A Perspective on Darwinian Psychology: The Importance of Domain-General Mechanisms, Plasticity, and Individual Differences

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In this paper a theory of Darwinian psychological adaptations as motive dispositions with an affective core is developed, and it is argued that 1) there is significant plasticity in these mechanisms; 2) in addition to domain-specific evolved motive dispositions, there are a variety of domain-general cognitive and emotional mechanisms; 3) humans are capable of developing motive dispositions which are not adaptations; 4) the relationship between evolved motive dispositions and behavior is very tenuous so that the explanatory power of Darwinian psychology is very weak; 5) individual differences in human psychological characteristics are evolutionarily meaningful and are linked to mechanisms which assess the resource value of intraspecific genetic and phenotypic diversity.

KEY WORDS: Darwinian psychology; Personality psychology, Plasticity, Individual differences.

> The basic structure of man's behavioural equipment resembles that of infra-human species but has in the course of evolution undergone special modifications that permit the same ends to be reached by a much greater diversity of means (Bowlby 1969, p. 40).

In a recent review, Buss (1991) has noted that views on the relation between evolution and psychology have ranged from the proposal of many learning theorists that there exist a few domain-general mechanisms which result in "more or less arbitrary psychological structures during ontogeny," to the view that "natural selection created many domain-specific psychological mechanisms that solve particular adaptive problems" (p. 462), the latter view associated with Cosmides and Tooby (1987) (see also Tooby and Cosmides 1990a, b) and Symons (1989; in press). Proponents

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of the importance of domain-specificity have tended to downgrade the importance of domain-general mechanisms and developmental plasticity. Moreover, they have stressed the idea that Darwinian psychological (DP) adaptations are species-typical traits, so that individual differences are viewed as mere noise in the system resulting from evolutionary processes unrelated to the evolutionary function of the adaptation. Moreover, because of the fundamental importance of understanding DP adaptations which evolved in the Pleistocene or before, this view has been used to challenge the importance of using reproductive success (RS) as an important dependent variable in the evolutionary analysis of contemporary societies.

In the following I will attempt to address these issues by developing a perspective intermediate between the arbitrary psychological content implied by many learning approaches and the view that psychological phenomena are adequately characterized by a host of adaptations to recurrent events in the Pleistocene environment. The perspective developed here is compatible with the argument of Cosmides and Tooby (1987) that the idea of a generalized fitness maximizer is incoherent, but it argues for the importance of domain-general mechanisms and is consistent with the existence of a relatively delimited set of evolved Darwinian psychological adaptations. Moreover, it incorporates a robust notion of plasticity into Darwinian psychology (as emphasized also by Alexander 1990; Turke 1990), and proposes a robust evolutionary role for individual differences in psychological traits. Finally, it is argued that studies of RS in contemporary societies are often an important undertaking independent of any knowledge of Darwinian psychological adaptations.

A THEORETICAL PERSPECTIVE ON EVOLVED PSYCHOLOGICAL ADAPTATIONS AND THEIR RELATIONSHIP TO DOMAIN-GENERAL MECHANISMS

1. Outline of the Theory

An essential proposal is that the psychological manifestation of DP adaptations often involves motivation and affect. Thus whatever domain-general cognitive abilities humans may have developed as psychological adaptations, a crucial subset of these adaptations must function as motivators to engage in adaptive behaviors in the environment of evolutionary adaptedness (EEA). As a thought experiment, imagine an evolved cognitive algorithm which would be able to detect cheaters (exploiters) during resource exchange interactions. In order to be effective it would also have to motivate the person to alter the situation. Simply knowing that one is being exploited is not enough to engage in adaptive behavior. A motivating device is necessary, and it is for this reason that so much of the psychological research in the areas of altruism and prosocial behavior is concerned with emotions such as guilt, empathy, sympathy, as well as negative emotions resulting from non-reciprocated altruistic behavior (Charlesworth 1990; MacDonald 1988).

Evolution seems to have resulted in an array of affective motivational systems which are triggered by specific types of stimulation (e.g., the taste of sweet foods, the pleasure of sexual intercourse, the joy of the infant in close contact with its mother) (see also, Tooby and Cosmides 1990a) and it is difficult to see or even conceptualize how it could have done otherwise. Whatever the fitness maximizing devices are, at a fundamental level they must include motivational systems, and motivation, virtually by definition, involves affect: "A goal may be defined as a mental image or other end point representation *associated with affect* toward which action may be directed" (Pervin 1989, p. 474, my italics).

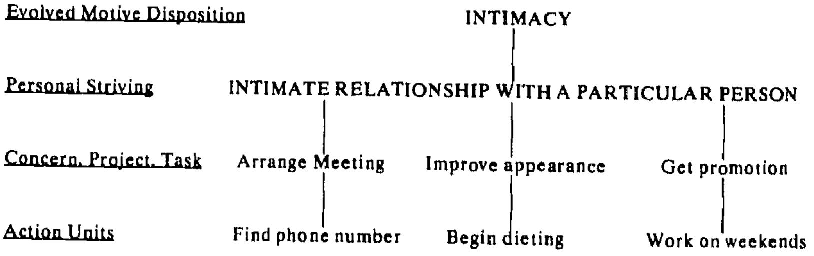
The proposal, then, is that domain-general fitness maximizing adaptations, whatever their cognitive components, would perforce be in the service of discrete affective goals which evolved in the EEA, involving perhaps positive feelings in response to parenthood or in sexual attraction to nubile females. The issues surrounding fitness maximizing devices then reduce to the basic question of the structure of these evolved affective systems their plasticity (manipulability) and the interactions among them.

As a means of conceptualizing these evolved motivational systems and the role of domain-general cognitive processes in them, the scheme of Emmons (1989) is useful (see Fig. 1) (see also Bowlby's (1969) discussion of plan hierarchies). Emmons has developed a hierarchical model in which

FIGURE 1. Hierarchical model of motivation showing relationships between domain-specific and domain-general mechanisms (after Emmons 1989).

Level 1	EVOLVED MOTIVE DISPOSITIONS *(Domain-Specific Mechanisms)*
Level 2	PERSONAL STRIVINGS *(Direct Psychological Effects of Domain-Specific Mechanisms)*
Level 3	CONCERNS, PROJECTS, TASKS *(Utilize Domain-General Mechanisms)*
Level 4	SPECIFIC ACTION UNITS *(Utilize Domain-General Mechanisms)*

EXAMPLE:



personal strivings, and a variety of other lower level actions and goals are in the service of *motive dispositions* at the highest level. I propose here that evolved motive dispositions (EMD's) are biological adaptations and constitute the most fundamental human biosocial goals. Lower level goals and many of the domain-general and domain-specific cognitive processes utilized in obtaining them are proposed as functioning in the service of these biosocial goals which are fundamentally affective in nature. The abilities to perform these latter tasks constitute a set of lower level adaptations, many of which are proposed to be domain-general mechanisms.

Thus, following Symons (in press) and Buss (1989), one could propose that males prefer nubile females as a result of a DP adaptation which is psychologically instantiated as an EMD characterized by positive affective responses (including pleasurable sexual arousal) toward copulation with nubile females, anticipation of copulation, representations of nubile females, etc. A male with the affective goal of copulating with such females would than pursue a wide range of lower level goals, involving perhaps resource accumulation and exchange, which would facilitate this higher level goal.

Success and failure at these lower level goals are accompanied by appropriate affective, motivating responses (e.g., emotions such as joy, hope, regret, sorrow, anxiety, pride, or guilt) related to success or failure at obtaining particular resources in the service of higher level EMD's. As a result, emotions as human adaptations need not be linked to recurring structures of the EEA, a necessary condition for being an adaptation according to Tooby and Cosmides (1990a, b). In order to be an adaptation, emotions need not be domain-specific but can be linked to any event which facilitates or impedes the acquisition of higher level EMD's. Thus, a man might be happy as a result of getting his car fixed because this would help him obtain parental affection or impress his girlfriend. The need to fix one's car is not a recurrent event in the EEA, but such an event can be meaningfully related to human biosocial goals.

Emotions as adaptations thus are often not tied to discrete situations which were recurrent in the EEA, and, indeed, in our day-to-day behavior emotions would appear to mostly function in the service of lower level, non-EEA goals. Emotions are adaptations which, in addition to their role in EMD's, motivate behavior and respond to a host of unforeseeable situations and micro-events in our day-to-day lives—events far removed from anything experienced in the EEA. An essential feature of emotions as adaptations, then, is that, like plasticity and domain-general cognitive mechanisms generally, they are geared to producing adaptive behavior in environments whose contours cannot be predicted and are not recurring.

Moreover, what counts as a resource and what strategy to pursue could be determined by domain-general cognitive processes. Thus in one context accumulating money through shrewd bargaining may be an excellent means of attaining an EMD related to reproduction because the money can be used, e.g., to purchase concubines, while in another context capturing females in warfare may be the best method, while seduction is the best strategy in another context. Thus humans are indeed "flexible strategizers" (Alexander 1987), but their goals have been profoundly shaped by their evolutionary history.

Domain-general cognitive and learning processes would be utilized in the service of obtaining both EMD's as well as lower level goals. The *g* measure of general intellectual ability obtained from IQ scores is a good candidate for such a generalized mechanism. Individuals with a high *g* (and all humans compared to, say, chimpanzees) are able to solve a wide variety of verbal, spatial, and mathematical problems with minimal constraints or biases in the types of problems which can be solved. *g* may involve, for example, speed of information processing which is useful in a wide range of cognitive tasks which may in addition call on additional specific mechanisms peculiar to each task.

A complete list of fundamental EMD's is a major desideratum of research, but there is persuasive evidence regarding at least some of these dispositions.

Panksepp (1989) has proposed five independent brain systems underlying the emotions in mammals. The Foraging-Expectancy system is an appetitive system which functions to bring animals in contact with the resources required from its environment. As indicated by studies of self-stimulation, it is essentially a reward system which functions by giving the animal a subjective feeling of pleasure when the reward is obtained and a sense of positive expectancy in anticipation of the reward. The Anger-Rage system underlies defensive and predatory aggression and rage. The Fear-Anxiety system responds to perceived threat with fear/flight. The Separation-Distress-Panic system is proposed to be a system which results in separation-induced distress vocalizations and is thus the system Bowlby's (1969) attachment theory was designed to describe. Panksepp also proposes a social-play circuit which underlies the play behaviors which commonly occur among mammals. This circuit is also a reward circuit which programs for the subjective pleasure involved in social play, such as rough and tumble play (Panksepp, in press).

This approach based on fundamental human brain systems is compatible with the evidence provided by personality research.[1] Thus Zuckerman (1983) and Gray, Owen, Davis, and Tsaltas (1983) propose that two basic, correlated traits of personality labeled sensation seeking and impulsivity fundamentally involve sensitivity to rewards (Panksepp's foraging-expectancy system). Sensation seeking involves attraction to novelty, danger, excitement, sexual variety, and disinhibition, and is phenotypically and genetically

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[1] The discussion is here restricted for the most part to what appear to be the basic appetitive and/or self-regulatory aspects of personality and does not include the emotionality system which reflects individual differences in the reactivity to stimulation (see Rothbart 1989; Larson and Diener 1987). The adaptive function of this system appears to be to energize behavior (MacDonald 1988).

correlated with sociability, impulsivity, extraversion, dominance, and aggression (see Fulker 1981; Zuckerman 1979). Moreover, it shows the evolutionarily predicted sex difference: i.e., females are expected to be the high investment, low risk sex compared to males, to be relatively less interested in sexual variety, and gain less by dominance and aggression. There is thus good reason to suppose that this system constitutes a set of basic EMD's which evolved as adaptations in the EEA.

A second trait revealed by personality research involves variation in attraction to the rewards of intimacy, affection, and nurturance. Individuals high on psychoticism (reversed) (Eysenck and Eysenck 1976) and reward dependence (Cloninger 1987) are strongly attracted to the rewards of intimacy, affection, and pairbonding, while those low on these dimensions are cold, impersonal, and lacking in empathy and concern for others. This trait is related to attachment (Bowlby 1969), and is hypothesized to function to facilitate paternal investment (MacDonald 1988; 1992).[2]

A third fundamental EMD, presumably more basic even than the appetitive goals discussed above, is a basic goal of self-preservation. The psychological manifestation of this basic sense of self-preservation is the behavioral inhibition system (BIS) (Panksepp's fear-anxiety system), proposed by Gray (1982) as a biological system which responds to perceived threat with behavioral inhibition and the initiation of fight or flight behaviors. The affects associated with the BIS are fear, tension, and anxiety. Since the BIS is fundamentally an avoidance system rather than a reward system, it operates in a quite different manner than the previously described appetitive systems, and the affects associated with it are negative and aversive. The organism behaves in such a manner as to remove the affect rather than to obtain the affect as in the former cases. As predicted by evolutionary theory, there is developmental evidence that girls are higher on behavioral inhibition than boys (Rothbart 1989; Kagan, 1989).

[2] The hypothesis that there was evolution of pairbonding in human evolution is controversial (e.g., Alexander and Noonan 1979). The considerations in favor of the pairbonding hypothesis are as follows (see MacDonald 1988; 1992): 1) Other proximal psychological mechanisms for facilitating paternal investment seem inadequate. For example, the concealed ovulation hypothesis (Alexander and Noonan 1979) predicts only that males will invest until they are sure that the female is pregnant, but meaningful paternal investment among humans must continue long after birth. In fact, the period of paternity uncertainty is the period of lowest need for paternal investment. 2) The psychological data referred to in the text indicate the existence of a psychological system predisposing individuals to form intimate affectional relationships. 3) There is significant cross-cultural universality to this system (see also Eibl-Eibesfeldt 1989). 4) There is genetic variation for this system (see text). 5) The psychological evidence bears out the evolutionary prediction that females will be more strongly attracted to affectional bonds than males (because they are expected to be more discriminating than males in selecting mates) (see also Hinde 1984). 6) There is an association between warm affectional relationships in parents and high investment rearing of offspring in contemporary industrial societies (Belsky, Steinberg, and Draper 1991). 7) There is a similar association in the cross-cultural literature: societies in which males invest little in children are also characterized by lack of affectional involvement between spouses. These considerations strongly suggest that pairbonding continues to function to facilitate paternal investment among humans even in contemporary societies. This does not imply that humans are obligately monogamous. The point here is that because of human developmental plasticity the affectional pairbonding mechanism can be facilitated or inhibited in an adaptive (or maladaptive) manner, at least partly as a result of socialization contingencies.

Some of the stimuli which activate the BIS appear to be the result of innate biases resulting from DP adaptations, such as the common fear of snakes (Gray 1982), loss of physical support, or, presumably, loss of attachment objects (see Bowlby 1969). However, the BIS is a highly domain-general system in that it may be activated by any perceived threat to the self. Thus tension, fear, and anxiety could result from complex, domain-general cognitive processes which result in a perceived threat to the individual, as when an individual learns that his company is the target of a hostile takeover attempt or when an individual believes that engaging in fornication or adultery will result in an eternity spent in Hell. The BIS, like the capacity for low level goals to acquire emotional significance, is thus not adequately described as an adaptation to recurrent specific features of the EEA but is an adaptation for motivating the behavior of an organism in possession of a wide range of domain-general cognitive processes which can reliably assess perceived personal threat in non-recurring situations.

Digman (1990) provides evidence that these traits have been found in a large number of factor analytic studies of personality performed over the last 50 years. Although there is no claim here that this set of EMD's constitutes a complete set of DP motivational systems[3] or that all DP adaptations involve affective motivational systems, this set of EMD's is sufficiently theoretically and empirically grounded to make some general assertions related to the broader question of the generalizability of fitness maximizing mechanisms: (a) whether DP mechanisms are plastic and manipulable and (b) the relation between EMD's and behavior, including the question of whether there can be non-DP motive dispositions in Emmons' (1989) sense; i.e., whether some human goals can assume equal or higher places in individuals' goal hierarchies than the EMD's resulting from DP adaptations.

2. The Plasticity of Evolved Motive Dispositions

The research upon which this set of EMD's is based consists both of investigations of these systems viewed as species-typical traits as well as investigations of individual differences. Thus Gray's (1982) research is an attempt to understand the neurological and psychopharmacological aspects of the mammalian BIS, but he also explicitly relates variation in this dimension to human personality variation.

Within the latter tradition, then, the BIS (and the other EMD's men-

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[3] Efficacy and striving for competence appear to meet the qualifications for EMD's, since many authors, especially White (1959) and Piaget (see Flavell 1985), have proposed that they involve essentially intrinsically rewarding affective motivation. The adaptive function of this system is presumably to provide a self-starting mechanism to motivate the child to learn about and master the environment without a need for continuous shaping via reinforcement. Competence is a dimension of the self-esteem system (Harter 1983), an affective system which seems particularly attuned to adaptive interactions with the environment: High self-esteem occurs consequent to achieving EMD's. In addition, many of the descriptors of the personality dimension of Will or Will to Achieve (Digman 1990) would appear to involve competence motivation. This dimension is independent of the other dimensions mentioned here.

tioned above) may be considered to be an individual differences dimension with both genetic and environmental sources of variance (see also below). This environmental variance implies plasticity—the idea that the observed level of a trait can be altered depending upon which environment is experienced (from the set of all normally experienced and even abnormal, extreme environments). Behavior genetic studies attempt to sample a representative range of environments normally encountered in a given society (not the effects of extreme environments), and within these studies environmental variance typically accounts for at least half of the variance for personality dimensions (see Digman 1990; Plomin and Daniels 1987 for summaries), indicating considerable plasticity in these EMD's.

As a more detailed example of plasticity in EMD's, there is evidence that the goal of close, intimate relationships (bonded attachments) is strongly influenced by environmental events which may or may not be present early in development. Attachment is an environment-expectant system in the sense that the biology of the system programs essentially for affective responses to expected environmental variation. Rapid historical alterations in the degree to which close, intimate relationships typify a society indicate the plasticity of this EMD, and the results of research on children reared without attachment objects also indicate profound effects on this system (Bowlby 1969). When there is no elaboration of this reward system, individuals tend not to be strongly attracted to the rewards of intimacy. In cultures where the pair bond is of no importance for reproduction (the vast majority of human societies prior to Western influence (MacFarlane 1986)), socialization influences are then able to de-emphasize the extent to which close, intimate attachments become an individual goal and thus become a criterion for mate choice (MacDonald 1988).

In addition, actual environmental influences on the affectional system are likely to be underestimated by behavior genetic research, since the range of environmental variation cross-culturally is likely to be much greater than within one culture. I have argued (MacDonald 1988) that normative patterns of child rearing in many human cultures have been characterized by parent-child aloofness and rejection of children, and that the magnitude of these between-society environmental differences, which are analogous to average effects of adoption in adoption studies, are not captured by behavior genetic studies performed within a given culture.

Thus the fact that the capacity for close, intimate attachment developed in the EEA (Bowlby 1969; see footnote 2) is compatible with manipulation of the attachment system in ways that could affect adaptiveness in non-EEA environments. As a result, one might say that attachment is an adaptation but, because of its plasticity, individuals can be programmed so that adaptive (and sometimes maladaptive) behavior occurs in non-EEA environments. Individuals with highly elaborated affectional reward systems and who have a sense of secure trust in their caregivers will then use a variety of means to attain these affective goals and thereby facilitate paternal investment.

Similarly, the aggression system appears to be greatly facilitated by socialization during development by the provision of aversive events, and this is also the case with other mammals (see MacDonald 1988, for a review). In non-EEA environments where aggression is a central aspect of public policy and where the resources attainable by aggression are much more crucial to reproductive success than was the case in the EEA (e.g., ancient Sparta and many intermediate-level clan societies) normative child rearing patterns have included provision of very high levels of painful, aversive stimulation during development. This programming of development to meet immediate environmental demands is the very essence of human behavioral ecology.

It should also be noted that plasticity itself must be viewed as an adaptation (e.g., West-Eberhard 1989; see also Alexander 1990), although its conceptualization requires some comment. The existence of developmental plasticity would appear to imply that the ability to program individual development in response to contingencies in the immediate environment was itself adaptive in the EEA. The model of human plasticity which has been utilized in human research is one of continuous variation (e.g., Lerner 1984; MacDonald 1985, 1989) rather than a set of discrete behaviors elicited by particular environmental cues.[4] It is thus a mechanism for the production of individual differences, another indication of the importance of individual differences in human evolution (see also below). Plasticity is, however, a double-edged sword (Bowlby 1969; Lerner 1984; MacDonald, 1985): because development is less constrained by the genome, it is open to unforeseeable environmental influences which may be maladaptive. Clearly, however, human developmental plasticity is not limitless, and there is evidence for a decline in plasticity in the adult years.

Plasticity as an adaptation is not a response to statistical regularities of the EEA, a necessary aspect of conceptualizing adaptations and evolutionary design according to Tooby and Cosmides (1990a). The optimum adaptation to statistical regularities of the environment (termed *invariances* by Tooby and Cosmides 1990a, p. 389) would be the production of phenotypic and genetic uniformity and insurance against environmental influences on individual differences. Such a characterization would appear to apply to basic cognitive and motor development, since these basic skills appear to

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[4] West-Eberhard (1989) distinguishes continuous phenotypic plasticity from bimodal or polymodal plasticity. The classic example of continuous plasticity is that of accommodating and amplifying features via correlated shifts. Thus, a mutation which shortened the front legs of a goat resulted in a large number of compensatory changes in morphological traits resulting from the fact that the animal now walked on its rear legs. West-Eberhard indicates that such compensation occurs during normal development as a response to both genetic and environmental changes. These phenotypic compensations were possible because of plasticity but clearly this is not an example of facultative traits responsive to particular environmental contingencies. Nor is the phenotype a response to recurring environmental contingencies, but rather to an unpredictable genetic mutation. The example illustrates well the idea that plasticity facilitates adaptation to uncertainty. Another class of examples illustrating the importance of plasticity in adaptation to uncertain environments comes from the literature on indeterminate body size (see Sebens 1987), where body size in many organisms can be finely tuned to environmental contingencies.

be canalized, so that only extreme deviations from expected environments can cause disruptions (McCall 1981; Scarr and McCartney 1983). However, plasticity is a means of ensuring that organisms can adapt to environmental uncertainty and lack of recurring structure within a finite range. It is thus an adaptation with a built-in potential for high cost, but clearly one whose benefits must have outweighed its costs in the EEA. The important points are that phenotypes are underdetermined by genotypes and EMD's are manipulable. Research can then determine whether these manipulations are adaptive in non-EEA environments.

Another type of plasticity, also an adaptation to environmental uncertainty, is represented by learning, and this is the case even for learning which is characterized by evolved channeling mechanisms (see Alexander 1990). Wcislo (1989) notes that learning is a mechanism which allows animals to exploit novel situations: "for populations to respond genetically is a *non*-necessity" (Wcislo 1989, p. 139, italics in text). For example, the proposition that girls may learn gender-appropriate behavior from their same-sex parent presumably implies a mechanism which directs the attention of girls to the behavior of mother rather than father (Tooby and Cosmides 1990b).

There appear to be several evolved mechanisms which channel social learning, including the warmth, power, similarity, and dominance of the model (MacDonald 1988). However, the content of what is actually learned and the behavioral output are completely underdetermined, since what is learned is limited only by the range of behaviors the mother actually engages in. The content of this type of learning and the behavior actually engaged in, then, are not responses to recurring environmental regularities in the EEA, but the result of selection for adaptation to environmental uncertainty. It is essentially a rule for the transmission of cultural variants whose nature is unspecified by the genetic program (See Boyd and Richerson 1985; Pulliam and Dunford 1980), and thus constitutes a domain-general psychological mechanism. In conjunction with EMD's, the domain-general learning device is thus able to pursue both lower and higher level goals (including EMD's) and may or may not result in adaptive behavior in non-EEA environments.

RELATIONSHIPS BETWEEN EVOLVED MOTIVE DISPOSITIONS AND BEHAVIOR

It has been argued that the elucidation of DP mechanisms is the road to greater predictability of behavior. Cosmides and Tooby (1987; see also Symons, in press) state that "in the lifetime of any particular animal, it is the proximate mechanisms that actually cause behavior—not natural selection. If these proximate mechanisms can be understood, behavior can be predicted more exactly; understanding the fitness-promoting strategies studied by evolutionary theorists allows only approximate prediction. Behavior correlates exactly with proximate mechanisms, but only approximately with the fitness-promoting strategies that shaped those mechanisms'' (pp. 282–283). The point of the following is to show that relationships between DP and behavior are actually quite complex and that DP must be supplemented by studies of fitness-promoting strategies in all human societies.

1. The Limitations of DP as an Exclusive Method of Evolutionary Analysis

Symons (1989, 1990) has proposed that the only interesting, significant, or indeed, meaningful question raised by the application of Darwinism to human affairs is ''whether differential reproductive success historically influenced the form of the phenotypic feature'' (1989, p. 137). This is so if we are really studying adaptations, since adaptations are by definition the result of natural selection for particular mechanisms which increase fitness in some EEA. ''The measurement of reproductive differentials contributes to the analysis of adaptation only insofar as such measurement sheds light on phenotypic design'' (pp. 137–138).

Specific instances where investigators have measured differential reproductive success in human societies based on resource control, polygyny, polyandry, etc. (termed Darwinian Social Science (DSS)) are thereby excluded from the realm of appropriate endeavors because there is little reason to suppose that there is some psychological mechanism which resulted in, e.g., polyandry, as a result of natural selection (i.e., evolution acting on heritable variation).

Implicit in this view is an emphasis on the reconstruction of Pleistocene adaptations as the key issue in applying evolutionary biology to humans (see also Cosmides and Tooby 1989; Tooby and Cosmides 1989). Human adaptations evolved during this period, so that individual differences in RS which occur after this time must be the result of these adaptations interacting with more recent environments. As a result, individual differences in RS in contemporary societies may or may not be related to some Pleistocene adaptation. DSS is thus nonpredictive, and even if the hypothesis is confirmed, ''such data are unlikely to serve as the foundation of a robust, evolution-minded science of human affairs because such data do not illuminate phenotypic design'' (Symons 1989, p. 140).

Several writers have noted that studies of RS often illuminate psychological design (Alexander 1990; Betzig 1989; Irons 1990; Turke 1990). The following argues in addition that the study of reproductive competition is important in its own right independent of the psychological mechanisms involved. The defenders of DP as an exclusive method of evolutionary analysis implicitly adopt a deterministic model in which human reproductive behavior is a determined outcome of DP psychological processes (viewed as species-typical traits) combined with some unspecified contextual features of the environment. Within this perspective, it is relatively unimportant to focus on reproductive success as a dependent variable because the evolutionary events of interest occurred during the Pleistocene. Information on reproductive success in more recent environments is mildly interesting in much the same way in which current eating habits shed information on the structure of Pleistocene adaptations: behavior in the present environment is a deterministic outcome of these Pleistocene adaptations in the context of modern environments in which food is readily available and can be engineered to appeal to any appetite. It is these Pleistocene-derived appetites that are the main focus of an evolutionary approach, however, not whether people's appetites are associated with RS in contemporary societies. The result would then be a deterministic sociobiology where one can begin with DP and predict behavior in different contexts and even at higher levels of analysis, what Barkow (1990) refers to as "vertical integration," and including such phenomena as social controls and even ideological structures.

The contrary position is that 1) the regulation of reproduction varies between human societies; 2) this variation is associated with massive differences in social structure (e.g., family structure, demography, the status of women, and the socialization of children); and 3) the social regulation of reproductive behavior is underdetermined by any known ecological theory either alone or in combination with proposed Darwinian psychological adaptations. Minimally, the implication is that until a deterministic evolutionary theory of social processes is provided, the measurement of the regulation of individual differences in RS is important for the evolutionary analysis of culture.

The most notable deficiency in the deterministic theory is the lack of ability to explain the enormous variation in the regulation of reproduction seen among stratified societies. This variation is important, since it is associated with differences in demographic patterns, marriage practices, rearing of children, and the status of women (MacFarlane 1986). Explanations of this variation in terms of DP are vacuous without specifying contextual variables which differentiate societies with very different reproductive patterns and showing how the contextual variations are explainable from a knowledge of DP, perhaps in conjunction with some set of external ecological variables.

A theory of these phenomena which is consistent with evolutionary theory (but not determined by it) is that social controls and ideological structures regulate reproductive behavior and do so in a manner which is underdetermined by external ecological factors in combination with a knowledge of DP psychological adaptations (MacDonald 1988, 1990, 1991). Briefly, evolutionary theory is highly compatible with the idea that the regulation of reproduction is an extremely important human interest and that individuals in a stratified society have conflicts of interest over the regulation of reproductive behavior depending especially on their control of resources. However, evolutionary theory (in combination with any known ecological variables and/or any set of universal DP psychological mechanisms) fails to predict the outcome of this conflict. Social controls supporting mating arrangements along a continuum ranging from egalitarian to despotic are in the interests of many individual members of human societies, so that their imposition on others is always a possibility. There is thus no biological reason to suppose that one or the other will be characteristic of a given society.

Since DP psychological adaptations related to mating behavior are typically viewed as species-wide central tendencies of behavior (e.g., Tooby and Cosmides 1990b), a knowledge of DP is insufficient for predicting the nature of these social controls. Social controls regulating mating behavior are the outcome of political processes, and DP does not dictate a unique result for these outcomes, any more than a knowledge of DP could predict the outcome of the Russian revolution: If the Tsar had won, no evolutionary laws would have been broken. Nonetheless, the actual result was that a relatively egalitarian society was created.

Moreover, just as one might wish to measure the success of a socialist revolution by measuring disparities in control of resources before and after the revolution, one would want to measure relative differences in RS depending on control of resources in reproductively egalitarian versus anti-egalitarian societies, and this would be so whether or not we knew anything (or everything) about DP. Such data would be essential to the very important scientific hypothesis that indeed it was the suppression of reproductive competition in some stratified societies which resulted in certain characteristic demographic profiles, family structures, etc. DP is thus essentially irrelevant to the question of how this conflict of interest over reproductive behavior is resolved.

Another way to view this is that social controls are often quite insensitive to genotypic or phenotypic characteristics of the individuals to whom they apply and cannot be analyzed reductionistically (i.e., as a genetic characteristic of individuals): Thus, even though there is every reason to suppose that males retain polygynous tendencies as a result of DP (D. Buss 1989; Symons 1989), they may be effectively prevented from being polygynous (MacDonald 1990). Knowledge of DP is not able to predict this result.

The position that a knowledge of DP is the only important goal of an evolutionary analysis is thus actually forced to presuppose a very powerful, deterministic theory—one which at present we do not possess. In the absence of such a theory, it is more an act of faith than a scientific proposal. As mentioned above, the minimum implication is that until a deterministic evolutionary theory of social processes is provided, the measurement of the regulation of individual differences in RS is important for the evolutionary analysis of culture. Moreover, the usefulness of understanding these regulatory processes in providing explanations for structural variation between societies is independent of knowledge of DP psychological mechanisms.

The foregoing proposes an explanation which is consistent with evolutionary theory but not determined by it, and I would suggest that not uncommonly evolutionary/ecological explanations are of this type. For example, there are two commonly accepted mechanisms for sexual selection which are compatible with evolutionary theory, female choice and intrasexual competition (Trivers 1986). Nevertheless, there is no deterministic theory which can predict which of these phenomena will occur in particular species, or, indeed, whether sexual selection will occur at all (Endler and McLellan 1988). Similarly, any number of mating arrangements in stratified societies ranging from egalitarian to anti-egalitarian are consistent with evolutionary theory as well as the existence of a universal set of EMD's, but none are predictable from these considerations. One could suppose that theory is simply not sufficiently developed at this point, but at present we must live with a theoretical structure that is fundamentally nondeterministic.

2. Can There Be Non-DP Motive Dispositions?

Lack of predictability of behavior from DP would also occur if the highest level human goals (motive dispositions in Emmons' (1989) sense) were not restricted to those which were EMD's. If such non-DP motive dispositions can exist, then they can compete with and even supersede DP motive dispositions and be an important source of human plasticity.

There is reason to suppose the existence of such non-DP motive dispositions and that they can successfully compete with EMD's. Richerson and Boyd (1989) have argued that personal ideologies and any associated behavior can depart radically from that predicted by an optimality model. Moreover, personal ideologies appear to be important for the social imposition of monogamy (MacDonald 1983; 1988; 1990) and may therefore influence whether one behaves in conformity with DP proclivities. Although there is a large main effect such that personal ideologies often serve evolutionary goals (i.e., are used in the service of DP affective goals), personal ideologies are irreducible to DP psychological traits of individuals, are underdetermined by biological theory, and interact with but are independent from social controls on individual behavior. Thus individual males and even entire cultures have adopted ideologies of male sexual restraint despite the apparent existence of DP adaptations toward male sexual promiscuity and despite the fact that such behavior is not optimal for wealthy males.[5]

These results suggest that ideologies can act as motive dispositions; i.e., that they can become goals on a par with EMD's resulting from human adaptations and in potential conflict with them. As a result, individuals may pursue a variety of lower level goals (e.g., attending church, refraining from sex during Lent, etc.) in order to obtain psychological rewards related, for example, to the belief that these behaviors are efficacious in achieving religious salvation, despite the fact that they may in fact be contrary to individual fitness. These ideological goals often occur in conjunction with social controls regulating reproductive behavior and often appear to result in an internal source of motivation in conformity with externally imposed social controls.

[5] Moskowitz (1978) also points out the role of religious ideology in influencing which foods are actually eaten, quite independent of DP adaptations affecting their hedonic quality.

Interestingly, one means by which ideologies appear to be effective in influencing behavior is by inculcating a sense of personal threat in the person. The BIS has been described above as a system which can be activated by a wide range of domain-general cognitive processes which result in a perceived feeling of personal danger. Western religious ideology, which has attempted to control sexual behavior in ways that result in non-fitness maximizing behavior for wealthy males (MacDonald 1990), has always emphasized not only the positive attraction of religious devotion, but also the negative consequences to those who violate religious standards of appropriate behavior (e.g., going to Hell). Stone (1977) states the fear of God was a potent force for sexual restraint in 17th-century England. The commonness with which a wide variety of religious ideologies (e.g., witchcraft and voodoo in many African societies (Levine and Levine 1966)) attempt to control behavior by invoking a sense of personal danger by the violation of ideological strictures is a testament to the domain-general nature of the BIS as a DP psychological adaptation.

3. Conflicts Among Evolved Motive Dispositions

There may be conflict among EMD's so that behavior in any given situation is difficult to predict. For example, an individual male may well have a conflict between the EMD of intimacy and the EMD of sexual variety. A man's pursuit of the DP goal of sexual variety may be perceived as endangering his DP goal of intimacy, since his spouse may view the situation as a threat to continued investment and terminate the relationship. Or the man may believe that the pursuit of sexual variety is personally threatening because of the possibility of contracting a fatal sexually transmitted disease or the possibility of enraging another man, or incurring the wrath of the authorities, etc. In such a situation the DP goal of self-preservation (i.e., the BIS) is triggered and conflicts with other DP motivational systems.

The prediction of behavior in such cases depends on the relative strength of the EMD's, and this in turn depends at least in part on the developmental history of the individual. We have already argued for the importance of environmental influences and developmental plasticity in affecting adaptive developmental outcomes. Such a perspective implies a robust role for individual differences in an evolutionary view of development, and the following attempts to provide an outline of an evolutionary perspective on individual differences, including genetic variation.

AN EVOLUTIONARY PERSPECTIVE ON INDIVIDUAL DIFFERENCES

1. Toward An Evolutionary Theory of Intraspecific Diversity

Finally, a strong link between behavior and a universal set of DP mechanisms is unlikely because of the importance of genetically influenced individual differences in virtually all of the behaviors of interest to psychologists. In their attempt to develop a theoretical approach based exclusively on DP, Cosmides and Tooby (1987; see also Tooby and Cosmides 1990a, b) concentrate on species-wide invariance in psychological adaptations, including personality. This approach ignores the importance of individual differences in psychological mechanisms and the role of genetic variation as an adaptive process which produces these individual differences.

The range of individual differences is truly enormous. Plomin, DeFries, and Fulker (1988) find that even after eliminating the highest and lowest individuals per 1000, the range ratio for adult memory span is 2.5:1; for Wechsler IQ, 2.9:1; for the Child Behavior Checklist, a clinical diagnostic inventory measuring a wide range of social behaviors including aggression, anxieties, and phobias, 34:1. Of direct relevance to the discussion of EMD's described above is the finding of a high degree of within-sex variation in sensation seeking (Zuckerman 1979) and attraction to affection (Cloninger 1987). We have also commented on the enormous range of individual variation in the affectional systems seen cross-culturally, a range which I would suggest stretches from normative sociopathy in many cultures at the intermediate level of economic production (see, e.g., Levine and Levine 1966) to normative family relations based on affection in modern industrial societies and in many foraging societies (see MacDonald 1988, for a review). Also noteworthy is that the rate of twinning, theoretically associated with low investment parenting practices (Rushton 1988), ranges from 57/1000 in parts of Nigeria to 2/1000 in Oriental populations (Bulmer 1980).

Evolutionary theory is clearly a theory which is most easily related to the central tendencies of behavior, such as the centrality of self-interest in moral reasoning, and the ways by which these central tendencies of behavior differ depending on age and sex. Nevertheless, genetically influenced individual differences are real, they are evolutionarily meaningful (see below), and they constitute another reason why the link between DP and behavior will be tenuous in a great many domains of behavior.

Thus the DP prediction that males will tend to be sensation seekers and risk-takers is a prediction about average sex differences and is certainly not disconfirmed by the existence of many men who are quite cautious and by some women who are risk-takers. Although directional selection is undoubtedly important in producing this sex difference, there is a very large overlap between the sexes and considerable genetic variation. As conceptualized here, the mechanism for producing sex differences clearly does not function as a switch which can activate two entirely different morphs, but rather creates a broad range of genetically influenced individual variation which, on average, conforms to evolutionary predictions.[6]

[6] Recently Gangestad and Simpson (1990) have argued for a bimodal, frequency-dependent conceptualization of female sexual behavior. If this proves to be the case it would provide further evidence for the adaptive significance of genetic variation in personality.

In attempting to assess the role of individual differences in evolutionary theory, one might note that fundamental evolutionary theory implies that organisms will be obsessed with genetic variation and its expression in a wide array of phenotypic traits. The entire modern theory of evolution implies that organisms will develop adaptations which allow them to determine commonality of genetic self-interest. The appraisal of genetic differences between organisms and consequent self-interested behavior on the basis of phenotypic variation is thus the basis of individual adaptiveness and the evolution of the kin group as a unit of selection (see L. W. Buss, 1987). It is difficult to understand why, for example, phenotypic similarity for IQ and a host of other highly heritable characteristics would be criteria for assortative mating (see Thiessen and Gregg 1980) if the only function of genetic variation is to protect against pathogens or is random noise. Why should organisms be interested in this variation at all and why should they, oftentimes, attempt to maximize the representation of their own genetic variants in subsequent generations? If keeping genetic variation in the population per se were the only goal, as would be the case if, e.g., pathogen protection were the only criterion, why not always adopt the rule that one should benefit uncommon genotypes (including individuals with mildly deleterious genetic disorders which lower individual resource competitive ability) so that maximum diversity is maintained?

On the contrary, the most parsimonious view of the behavior of many individuals, such as intensively polygynous males in many traditional stratified societies, is that they are behaving in a manner which is most likely to restrict the genetic variance in the population (i.e., sire a disproportionate share of the offspring; e.g., Dickemann 1979). Phenotypic variation must be seen as containing cues such that individuals possessing genetic variants can engage in self-interested behavior toward others. On the other hand, if genetic variation represents merely random noise and/or pathogen protectors, it is difficult to understand the development of this elaborate machinery.

Behavior and personality thus evolve in part in order to respond to and manipulate genetic diversity. As Buss (1991) notes, personality is an adaptive landscape in which "perceiving, attending to, and acting upon differences in others is crucial for solving problems of survival and reproduction" (p. 471). Therefore, genetic diversity itself cannot entirely be random noise. In support of this idea, Buss (1991) notes that the vast majority of personality trait terms are evaluative, indicating a person's potential value as a resource to others. Indeed, if kin selection theory (Hamilton 1964) and genetic similarity theory (Rushton 1989a) are correct, genetic variation is always a potential resource for individuals. If genetic commonality were of overriding importance in human affairs there would be no need to develop this vast array of discriminitive mechanisms and no rationale whatever for the existence of phenotypic variation.

However, it is precisely because the organism must assume that there is genetic variation related to fitness differences and that fitness is important—precisely because competition among genetic variants has always existed and is indeed the driving force of all of evolution—that the study of genetically based individual differences (and fitness differences associated with them) must be of prime importance. Quite simply, whatever the adaptive reason for significant levels of genetic variation, this variation constitutes the playing field upon which the evolutionary game is played and it's the only game in town; the battle over the structure of the rest of the genome has already been won. And, as indicated above, the playing field which remains, i.e., the range of genetic variation in the population, remains quite large.

This basic logic does not imply that all of the genetic variation in a trait must be associated with fitness differences or must be the result of processes which are nonrandom with respect to phenotypic variation in the trait. It is thus logically compatible with the hypothesis that at least some of the genetic variation in, e.g., personality, is the result of random processes or selection for pathogen protection. It does, however, imply that organisms should always behave *as if* the variation may reflect fitness differences; i.e., it implies that organisms should evolve mechanisms for detecting when particular examples of genetic diversity (and, indeed, phenotypic diversity) can contribute to individual fitness. If they never did, there would be no point in developing these mechanisms and the entire superstructure of modern evolutionary theory would fall.

I suggest that two basic types of mechanisms have evolved for discriminating and behaving on the basis of genetic and phenotypic diversity. The first is encompassed by kin selection theory (Hamilton 1964) and, more broadly, genetic similarity theory (Rushton 1989a, b). Cost/benefit decisions related to interactions with others are expected to be weighted by the degree of genetic relatedness, and, in the case of nonrelatives, should be weighted on the basis of phenotypic similarity in highly heritable traits. (One of the benefits of assortative mating on the basis of kinship is that genetic variants which are not expressed as observable phenotypic variation or are not valued as resources are pulled along anyway.) This class of behaviors thus ranges from directly aiding close biological relatives, to reciprocity and attempts at exploitation in cases where the commonality of genetic interest does not influence the decision.

Considerations of genetic similarity will always be an available strategy for fitness maximization but in many cases it must be balanced with a second class of strategies. Individuals are also expected to develop mechanisms to discriminate and take advantage of others' phenotypic and genetic characteristics independent of the extent to which individuals share genes. A prime example of this would be female mate choice, proposed originally by Darwin as a mechanism of sexual selection. (See Trivers (1986) and Kirkpatrick (1987) for examples from the animal literature.) Thus it might be in a woman's interest to marry a wealthy man even if she were completely dissimilar from him genetically and phenotypically. Moreover, this is the case even if being a millionaire was not heritable: Thus in many stratified human societies economic resources were typically inherited independent of the phenotypic (apart from birth order) and genetic characteristics of the child (e.g., through primogeniture). In arranging marriages it was the phenotype of being a wealthy heir which determined an individual's value on the marriage market, and this was assessed independent of his genetic characteristics. Younger sons, for example, who could not be expected to be heirs, had little opportunity on the marriage market throughout European history—certainly much less than that predictable on the basis of genes shared with the heir (see, e.g., Duby 1978; Hollingsworth 1965).

People thus appear sensitive to the phenotypic resource value of others, independent of genetic variation. As further examples, Mackey (1980) finds that there is a tendency for males to divorce their wives and marry women who are younger than the first wife. Also many clinicians have noted that people attempt to prevent their spouses from increasing their resource value on the marriage market by, e.g., exercising or losing weight.

Besides assessing the phenotypic resource value of others, others' genetic characteristics may be a criterion of assortment. Thus if a woman were not interested in paternal economic or psychological investment, it would be in her interests to ensure that the biological father possessed advantageous, highly heritable traits, especially if she were phenotypically (and genetically) like him on other traits. As Trivers (1986) notes, where the male invests little beyond his sex cells, the female has only to decide which male offers the ideal genetic material for her offspring. She would behave in the same manner as a horse breeder who attempts to find the best stallion for his mares: he bases his judgment not on the phenotypic similarity or genetic relatedness of his mare to the stallion, but on the racing record and breeding value of the stallion.

As an indication that humans are sensitive to genetic variation independent of genetic similarity, Draper (1990) finds that !Kung women have responded to the novel environment of stable, plentiful provisions and social stratification by having children with Bantu men who have higher social status than !Kung men. Despite the complete lack of paternal investment by the Bantu fathers, these babies have increased survivorship compared to the full !Kung babies. The !Kung mothers appear to be choosing males solely because of their phenotypic traits (and the genes which affect the expression of the traits), not because the males will invest in their offspring. It is presumably also for this reason that prospective sperm donors are carefully screened for their intelligence and other heritable traits, and suggests that a sperm bank where the sperm is contributed by eminent men would be very attractive to women who are not interested in paternal investment.

In addition, as Jensen (1989) notes, there could be trade-offs among genetic similarity and the resource value of phenotypic and genetic diversity such that different partners in assortative and non-assortative mating evaluate different traits differently. For example, Trivers (1986) reviews examples in which parental investment is essentially traded for genes influencing physical attractiveness among animals. In this vein, it is noteworthy that many highly heritable anthropomorphic characteristics are much less associated with friendship assortment than are education and attitudes (Rushton 1989b). The suggestion is that the latter are more valued as resources in human friendship interactions than the former. Moreover, the history of marriage in the European Middle Ages indicates the complicated trade-offs in the marriage market between social status, biological relatedness, and control of economic resources (see, e.g., Duby 1978). The prime resource was social status, so that heiresses could expect to be able to marry a non-inheriting younger son of a higher ranking noble, and the daughters of the upper nobility were welcomed as wives by the lower nobility. The marriage alliances would then create political ties between the families which were facilitated by the newly created ties of biological relatedness between the families. In fact, the importance of social status as a resource resulted in a gradual deemphasis on assortative mating based on close kinship ties. Whereas early in the Middle Ages, the ideal marriage partner would come from a closely related branch of the extended family, the nobility gradually cut the ties between themselves and their kinsmen in favor of class endogamy with other members of the nobility (see Verdery 1988). When extended kinship ties were no longer needed to maintain social status, the best strategy for mating for the nobility was to create biological and political ties with other aristocratic families.

This strategy was the antithesis of maximizing genetic commonality between mates. Rather, it was a strategy which aimed at maximizing the resource of social status while at the same time taking advantage of the newly created biological ties. In the long run it was undoubtedly a much better strategy for maintaining genetic control over the ultimate resource, i.e., social status, than pursuing the old practice of endogamous marriages among closely related kin. Like the shift in !Kung reproductive practices mentioned above, the change to this practice was too rapid to be due to natural selection but would appear to be the result of domain-general cognitive processes aimed at maximizing the newly created resource of social status in a society with a stable aristocracy where extended family kinship ties were relatively unimportant. Since there appears to have been a positive correlation between social status and RS in Europe at least until the modern period (Hanawalt 1986; Herlihy and Klapische-Zuber 1985; Hollingsorth 1965), the nobility also increased their RS by maximizing social status.

The general point is that human genetic and phenotypic diversity constitutes a resource environment for individuals. The fundamental rule is not necessarily to match one's genes with others in order to facilitate altruism (as proposed by kin selection theory and genetic similarity theory), but to maximize RS (or more precisely, to attain one's EMD's in the present sense of that term). Minimally, one must assume that DP adaptations will be highly sensitive to the resource environment represented by individual diversity and mechanisms will evolve in order to take advantage of this diversity. However, in the context of this discussion, it is also reasonable to suppose that domain-general cognitive devices are able to respond to this diversity in order to facilitate the attainment of EMD's (as well as non-DP motive dispositions; see above), by for example, scheming to attain resources related to social status. It is an empirical question whether the results are adaptive in any particular context, but clearly there are various ways of attaining these motive dispositions by exploiting this diversity.

The general theory for understanding the methods by which individuals interact with the phenotypic and genotypic resource environment represented by human diversity may be termed "intraspecific diversity theory"; i.e., the theory of the manipulation of within-species diversity as a resource environment. The methods individuals use to manipulate this diversity range from assortment and discrimination on the basis of phenotypic similarity and genes identical by common descent to methods which evaluate this diversity solely in terms of resource potential to the individual without consideration of possible genetic or even phenotypic commonality. To the extent that these relationships are entered into voluntarily, the fundamental principle of all of these methods of dealing with diversity is reciprocity. While much research needs to be performed on the methods involved, the theoretical considerations and empirical support provided here are sufficient to warrant the inclusion of these methods as supporting the general importance of individual differences in an evolutionary view of human affairs.

Moreover, these historical and anthropological examples provide support for the ideas that 1) the importance of human assortment based on commonality of genes can be swamped by the importance of a variety of other resources, including especially, social status and economic resources; 2) human strategies for coping with intraspecific diversity are not rigidly programmed genetically but are able to rapidly adapt to new resource opportunities, presumably via domain-general cognitive processes as a necessary condition.

2. Evolved Mechanisms for Human Diversity

There are several reasons for supposing that genetic and phenotypic variation for a variety of traits (and associated phenotypic cues) would itself be an important outcome of natural selection beyond; for example, natural selection for genetic variation important for pathogen protection (see also Gangestad and Simpson 1990). The impressive level of plasticity among humans, discussed above, implies mechanisms for producing individual phenotypic variation both within and between societies. Moreover, the evidence cited there indicates that societies are able to adaptively program individual development. The resulting individual differences are the very essence of human behavioral ecology, and indeed, without such a conceptualization one is forced to suppose that there are at best only a very few human ecological niches which evolved in the EEA, perhaps restricted to categories such as sex or age.

The conclusion of this line of reasoning is that phenotypic variation itself is unlikely to be the result of merely random genetic variation or genetic variation related exclusively to very broad evolutionary functions such as pathogen protection. In other words, the fact that there is plasticity in, for example, human personality, strongly suggests that individual variation is functional and clearly the function cannot be the purely genetic function of protecting against pathogens (since the variation is merely phenotypic). Moreover, this phenotypic variation allowed by plasticity has evolved within the context of genetic variation for personality. Genetic variation and phenotypic plasticity are thus likely to be two aspects of the solution to the same evolutionary problem: the difficulty of dealing with uncertain, complex environments. Wcislo (1989) notes the close connection between plasticity and adaptation to environmental heterogeneity: "Behavioral adaptability is important in evolution because the activity of individuals has the potential to diminish or exacerbate the influence of external environmental heterogeneity" (p. 159).

Thus, 1) there appears to be a mechanism (plasticity) which promotes the production of individual differences within a delimited reaction range; 2) this mechanism evolved in the context of genetic variation which also influences individual differences. These considerations make it plausible to suppose that genetic variation influencing phenotypic variation in personality is not merely random, and that it has other functions, perhaps in addition to protecting against pathogens.

The question of the adaptive significance of genetic variation and the related question of the evolution of sex continue to stir debate and a wide range of theoretical treatments has appeared (e.g., Burger, Wagner, and Stettinger 1989; Buss 1987; Endler 1986; Hamilton 1980; Lande 1977, 1980; Tooby, 1983). In this vein, it is noteworthy that there is continuing interest in the hypothesis that one reason genetic variation may be adaptive is because it allows organisms to adapt to a wider range of micro-niches and environmental variation. Traits under selection in fluctuating (i.e., uncertain) environments show relatively high heritabilities (Burger et al. 1989), and Williams (1975) has provided evidence that some organisms facing uncertain environments and resource scarcity resort to sexual reproduction, a mechanism which maximizes variability.

It is thus quite possible that genetic variation in personality and its correlated phenotypic variation, as well as the phenotypic variation resulting from plasticity, serve to enable humans to produce a wide range of variation in response to immediate environmental contingencies (within a delimited range) and thereby occupy a wide range of possible niches in the human and nonhuman environment. Futuyma and Moreno (1988) provide examples from a variety of animals in which intraspecific genetic variation is associated with variation in habitat preference, and Hedrick (1986) reviews evidence indicating that genetic variation is linked with environmental heterogeneity.

These findings do not imply that all genetic variation is linked with adaptive function or that coping with environmental uncertainty and maximizing the fit between organism and environment are the reasons for the evolution of sex. As a minimally sufficient argument, it merely suggests that, given that genetic variation exists, organisms are able to utilize this variation in adaptive ways. These mechanisms may be unrelated to the original function of the mechanisms which evolved to preserve or enhance genetic variation.

As indicated above, the existence of human phenotypic plasticity is highly compatible with the environmental complexity/uncertainty hypothesis. Indeed, it is quite likely that the existence of very high levels of plasticity would impose an enormous cost on organisms which were unable to utilize this plasticity in an adaptive manner; i.e., by programming development in an adaptive manner. The same may be said for domain-general cognitive adaptations which can be used in pursuit of EMD's. Both of these classes of mechanism appear to function as adaptations for optimum adaptation to life in complex, fluctuating, uncertain, multi-niche environments, and it is quite reasonable to suppose genetic variation for behaviors related to personality serves the same function. The best bet for humans may have been to hedge one's bets and to evolve 1) mechanisms for retaining a wide range of genetic variation, 2) plasticity which enables a very close tracking of immediate environmental contingencies by modifying genetic predispositions within limits, 3) domain-general cognitive devices which are able to take cognizance of and respond adaptively to a wide range of environmental contingencies while generally being in the service of EMD's. In short, genetic variation and individual differences must be seen within a wider context of human adaptation—a context which includes plasticity and domain-general cognitive processes.

3. Personality and Individual Differences

In the area of human personality we have already noted evidence for substantial heritability of personality, and there are several evolutionary and genetic reasons which are compatible with the idea that there is considerable additive and non-additive genetic variance for personality related to adaptive function (See also Buss 1991).

(1) It is conceptually plausible to suppose that optimizing selection for personality occurred, since extremely high or extremely low individuals would appear to be at a disadvantage but with the result that there is a broad range of genetic variation in the middle of the distribution (see Travis 1989). Extreme sensation seeking, for example, would tend to result in dangerous risk-taking and impulsivity, while individuals who are extremely low on these appetitive traits would lack motivation to pursue goals related to the ac-

cumulation of sexual and personal resources. Extremes in either direction would appear to be maladaptive so that there is good reason to suppose that there has not been selection for an "ideal" personality type.

On the other hand, the wide diversity of intermediate individuals resulting both from genetic variation and developmental plasticity would be able to occupy different social roles and have differing balances between caution and impulsivity. Optimizing selection is theoretically expected to be associated with higher levels of additive genetic variance than directionally selected traits (e.g., B. Charlesworth 1987; Travis 1989). For example, Charlesworth notes a heritability of 0.40 for clutch size in birds, a trait which is quite possibly under stabilizing selection.

(2) One of the consistent findings from personality research is that there tend to be low phenotypic and genetic correlations among first-degree biological relatives (Plomin and Daniels 1987). As an explanation of this finding, Lykken (1982, 1987) has proposed that genetic influences on personality be conceptualized as resulting in what he terms "emergenesis." Personality is emergent in the sense that it results from interactions between a relatively low number of genes, with the result that while there is substantial resemblance among monozygotic (MZ) twins for an emergent trait, the scores of dizygotic (DZ) twins are uncorrelated. Such a conceptualization is highly compatible with the idea that there is no "ideal" personality type, but rather that the genetic mechanisms underlying personality are designed to produce high levels of variation, presumably within some boundaries. Recently Tellegen, Lykken, Bouchard, Wilcox, Segal, and Rich (1988) found evidence for a significant non-additive genetic influence compatible with an emergenic model on several personality traits (Positive Emotionality, Control, and Social Potency). These traits appear to be related to extraversion, sensation seeking, and impulsivity which appear in many personality scales and are proposed as a set of EMD's here. For example, Tellegen's higher order factor of Positive Emotionality is strongly related ($r = 0.79$ for females; $r = 0.76$ for males) to Eysenck's extraversion (Tellegen 1982).

(3) Genetic variance and significant heritability are common for many behavioral, morphological, and physiological traits in populations of animals, including components of fitness (e.g., Istock 1983). Even in traits under directional selection, significant additive genetic variance is expected if there are negative correlations among components of fitness (B. Charlesworth 1987) or frequency dependent selection (see Gangestad and Simpson, 1990). Negative correlations among the biological systems underlying personality may well occur, since more than one biological system may influence phenotypic personality dimensions (MacDonald 1988). Thus the phenotypic trait of introversion-extraversion may be a complex outcome of genetic systems underlying sensation seeking/impulsivity as well as the BIS and, quite possibly, emotionality. Certainly at a conceptual level it is reasonable to suppose that genes which promote sensation seeking/impulsivity would also be negatively correlated with behavioral inhibition, since these systems function

as a sort of "stop-go" system. Indeed, the low familial correlations for personality measures mentioned above, as well as low correlations for personality between friends (Rushton 1989b) are consistent with the theory that phenotypic measures of personality are influenced by more than one genetic system which has been under natural selection (McGue 1990; see also Humphreys 1970).

(4) Humans engage in positive assortative mating for a wide range of traits (see, e.g., Rushton 1989a). Assortative mating is presumably a mechanism by which individuals attempt to maximize genetic representation in the next generation while still avoiding the costs of inbreeding (Thiessen and Gregg 1980). The result of this tendency is to maintain high levels of genetic variation in the population. Here genetic variation in the population is maintained as a result of individually adaptive processes related to the resource value of specific traits for others (Rushton 1989a, b). The mechanism implies cue detection mechanisms which are geared to phenotypic variation, not to random genetic noise or variation in pathogen protectors.

Interestingly, the value of these traits as resources to be acted on results from the existence of genetic diversity in the trait: if there was genetic uniformity, there would be no evolutionary rationale to engage in assortative mating for the trait. However, the consequent adaptive behavior itself results in genetic diversity. In such a situation it is not the case that the trait variation is the result of random noise or the secondary result of, e.g., pathogen protection.[7]

(5) It is theoretically plausible to suppose that socially imposed monogamy results in an increase in genetic variance in stratified societies compared to societies in which individual males are allowed to maximize their access to fertile females based on control of resources or political power. On the assumption that wealthy males are not a random sample of their gene pool, large disparities among males in control of sexual resources and consequent enforced bachelorhood for many males would result in a restriction of genetic variation compared to a society with enforced monogamy. In this case, therefore, societal-level processes involving social controls and ideology (see MacDonald 1983; 1990) could have effects on genetic variance in the population.

4. Conclusion

The consequence of all of this is that the search for DP mechanisms conceptualized exclusively as essentially species-wide, genetically invariant traits is likely to be only a part of the picture. It follows also that the attempt

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[7] Nevertheless, without further argument there is no reason to suppose that the variation produced by assortative mating, while the product of an adaptive process, is itself adaptive. It is thus different from the examples in the preceding discussion. There it was suggested that variation itself was adaptive (emergenesis) or that the structure of personality as an adaptation resulted in genetic variation (stabilizing selection, negative correlations between components of fitness).

to develop a powerful predictive science based on these genetically invariant mechanisms, with no consideration of either environmental or genetic sources of variation in these mechanisms simply ignores the great mass of empirical data on personality. Moreover, even if one supposes that all of the variation in human personality is essentially random variation, at the very least the extent of empirically found variation indicates that there will be a very large error term in this type of research.

Besides the issue of genetic and environmental influences on individual differences, another major source of individual differences in behavior related to EMD's results from variation in the myriad lower level cognitive processes related to the higher level motive dispositions in Emmons' model. For example, different individuals have available different information on which to base a decision: a decision regarding the pursuit of sexual variety (presumably a DP tendency for males) may be quite different depending on knowledge of sexually transmitted diseases. Moreover, the large individual differences in IQ mentioned above are compatible with enormous variation in the ability to pursue both lower and upper level goals because of these individual differences.

DISCUSSION

Clearly the above discussion of motivational systems is compatible with the finding that mechanisms which evolved to maximize RS in ancestral environments often function to maximize RS in contexts far removed from the EEA. Evolved motivational systems in males involving attraction to sexual variety and an interest in paternity certainty combined with domain-general cognitive mechanisms would be sufficient to explain the difference in mating practices between societies characterized by ecologically imposed monogamy (typical of many foraging societies) to resource polygyny in the great majority of human societies with higher levels of economic production (presumably an adaptive response in the sense of Betzig 1989). Domain-general mechanisms in pursuit of this EMD could facilitate a wide range of cost/benefit decisions pertaining not only to control of females but to other resources as well. Thus a man haggling over the cost of bridewealth may use the same domain-general cognitive mechanisms in order to calculate how much money he can afford in dowry payments for his daughters, negotiate for the ownership of land, or for the purchase of a trivial item for a friend.

The generalizability of human adaptations to new environments is supported by evidence that in fact humans tend overwhelmingly to behave adaptively in environments far removed from the EEA (see Irons 1990; Turke 1990). Moreover, very rapid changes in adaptive response can occur. The example of the change in !Kung mating practices described above is relevant, since Draper (1990) finds that !Kung women have responded to the novel environment of stable, plentiful provisions and social stratification by having children with Bantu men who have higher social status than !Kung men. These women are able to rapidly shift from a mating style where high paternal investment was required to one where there is no need for paternal investment. They also appear sensitive to the economic shift in the changed value of females in a stratified social system. Similarly Voland, Siegelkow, and Engel (1991) found that during the 18th and 19th centuries German families at the top of the social hierarchy appeared to invest more highly in daughters than sons despite the evolutionary expectation that such families would prefer to invest in sons. The authors note, however, that such a strategy conforms to a cost/benefit model because in fact the opportunities for males to reproduce in this particular historical context were very limited.

Indeed, the very commonness of apparent fitness maximizing behavior in a wide range of human societies is testimony to the difficulty of developing contexts in which fitness maximizing does not occur. The DP mechanisms discussed here, with the exception of the affectional systems, appear to be phylogenetically ancient, since they appear to be homologous to systems which occur among reptiles (MacLean 1990). They are thus adapted, perhaps with some modifications, to a very wide range of environments over a very long period of evolutionary time. It is thus not surprising that socially imposed monogamy has often (and perhaps most successfully) been accompanied by high levels of social controls on sexual behavior and by the intensive inculcation of an ideology of sexual restraint, conjugal affection as the basis of marriage, and monogamy as a moral and religious ideal.

The above account is also highly compatible with the possibility that some non-EEA environments will result in situations where fitness maximization does not occur. The aim of research must be to find (a) to what extent does fitness maximization occur in particular human societies (with no assumption that it will always occur); (b) if indeed fitness maximization occurs, how are DP and domain-general mechanisms utilized to this end; i.e., how are EMD's, personal ideologies, and other cultural manipulations of behavior based on the plasticity of behavioral systems recruited in the service of fitness maximization; (c) in societies where fitness maximization does not occur, precisely how are these mechanisms manipulated (e.g., via social controls and ideology) so that fitness maximization does not occur.

The above analysis has assumed that there is no variation in the EEA for humans. However, this is highly questionable (Irons 1990). The opposite hypothesis would be supported by finding evidence for different genetically-based fitness maximizing mechanisms among different groups subject to different contextual demands (e.g., intermediate level societies versus stratified societies versus hunter-gatherers). The implication would be that these different groups were under different selective pressures and had developed very different rules as a result. (See Rushton 1985, 1988 for an evolutionary perspective on intergroup differences in humans.)

It is unlikely that natural selection has essentially ceased since the Pleistocene, given the finding of massive individual differences in RS in highly productive economies such as many of the stratified societies of Eurasia (Betzig 1986; Dickemann 1979; Weisfeld 1990). The common finding of ethnic differences in temperamental variation in behavioral inhibition (e.g., Kagan, Kearsley, and Zelazo 1978) suggests that different human groups have been under quite different selection pressures, as does the finding of enormous cross-cultural differences in the rate of twinning referred to above. Genetic drift is also a (rather doubtful) possibility for these differences, but whether through selection or drift, the result is genetic variation in DP motivational mechanisms.[8] The quest for a universal set of genetically invariant mechanisms which evolved in the Pleistocene is quite likely to be illusory.

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[8] This type of example suggests that the principle means by which EEA mechanisms have been molded in non-EEA environments is not the development *de novo* of mechanisms but by directional selection on genetic variation for pan-human mechanisms.

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