysis also aligns the study of individual differences more closely with the search for general laws that occupies most of psychology. One important direction for this rapprochement involves identifying stable classes of environmental factors that consistently moderate phenotypic expression. Hypotheses derived from evolutionary theory, such as the environmental conditions under which nepotism will and will not occur, provide one means for identifying such factors.

In this context, assessment methods are needed that produce interpretable central tendencies for comparative analysis. One such method can be derived from the act frequency approach (Buss & Craik, 1983a, 1984), in which frequencies of acts within certain categories (e.g., dominance or aggression) are recorded by observers in the natural audience over a specified period of observation. Across persons and environments, these frequency counts yield "modal human tendencies" (Buss & Craik, 1983b, p. 396). The concept of modal tendency is perhaps more appropriate than "species-typical commonality" because the presence of a central tendency rarely precludes individual variation for behavioral categories. Indeed, by identifying the degree of variation, these methods can specify the degree to which different traits approximate species typicality.

From this perspective, emphasis on central tendencies as well as on variability highlights the relatively neglected descriptive task that faces personality psychology. The finding that altruistic acts may occur twice as frequently as do aggressive acts, for example, or that the ratio of the two modal frequencies may be predictable from environmental factors such as population density and longevity, shows important descriptive characteristics of our species even prior to causal analysis. Different modal tendencies within different classes of environments yield general laws in the form of hypothetical propositions, or "if . . . then" statements, and suggest that individual variation

deriving from stable occupancy of different environments may be systematic and predictable rather than random or capricious. Even more transient interindividual and intraindividual differences may be traceable to such "if . . . then" algorithms. This scheme grants a central role to individual variation in the context of these contingent relations.

Detailed analysis of species-typical problems provides another promising focus for this integration. Because the majority of humans enter into marital relationships, mate selection comes close to being a species-typical problem. In this context, exogamy (mating with individuals who are not closely related) appears to be a species tendency that roughly delineates the boundaries for mate choice. Within (or we might say outside) these boundaries, however, individual differences become crucial in the specific selections that are made.

Individual selections may be governed by the species-typical search for the similar, or what Thiessen (1979) has called "assortative narcissism" (p. 102). Empirically, individuals do tend to select mates who are similar with respect to age, ethnicity, religion, intelligence, attitudes, and personality characteristics (Buss, 1984a, 1984b; Eckland, 1968; Vandenberg, 1972). Individual differences in decisions (e.g., each individual tends to choose a mate who possesses a similar constellation of traits) are driven in part by the species-typical solution (e.g., assortative narcissism) to a common human problem (e.g., mate selection).

These individual choices, however, may be fundamentally mediated by existing hierarchies and individual placement within them. Genetic differences can create phenotypic differences (e.g., in dominance) that in turn lead to group structure (hierarchy), which because of its close link with assortative mating leads back full circle to increase genotypic variability in subsequent generations. This highlights the intriguing ways in which causal links between species-typical traits and individual differences can be identified across levels of analysis.

Beyond the tangible benefits derived by personality psychology, integrative efforts of this sort can modify the strongly typological themes that dominate some (although not all) evolutionary approaches to our species. Typological statements that "the traits of human nature" include altruism and aggression (Wilson, 1978, p. 34) are inadequate as they stand without specifying (a) the level of analysis to which they apply (group structure, phenotypic invariant, genotypic invariant), (b) the environmental contingencies that could yield statements in the form of invariant hypothetical propositions, and (c) the range of individual variation (both genotypic and phenotypic) commonly found with respect to each hypothesized species-typical trait.

From this perspective, species-typical characterization is incomplete without accompanying statements about within-species dispersion. The basic tenets of evolutionary biology have required both lines of thinking since Darwin's initial 1859 formulation that emphasized both variation and selective character retention. Current conceptions in psychology should require no less.

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