GENE-BASED EVOLUTIONARY THEORIES IN CRIMINOLOGY*

LEE ELLIS  
Minot State University

ANTHONY WALSH  
Boise State University

In the past 20 years, several theories of criminal (and antisocial) behavior have been proposed from an evolutionary perspective, some of which specifically stipulate that people vary in their genetic dispositions toward criminality. It is these theories, herein called gene-based evolutionary theories, that are the focus of this article. Two categories of gene-based evolutionary theories are described. One category is crime specific, pertaining to the offenses of rape, spousal assault/murder, and child abuse/neglect. The second category consists of two general theories of criminal and antisocial behavior: the cheater (or cad vs. dad) theory, and the r/K theory. In addition to assuming that genes contribute to variation in criminal (and antisocial) behavior, all five of these theories assume that natural selection has acted on human populations to open up reproductive niches for individuals and groups who victimize others. While the theories are still far too new to have been fully tested, we derive some of the most obvious hypotheses from each theory and explore the relevant empirical evidence. We show that while gene-based evolutionary theories often make predictions similar to strictly environmental theories, they also lead to unique hypotheses, several of which have at least some support.

According to modern (or gene-based) evolutionary theory, natural selection can operate on traits only if the traits are genetically influenced (Daly and Wilson, 1983:341) and only if the genes are not universally present in a population (Browne, 1995:985). In the case of behavior, nearly all of the effects of genes are quite indirect because they are mediated through complex chains of events occurring in the brain. This means that there are almost certainly no genes for something as complex as criminal behavior. Nevertheless, many genes may affect brain functioning in ways that either increase or reduce the chances of individuals learning various complex behavior patterns, including behavior patterns that happen to be

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* We thank Linda Mealey, Edward Miller, Alan Widmayer and Linda Ebertz for helpful suggestions.
so offensive to others that criminal sanctions have been instituted to minimize their recurrence (Ellis, 1990d).

This review may not appeal to most criminologists because it rests on the assumption that genetic factors influence criminal behavior. A survey found that only about 20% of criminologists are receptive to the notion that genetic factors have important influences on criminal behavior (Ellis and Hoffman, 1990). For those who are open to persuasion on this point, several recent reviews may be consulted for supportive evidence (Bock and Goode, 1996; Carey, 1992; Eysenck and Gudjonsson, 1989:108; Lykken, 1995:92; Mealey, 1995:526; Raine, 1993; Walters, 1992:604). The evidence is particularly strong in the case of offenders who exhibit antisocial behavior prior to puberty and persist in doing so throughout adolescence and early adulthood (Cadoret and Stewart, 1991; Cadoret et al., 1995; Moffitt, 1993; Willerman et al., 1992). Evidence of genetic influences on serious and persistent criminal and antisocial behavior has now come from general family studies (Jones et al., 1980), twin studies (Cloninger and Gottesman, 1987; Rowe, 1990), adoption studies (Carey, 1992; Cadoret et al., 1995; Raine and Dunkin, 1990:638; Willerman et al., 1992), and one study of twins reared apart (Grove et al., 1990).

One reason most criminologists are skeptical about genetic influences on criminal behavior is that it seems improbable that behavior that is defined differently in every society could have a genetic foundation (see Walsh, 1995a:174). In other words, why would genes affect behavior that is circumscribed by laws that vary from one society to another? Much of the answer lies in the fact that in nearly all societies with written criminal statutes, there are a fairly standard set of “core behavior patterns” that are criminalized (Ellis, 1990a:19; Eysenck and Gudjonsson, 1989:1). These criminalized acts have in common the fact that they directly harm other societal members, either physically or by damaging or confiscating property. While most societies go on to criminalize numerous other “peripheral” acts, the core offenses remain almost universally criminalized. This means that as long as one focuses on so-called victimful offenses (i.e., violent and property crimes), it is possible to maintain that there is little variation from one society to another in what constitutes criminal behavior (Ellis, 1990a).

The similarity in what constitutes victimful crimes in all societies may be compared to the extent of agreement among psychological and psychiatric clinicians on another socially defined concept: mental illness. Despite continued disputes over precisely how to define and identify schizophrenia, unipolar and bipolar depression, phobias, alcoholism, and so on, the essential “core” of each of these mental conditions is sufficiently clear to
have allowed researchers to investigate the possibility of their being influenced by genetics. The results of these studies have consistently implicated genetic factors in most major forms of mental illness (reviewed by Andrews et al., 1990).

If genetic factors influence people's varying probabilities of criminal behavior, as current evidence suggests, why would such genes exist? Obviously, environmental theories cannot address this question because they assume that there are no such genes. For those willing to set aside environmental theories as incomplete (but not necessarily incorrect), a fascinating possibility presents itself: Perhaps some evolutionary forces are responsible for the existence of genes that promote criminal behavior. In other words, persons who are highly disposed toward crime might be able to reproduce at fairly high rates, at least under certain conditions, such as when the chances of being identified or punished are fairly low (e.g., in large cities as opposed to small communities).

As this review will show, recent explorations of this possibility have gone far beyond Lombroso's (1896) suggestion that criminals are atavistic throwbacks to some primitive human life form. Not only did Lombroso know nothing of genetics, he also thought criminals were poorly adapted to life in complex industrial societies. Recently, several evolutionary theorists have argued that criminals may actually be better adapted for living in large modern societies than for living in small foraging or horticultural communities.

It is important to emphasize that the concept of genetic influence is not equivalent to genetic determinism and that genetic influence does not mean that a behavior pattern is unlearned. Breeding experiments with various animal species have shown that genes can and do influence learning (Gould and Marler, 1987). More precisely, the ability to learn and the disposition to learn some things more readily than others appear to have genetic foundations, and the responsible genes can respond to natural selection pressure (Kenrick, 1987). Presumably, varying capacities and dispositions to learn are present in animal populations to the extent these capacities and dispositions facilitate reproduction relative to animals whose behavior is more instinctually motivated. Especially in large mammals such as ourselves, numerous genetic programs appear to exist that affect how our brains function in ways that facilitate general tendencies to learn as well as tendencies to learn some things more readily than others.

Recently, a “Swiss army knife” model of how genes may influence brain functioning has been advocated (Cosmides and Tooby, 1992). According to this model, humans (and other animals) have evolved special modules and networks in their brains that incline them to learn certain behavioral responses readily. Thus, depending upon the particular environment to
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which humans are exposed, much of human behavior could be differen-
tially channeled in particular directions by genes that modify small behav-
ior-control modules in the brain. All of this learning could have been
shaped by natural selection forces to which numerous generations of
ancestors were exposed.

Whether this "Swiss army knife" model of the brain proves to be true or
not, everything in the theories that we are about to review is entirely com-
patible with the assumption that criminal behavior is largely learned
behavior. Nevertheless, these theories all share the assumption that for
both genetic and environmental reasons, people will vary in the ease with
which they learn some behaviors rather than others, including criminal
behavior. As one evolutionary criminologist put it, "Genes do not code
themselves for jimmying a lock or stealing a car—criminal acts must be
acquired by socialization and learning because the genome does not waste
precious DNA encoding the specifics" (Rowe, 1996:285).

MODERN EVOLUTIONARY THEORY

Two scientific breakthroughs from the nineteenth century are at the
heart of modern biology: One was Charles Darwin's theory of evolution,
which never dealt with the concept of genes. The other was Gregor Men-
del's discoveries, which eventually led to the field of genetics. Especially
after these two monumental discoveries were combined in the 1920s to
give rise to the so-called Modern Synthesis, they became enormously use-
ful for understanding how life on earth arose and how life has been trans-
formed into millions of species over billions of years (Blackburn and
Modern Synthesis arose various versions of gene-based (neo-Darwinian)
All versions of this gene-based theory of evolution have converged on a
simple but powerful idea: To the degree a particular characteristic is prev-
alent in a population, it is likely to have contributed to the reproductive
success of the ancestors of the individuals currently living. Increasingly,
this fundamental principle has been applied to the study of behavior (e.g.,
Buss, 1994; Wright, 1995), including criminal behavior (Ellis, 1990c).

A term that has come to be widely used in the applications of gene-
based evolutionary theory in the study of criminal behavior is kin selection.
Kin selection refers to the idea that individuals can often help ensure the
representation of their genes in subsequent generations not simply by hav-
ing offspring of their own, but also by helping other close genetic relatives
to have offspring. Of course, the best way to pass on one's genes to the
next generation is to have offspring of one's own who go on to do likewise.

Imbedded in the concept of kin selection is the realization that often
one cannot identify close genetic relatives with certainty. As we will dis-
cuss, this opens the door to numerous social strategies and counterstrate-
gies that animals, including ourselves, may use that affect not only one's
own reproduction, but that of others with whom one has contact.

APPLICATIONS OF GENE-BASED EVOLVOLUTIONARY
THINKING TO THE STUDY OF
CRIMINALITY

Two concepts that have received a great deal of attention from those
who are applying gene-based evolutionary theory to the study of criminal
and antisocial behavior are those of deception and cheating. Arguments
have been made that such behavior could often be advantageous to repro-
duction (e.g., Harpending and Sobus, 1987; Mealey, 1995; Rowe,
1996:278). The reasoning is as follows: If genes promoting altruistic
and cooperative behavior can evolve by natural selection, as some evidence
suggests (Rushton et al., 1986), genes could also evolve that predispose
organisms to take advantage of the altruistic and cooperative behavior of
others without reciprocating (Badcock, 1986; Thompson, 1980; Thornhill,
1979). This in turn could favor the evolution of attempts by altruists to
detect and punish (or ostracize) nonreciprocators. Through this escalating
set of social relationships may evolve reproductive strategies rooted in
deception and cheating (Cosmides and Tooby, 1992; Ellis, 1990b). If ten-
dencies to learn deceptive and cheating tactics are genetically influenced,
so too may be the tendencies to be vigilant against the use of such tactics
by others (Bond and Robinson, 1988:296).

Several evolutionary theorists have argued that the best way for cheat-
ers to avoid detection is for them to go so far as to even virtually deceive
themselves. Thus, self-deception may have evolved as a character trait
that helps cheaters fool others (Beahrs, 1991; Beckstrom, 1989:81;
Dugatkin, 1992; Trivers, 1991). In a number of social species, an "arms
race" of deception/cheating, and attempts to detect and foil such tactics,
may have given rise to the evolution of retaliatory tactics, which may exert
pressures for the evolution of even more subtle forms of deception and
cheating (Clutton-Brock and Parker, 1995). The human ability to commu-
nicate linguistically (especially in writing) may have evolved in part
because it facilitates the detection of cheaters and victimizers (Ellis,
1990b).

As this review will show, these arguments have allowed evolutionary
social scientists to deduce a number of novel hypotheses, several of which
are extremely relevant to criminology. The theories to be reviewed all
assume that for genetic reasons, if people (or other animals) are going to
be altruistic, they are most likely to be so toward close genetic relatives
and/or toward others who are willing to reciprocate. The theories also assume that most people are genetically capable of at least occasionally being deceptive, and that a significant minority of human beings (and other animals) may be genetically prone to be extremely deceptive and otherwise prone to take advantage of others, sometimes even close relatives and friends. When human deception and victimizing behavior reach high levels of harm, the term *criminal* is often applied to the behavior, and when offenders are sufficiently chronic in these activities, they are said to be *antisocial* or *psychopathic* (or *sociopathic*).

We now describe each of the five specific gene-based evolutionary theories of criminal and antisocial behavior with a focus on identifying testable hypotheses that may be derived from each theory. Many of the hypotheses derived from these theories overlap ones that can be derived from strictly social environmental theories, although we show that they go beyond them in some intriguing directions.

**EVOLUTIONARY THEORIES OF SPECIFIC TYPES OF CRIMES**

Two types of gene-based evolutionary theories of criminal behavior can be identified. One type focuses on specific crimes, such as rape, spousal assault, and child abuse, and the other type is applied generally to criminal and antisocial behavior. We discuss each of these two types in turn.

**RAPE (AND SEXUAL ASSAULT)**

Since the early 1980s, numerous theorists have proposed that sexual assault may have been favored by natural selection (Ellis, 1989b, 1991b, in press; Lalumiere and Quinsey, 1996; Shields and Shields, 1983; Thiessen, 1986; Thornhill and Thornhill, 1983, 1987, 1992; van der Dennen, 1992). These proposals basically assert that sexual aggression has been naturally selected to be exhibited predominantly by the sex that invests the least in each offspring conceived. In nearly all species, but especially among mammals, males are not directly involved in gestating offspring, nor do they invest nearly as much time and energy in their offspring after birth as do females. Successfully reproducing females, on the other hand, rarely escape making high parental investments.

Being relatively free of parenting responsibilities, males have more to gain in reproductive terms from having multiple sex partners than do females (Browne, 1995:995). Since males who succeed in having multiple sex partners generally reproduce more prolifically than males who have just one, it is important to consider the sort of tactics that may have evolved to assist males in securing multiple sex partners.

According to the evolutionary theory of rape, the male reproductive
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advantage derived from having multiple sex partners has resulted in natural selection favoring genes promoting brain patterns for "pushiness" in pursuit of sexual intercourse. In some males, genes may carry pushiness to the point of actual force, especially after less violent tactics fail to yield results. In other words, over generations, pushy males will probably be more successful at passing on their genes, including any genes coding for readily learning pushy sexual behavior, than will less pushy males. While these ideas may not be pleasant to contemplate, proponents of the evolutionary theory of rape contend that the dynamics of rape cannot be fully understood without taking into account its reproductive consequences. Further insight into the evolutionary theory of rape can come from considering various hypotheses derived from it.

**Hypothesis 1: Males should predominate in the commission of rape and sexual assault.** Even though females could at least occasionally gain in reproductive terms from being sexually assertive, especially with high-status males (Belsky et al., 1991), there is little doubt that males have the most to gain from sexual assertiveness. Because of the minimal investment of time and energy males must make in each offspring compared to what females must make, they always stand to gain more than females in reproductive terms from becoming pushy when it comes to sex, at least when other tactics are unsuccessful. Thus, evolutionary theory predicts that most sexual assaults will be committed by males, and this is clearly the case throughout the world (reviewed by Cohn, 1993; Ellis, 1989b:82, in press).

Strictly environmental theories make the same prediction, but they posit that differential socialization accounts for the gender difference in propensity to rape and that if each gender was identically socialized it would be equally likely (or unlikely) to rape. As explained more below, one problem with this explanation is that it fails to predict that forced copulations occur in numerous nonhuman species in which nothing akin to differential gender socialization exists, and in all of these species also, most of the assailants are males. Nonevolutionary theories may also point to gender differences in physical strength and aggressiveness to explain the gender difference in propensity to sexually assault. For evolutionary theorists, this begs the question of why these differences exist in the first place (i.e., What reproductive advantages do they confer?), and they would point out that strength and aggressiveness (sexual and otherwise) may be more pronounced in males due in part to these traits facilitating sexual intimidation.

**Hypothesis 2: Sexual assaults should not be exclusively a human phenomenon; males of other species should have evolved similar genetically promoted tendencies.** The two main alternative theories of rape are the feminist theory and the social learning theory (Ellis, 1989b). As noted above, these theories usually account for why nearly all rapists are males
by invoking differential socialization, which implies that sexual assault is a unique human phenomenon, an argument made by Brownmiller (1975:3) in her classic defense of the feminist theory. The evolutionary theory, on the other hand, leads to the opposite hypothesis: If genes contributing to rape have evolved in males because they can reproductively (and thus genetically) benefit from multiple matings more than females can, there is no reason to think that similar genes would not have evolved in other species. The evidence on the matter is clearly on the side of the evolutionary hypothesis. Forced copulations have been documented in numerous nonhuman species, and in all cases, males are almost always the assailants (Ellis, 1989b:45; Palmer, 1989; Thornhill and Thornhill, 1992:364). This is even true of some species of monogamous birds in which no significant sex differences exist in terms of size or physical strength (McKinney et al., 1983).

Hypothesis 3: Rape should be strongly resisted by female victims because it denies them the opportunity to choose sex partners who are most likely to help care for offspring. Feminist and social leaning theories of rape both assume that females want control over deciding with whom they have sex (Ellis, 1989b). However, these theories do not explain why such control would be important. Evolutionary theory offers an explanation for this desire by postulating that it has been strongly favored by natural selection. Females who tend to withhold copulating with a male until they are relatively confident that the male will help care for any offspring that are produced will be evolutionarily favored over females who copulate simply on the basis of sexual attraction (Townsend, 1995:175). In other words, because females gestate offspring and males do not, females have a lower ceiling than males do in terms of the number of offspring they can possibly have in a lifetime. One of the main things a female can do to raise this ceiling somewhat (although never as high as the male's) is to choose a mate who will help her care for offspring.

Supporting this reasoning, research throughout the world has indicated that females are much more cautious in choosing sex partners than is true for males (Buss and Schmitt, 1993) and much more interested in personality traits that suggest loyalty, commitment, and love of children than males are when identifying an ideal mate (Buss, 1994:32; Townsend, 1995). Further, this choosiness should be especially true of females who themselves expect to invest heavily in their offspring. Evolutionarily speaking, the differences in mating strategies by the average male and female create a tension in sexual relationships, and rape may be one of the unfortunate consequences of this tension (Thornhill and Thornhill, 1987:286).

Theoretically, male desires for multiple sex partners and female desires for males who are willing and able providers of resources for offspring have garnered a complex web of strategies and counterstrategies, although
always with a great deal of intra- and intersex diversity (Smuts and Smuts, 1993:29). The general (although not universal) female tendency to avoid mating with sexually philandering males could be one reason males are prone to exaggerate their likelihood of making monogamous commitments. These male exaggerations in turn could have favored females with keen abilities to "read" male sincerity, which could be countered by males taking deception to the point of self-deception (Tooke and Camire, 1991).

**Hypothesis 4: Victims of sexual assault should primarily be females of reproductive age.** According to evolutionary theory, rape victimization should be strongly associated with age. Specifically, the victims should be primarily of reproductive age. The evolutionary theory of rape would be seriously undercut by evidence of no correlation between age and rape victimization or by the discovery of even one society in which most sexual assault victims are not of reproductive age.

Strictly environmental theories of rape would imply that there should be at least some societies in which rape victims are not primarily of reproductive age. So far, no such societies have been found. Of the 17 studies that have investigated the link between age and rape victimization, all have found the most vulnerable age to be in the range of 15 to 35 years (reviewed by Ellis, 1989b50).

It should be noted that there is nothing in the evolutionary theory of rape that asserts that reproductive success constitutes a conscious motive for rape. Humans, like other animals, are generally prone to seek much more immediate goals (eating regularly, avoiding painful stimuli, copulating periodically).

**Hypothesis 5: In some societies, males who engage in forced copulations may not only reproduce relatively well, they could even out-reproduce males who only mate with voluntary sex partners.** A criticism lodged against the evolutionary theory of rape has been that the probability of rape victims becoming pregnant is too low for sexual assault to have been naturally selected (Harding, 1985:51). While additional research is in order, this criticism does not appear to be well founded. Most studies place the probability of becoming pregnant from rape at only slightly below the rate from voluntary intercourse (reviewed by Ellis, 1989b:47; also see Krueger, 1988:24; Winston, 1987). In addition, several studies have found that when all sexual outlets are considered (i.e., both voluntary and forced), rapists have more active sex lives than do males who only engage in voluntary copulations (Abel et al., 1989; Byers, 1988; Koss et al., 1985; Malamuth, 1986). This suggests that any genes inclining males to fall back on force and deception when voluntary copulatory tactics do not succeed would increase the representation of their genes in a population unless fairly effective countermeasures were instituted. (As discussed below, this latter
reasoning could help to explain why criminal justice sanctions for rape are often severe.)

It is important to note at this point that the evolutionary theory of rape (or of any other crime) does not offer a moral defense. In fact, as discussed in hypothesis 6, the very tendency most of us have to condemn rape (especially when loved ones are victims), may itself be part of an evolved counterstrategy against an act that threatens our own inclusive fitness (Ellis, 1990b).

**Hypothesis 6:** Penalties for rape will be severe to prevent genes conducive to rape from overtaking a population. Even if rape is part of a genetically influenced, evolved reproductive strategy, the complex behavior surrounding the offense is still learned. As such, the probability that someone will act on urges to commit a sexual assault is certainly subject to environmental influences, including the threat of punishment. Most criminal justice sanctions may be thought of as a set of evolved strategies whereby generally altruistic people collectively protect their reproductive interests against invasion by people who are minimally altruistic (Boyd and Richerson, 1992; Clutton-Brock and Parker, 1995; Ellis, 1990b). The typically severe penalties for rape may be a reflection of these efforts.

There is considerable evidence that many male would-be rapists are deterred by the punitive sanctions imposed on rapists. While studies have found that only about 10% to 20% of males admit to ever having committed rape (Yegidis, 1986), up to 70% admit to at least using deceptive and/or pushy tactics in order to achieve sexual intimacy in dating situations (reviewed by Ellis, 1996). Also, 25% to 50% of males concede that they might use forceful tactics if somehow assured that they would never be caught and punished for doing so (reviewed by Ellis, 1989b:6). About the only "natural" conditions that ever approximate such assurances come under warfare conditions. Numerous historical accounts have suggested that large proportions of males commit rape when the ability of victims and/or their relatives to retaliate is greatly diminished (Brownmiller, 1975:80; Ellis, 1989b:47; Shields and Shields, 1983).

**SPOUSAL AND “ROMANTIC TRIANGLE” ASSAULT**

Several evolutionary theorists have proposed that spousal abuse, assault, and homicide (here collectively called *spousal assault*) may have evolutionary underpinnings (Buss, 1994:156; Daly and Wilson, 1988:295; Ellis, 1990c; Weir, 1992:353). Spousal assaults cover offenses ranging from occasional slapping and threatening bodily harm to repeated attacks, and even murder. *Romantic triangle assaults* are assaults directed by one individual toward another person (usually of the same sex) in order to prevent the victim from gaining (or retaining) sexual access to a third individual (usually of the opposite sex).
Basically, the evolutionary theory of spousal assault asserts that such behavior will, in one way or another, have a great deal to do with propriety over sexual access. And the theory suggests that the sex that runs the greatest risk of misidentifying its progeny will be particularly prone to resort to assaultive tactics to ensure exclusivity in sexual access. Accordingly, the following hypotheses may be derived from the theory.

Hypothesis 1: Males should be the main offenders in the case of spousal assaults and romantic triangle assaults. Studies have repeatedly shown that except for minor forms of spousal abuse—for which male and female assault rates are nearly equal (Arias et al., 1987:88; Straus et al., 1980)—males are far more abusive toward their spouses and dating partners than are females (Browne and Williams, 1989, 1993; Roberts et al., 1993; Zawitz et al., 1993:25). This would be consistent with the fact that males have much more to lose reproductively from partner infidelity than do females. As explained below, while females whose partners are unfaithful can still accurately identify their offspring for the purpose of making parental investments, males cannot.

Hypothesis 2: Jealousy and suspicion of infidelity should be a key cause of spousal and dating assaults. As noted in hypothesis 1, the evolutionary explanation of spousal assault rests heavily on evidence that males are more likely than females to be the abusers, especially in the case of serious assaults and homicides. The evolutionary concept most often used to explain this pattern is that of cuckoldry (which refers to unwittingly helping to rear an offspring that is not one's own genetic descendant). Males can only infer that offspring are their genetic descendants by associating the offspring with the female(s) with whom they have had sex. To the degree a male's mate copulates with other males, he risks cuckoldry and thereby having his genes culled from the gene pool.

According to evolutionary theory, assaultive tendencies toward spouses and dating and cohabitating partners have been favored by natural selection as tactics for helping to maintain a mate's sexual fidelity (Smuts, 1992:11). If this is true, jealousy and suspicions of infidelity should be major causes of spousal assaults and homicides. Evidence from many countries indicates that the single most important motivation behind spousal and romantic triangle assault is sexual jealousy and suspicions of infidelity (Crawford and Gartner, 1992; Laner, 1990; Lepowsky, 1994).

Hypothesis 3: "Spousal assaults" should not be an exclusively human phenomenon. Unlike strictly environmental theories of spousal assaults, nothing in evolutionary theory excludes the possibility of similar tactics existing outside the human species. In fact, it would be surprising to find that only humans had evolved violent tactics for discouraging mates from copulating with other partners. Males have been observed attacking
females who show interest in other males and/or fail to be sexually receptive toward the assailant in at least four other primate species: hamadryas baboons (Smuts and Smuts, 1993), toque macaques (Dittus, 1977), stumptail macaques (Whitten and Smith, 1984), and rhesus macaques (Lindburg, 1983). Similarly, males sometimes severely wound one another over "breeding rights" (Dunbar, 1984:132) in ways analogous to romantic triangle assaults in humans.

**Hypothesis 4:** *Spousal assault should be highest in human populations that have fewer stable marriages, greater promiscuous sexual intercourse, and more children who do not receive the family name of the father.*

Although humans stand out among mammals in the degree to which males are directly involved in caring for offspring, throughout the world men still invest far less time and energy in caring for their offspring than do women (Oakes and Almquist, 1993:71; White, 1993:155). At least two factors have favored greater parental investment by human males relative to males of other mammalian species. One is the slow rate at which human infants develop out of a state of helplessness. This has favored the evolution of pair bonding and cooperation between both parents to share in child care (Lovejoy, 1981; Walsh, 1995a:203). The second factor consists of various cultural practices that have made it possible for human males to identify their offspring with greater certainty than is true of other mammals. Such nearly universal practices as marriage, moral prohibitions against premarital intercourse, and patrilineal naming practices could all have been selected because they foster parental investment by males (Schulz, 1994:200).

Despite these customs, human males still risk cuckoldry to a substantial degree. In some countries, between 1% and 3% of children appear to have been fathered by someone other than the male claiming fatherhood (Brock and Shrimpton, 1991; Sasse et al., 1994), while in other countries rates of misidentified paternity are estimated at between 10% and 30% (Birkhead and Moller, 1992; Hirsch et al., 1980). It can hardly be doubted that natural selection has severely disfavored males who make little effort to ensure the sexual fidelity of the female with whom they share parental responsibilities.

Assuming that spousal assault for infidelity is a relatively desperate measure for preventing cuckoldry, the following predictions can be made: Cultures (or subcultures) in which spousal assaults are relatively high should be those in which (a) marriage is uncommon or unstable, (b) prohibitions against pre- and extramarital intercourse are lax, and/or (c) children infrequently receive their father's family name. We were able to locate no scientific evidence specifically undertaken to test these predictions.

**Hypothesis 5:** *Spousal assault may prevent infidelity and/or pregnancy*
resulting from infidelity. In order for spousal assault to evolve by natural selection, there must be some way that such action at least occasionally benefits the assailant reproductively. There are at least two possibilities in this regard. First, victims could be so frightened and intimidated by threats of being beaten that they avoid the sort of activities that provoke it. In this connection, several researchers have identified what has been called trauma-induced bonding and dependency (or traumatic bonding) as an emotional response to extreme fear (reviewed by Ellis, 1989b:48). This concept has been invoked to help explain why battered wives often do not leave their husbands, even after repeated assaults (Dutton, 1995:189; Painter and Dutton, 1985).

Spousal assault could also serve the reproductive interests of the offender by causing the victim to suffer such severe emotional stress as to disrupt reproductive functioning (reviewed by Ellis, 1995). This disruption appears to include suppression of ovulation (Dunbar, 1984:67) and even the prevention of implantation of fertilized eggs onto the uterine wall (Huck et al., 1988). Perhaps spousal assault by men is sometimes part of an insidious evolved strategy that helps them avoid being cuckolded when mates have been unfaithful. (Keep in mind that evolutionary strategies are rarely conscious strategies.)

_Hypothesis 6: Women who become pregnant as a result of sexual infidelity may be subjected to such severe badgering by the men with whom they live that their pregnancy may be aborted._ Assaults on women by their spouses or lovers occur at alarming frequencies during pregnancy—estimates range from 4% to 20% (Helton et al., 1987; Norton et al., 1995; Parker et al., 1994). In several nonhuman species, stress during pregnancy is a significant cause of miscarriage (Huck et al., 1988; MacNiven and de Catanzaro, 1990; Miller and Riegle, 1985). Studies have shown that in some species the mere presence of males not responsible for a given pregnancy sometimes induces a miscarriage (Huck et al., 1988; Sackett, 1981:269; Wimer and Wimer, 1985:194). At the extreme, 80% of pregnancies among a herd of wild horses were found to have ended in miscarriage after a male new to the herd took over leadership and began harassing and sexually assaulting the mares (Berger, 1983).

Severe emotional stress also appears to induce miscarriages in humans (Scarpellini et al., 1994). The biochemical mechanisms by which this happens seem to involve high levels of stress hormones temporarily blocking the production of various sex hormones (such as progesterone) that are required to maintain pregnancy (MacNiven and de Catanzaro, 1990; Tupper et al., 1957).

Perhaps male tendencies to physically assault their spouses or lovers during pregnancy may have evolutionary functions similar to what has been documented for other animals. This hypothesis could be tested by
determining if unfaithful women experience higher rates of spousal assault during pregnancy than faithful women. To our knowledge, this hypothesis has never been tested among humans, although it would be consistent with evidence that domestic assaults during pregnancy are higher for unmarried teenage women than for women in general (Parker et al., 1994).

Overall, several hypotheses can be reasonably derived from the evolutionary theory of spousal (and romantic triangle) assault. Of the hypotheses tested thus far, they have been fairly well supported. Although we cannot exclude hypotheses derived from cultural theories for spousal assault, evolutionary theories, by documenting analogous behavior in other species, take the issue beyond cultural learning to suggest that such behavior is part of a general evolved strategy that humans share with other mammals.

CHILD ABUSE AND NEGLECT

Child abuse and neglect (including infanticide) is another type of crime that has received a great deal of attention from evolutionists in recent years (Belsky, 1993:424; Burgess and Draper, 1988; Daly and Wilson, 1985, 1987, 1994; Gelles and Lancaster, 1987). At first glance, neglecting or intentionally injuring one’s own offspring appears totally incongruent with evolutionary logic. However, there are a few conditions under which abusive actions toward one’s offspring could be favored by natural selection (Buss, 1995:18; Daly and Wilson, 1980:284; Ellis, 1990c:65). These conditions are specified by the following four hypotheses.

Hypothesis 1: Parents who have more children than they have resources needed to rear them should abuse and even abandon their children more than parents who have sufficient resources. Thus, when a family is large, poor, and/or has children who are closely spaced, child abuse and neglect should be particularly high. Studies of various animal species have found parents occasionally abusing, and sometimes even killing, their offspring. Consistent with the evolutionary perspective, the probability of parental abuse, neglect, and infanticide appears to increase when litter size is unusually large (Aguilera, 1990; Brooks, 1984), food is in short supply (Elwood and Ostermeyer, 1984; Hoogland, 1985), or nutritional conditions are poor (Porter and Wiemeyer, 1970).

Child abuse among humans has been shown to be significantly greater in large families than in small families (Daly and Wilson, 1985; Straus et al., 1980; Wolfner and Gelles, 1993; Zuravin, 1991). Also, child abuse and neglect has been found to be inversely correlated with family income (Walsh and Beyer, 1987; Whipple and Webster–Stratton, 1991; Wolfner and Gelles, 1993).

Hypothesis 2: A parent who lacks the assistance of the other parent in caring for offspring should be more prone toward child abuse, neglect, and
abandonment than a parent who has the other parent cooperating in providing child care. If one parent finds the other parent failing to assist either directly or indirectly in caring for their offspring, that parent may be favored for doing likewise. This would be especially true of parents who are young and have a reasonably high probability of attracting a new mate who will be more cooperative. In a recent piece on “parental effort,” Sozou and Houston (1994:251) wrote, “When two or more parents are cooperating to raise young, the optimal level of effort by one parent will, in general, depend on the effort of the other.” Coinciding with this reasoning, a study of egrets found that when one mate died, the surviving parent sometimes abandoned its offspring to the elements and re-mated to rear new broods successfully (Fujioka, 1986).

Among humans, studies have shown that child abuse (including infanticide) by parents is unusually common among couples who have never married or are separated or divorced (Daly et al., 1982; Walsh, 1991) and in families marked by excessive marital discord (Green, 1976; Reid et al., 1981). Long-term cooperation by both parents in providing child care would almost certainly be less for unwedded parents than for their wedded counterparts because their likelihood of remaining together is lower (Bennett et al., 1988; Bumpass and Sweet, 1989). We therefore expect a positive correlation between child abuse rates and rates of out-of-wedlock births, an expectation that has been supported by at least three studies (Simons et al., 1993; Walsh, 1990; Zuravin, 1988).

Hypothesis 3: Children who are less viable from a reproductive standpoint are likely to experience more abuse and neglect from parents than other children. Evolutionary theory leads to the hypothesis that parental investments will not always be equally distributed to all offspring. Theoretically, parents should behave toward each child in ways that roughly correspond to the child’s chances of eventually reproducing. If the chances are low, the parents should invest less in a particular offspring than if the chances are high.

Consistent with this deduction, human parents appear to discriminate in favor of offspring who are the most promising from the standpoint of their reproductive potential (Borgerhoff Mulder, 1987:30). For example, children with serious physical and mental handicaps typically receive less care and/or more abuse than their nonhandicapped siblings (Frodi, 1981; Lightcap et al., 1982).

Hypothesis 4: Children will be subjected to more abuse and neglect when no close genetic relationship exists between the child and the parent/guardian. Evolutionary theory posits that parental care has evolved because it contributes to the survival of the caregiver’s genes. Hence, there is less genetic advantage in rearing someone else’s offspring than in rearing one’s own (Daly and Wilson, 1994). Thus, one can expect that child abuse and
neglect will be experienced more by adopted children and stepchildren than by children raised by their biological parents. This expectation has been consistently borne out by research (Daly and Wilson, 1985, 1988:89, 1994; Lightcap et al., 1982). While the research on adopted children is much more limited than that for stepchildren, it too coincides with evolutionary expectations (Kempe, 1971; Wilson et al., 1980).

Strictly environmental theories are devoid of explanations for why step-parents and adoptive parents are more prone to engage in child abuse than biological parents. Currently, the only theory that predicts this observation is the evolutionary theory (Buss, 1995:18).

GENERAL GENE-BASED EVOLUTIONARY THEORIES OF CRIMINAL AND ANTISOcial BEHAVIOR

In addition to being applied to the study of specific offenses, gene-based evolutionary theories have been applied quite broadly in criminology (Ellis, 1987, 1990c; Harpending and Draper, 1988:313; McGuire et al., 1994:313; Raine, 1993:27). The possibility that evolutionary forces are behind general tendencies to victimize others does not mean that the most victimizing individuals will reproduce at unusually high rates under all conditions. There may be constraints upon which genes for such behavior can infiltrate a population's gene pool, and these constraints might vary from one set of environmental conditions to another.

Consider what might happen if a mutant gene arose in a small foraging society that inclined one of its members to be unusually aggressive toward other group members and/or to be disrespectful of other people's property rights. In a small society, this individual would probably be ousted unless he or she quickly learned to restrain his or her impulses. In a large society, however, this same individual might be able to act upon his or her antisocial impulses repeatedly without detection or ill consequences. Not only would he or she be able to find many more unwary victims in a large society, but the chances of being identified and punished would be less. This sort of reasoning has led to two distinguishable gene-based evolutionary theories of criminal and antisocial behavior: the cheater and r/K selection theories. Each is described below.

THE CHEATER (OR CAD vs. DAD) THEORY OF CRIMINAL AND ANTISOcial BEHAVIOR

In regard to sexual assault, we noted above that the sex that is not directly involved in gestating offspring can potentially have many more offspring than the sex that is. The time and energy males do not spend gestating offspring can be utilized in other reproductively significant ways,
such as competing in various ways with other males for access to females. In response to this strategy, females often seem to evolve tendencies to choose mates who appear willing and able to help them care for the offspring. Males respond by competing with other males to furnish evidence of their ability and inclination to provide parental care. Parental investment by males can be quite general and indiscriminate, such as providing protection to the group in which the mother and her offspring reside, or may be specific, such as provisioning food and shelter for his mate and her offspring.

Unfortunately for females, appearances can be deceiving, and it is often to the male's reproductive advantage to orchestrate this deception. In many species of animals, males have evolved what are broadly called alternative reproductive strategies (Bass, 1996; West-Eberhard, 1986); that is, within a species males have evolved the ability to reproduce in two or more distinctive ways. The most frequent alternative reproductive strategy yet documented involves males who minimize their parental investment in any specific offspring. Depending on the species involved, these extremely "low investing" males are called cheaters, floaters, sneakers, and satellites (Bass, 1996; Grahn et al, 1993; Katano, 1990). In some species, these males are also referred to as cads, thereby allowing the term dads to be used to describe males who assist females in caring for offspring and with whom females preferentially mate (Buss, 1994:23; Cashdan, 1993; Draper and Harpending, 1982).

According to the cheater (or cad) theory of criminal and antisocial behavior, a subpopulation of men has evolved with genes that incline them toward an extremely low parental investment reproductive strategy (Belsky et al., 1991; Burgess, 1991; Kofoed, 1988; Mealey, 1995; Raine, 1993:33). Since women will be favored for avoiding mating with these men, their cad strategy requires considerable deception or stealth. Much of this stealth takes the form of mimicking high investing (noncheater) males up to the point of the impregnation. Additional stealthy tactics include devious techniques for acquiring resources quickly and for gaining sexual access through almost any means that works (Raine, 1993:40).

According to the cheater theory, criminal and antisocial behavior is the human version of a low parental investment reproductive strategy. If this theory is true, criminals should be deceptive, irresponsible, and opportunistic in almost everything they do, and if genes are a major cause of this behavior, it would likely begin to manifest itself early in life. Theoretically, cad males will use just about any tactic that works to coax, trick and/or force numerous females to copulate, including thievery to acquire resources quickly, and will then shirk all long-term investments in offspring.

In a recent review of evidence pertaining to the cheater theory, Mealey
(1995) argued that males may come to a cheater strategy in one of two ways: Either they have genes that more or less compel them to adopt the strategy, or they may learn the strategy. She called those who are genetically inclined toward a life of cheating and crime primary sociopaths, and those who largely learned the strategy because of their rearing and circumstances secondary sociopaths. Lykken (1995) made the same distinction, but called the first category psychopaths and the second category sociopaths.

Whatever the source, Mealey contended that the cheater strategy will flourish in a population as long as the number of cheaters does not overwhelm the number of noncheaters in the population. This idea is similar to the fact that the number of predators in an ecosystem is always constrained by the availability of prey. Among the specific hypotheses that may be derived from the cheater theory are the following.

**Hypothesis 1:** Criminality and psychopathy should be more prevalent among men than among women. If criminality and psychopathy are manifestations of an evolved cheater strategy, they must be more prevalent among males than among females. Given the long gestation period in the human species, females simply must make a greater average investment in their offspring than males if they are to leave descendants in subsequent generations.

Consistent with this hypothesis, in all societies yet studied, men are more prone toward criminal and antisocial behavior than women, and the more serious and persistent the antisocial tendencies, the stronger the disparity is (reviewed by Ellis, 1988:535). A number of strictly environmental theories also have been offered to explain why males are more criminal and antisocial than females (reviewed by Ellis, 1989/90:19). However, these explanations all imply that environmental conditions could exist in which female crime rates will equal or exceed male rates. The fact that no such societies have yet been identified offers some support for the cheater theory.

**Hypothesis 2:** Criminals and psychopaths should be unusually promiscuous. According to the cheater theory, persistent criminals and psychopaths should be unusually prone to seek to have multiple sex partners (Belsky et al., 1991; Burgess, 1991:20; Kofoed, 1988). Consistent with this prediction, several studies have linked criminality and psychopathy with early onset of promiscuous sexual behavior (e.g., Elliott and Morse, 1987; Weiher et al., 1991) and unstable marriages (Robins, 1966:103).

**Hypothesis 3:** Criminals and psychopaths should be more inclined to commit sexual assaults than males in general. The cheater theory would predict that cheater males would experiment with any method that seems
to work for the purpose of copulating frequently with numerous sex partners. Accordingly, cads should resort more often than dads to more desperate and forceful copulatory tactics. The evidence to date is generally supportive of this hypothesis in the sense that rapists do not appear to be a special type of criminal. Rather, they generally exhibit all of the other major criminal and antisocial behavioral traits (Hall and Proctor, 1987; Knight et al., 1983; Rice et al., 1990).

Hypothesis 4: The cad strategy should be more pronounced among males in the prime of their reproductive careers than in later life. Evolutionary theorists have referred to the tendency for animals to adjust their reproductive strategies according to their age as an ontogenetic shift (Wilson, 1993). The assumption is that genetically regulated neurohormonal factors operate to affect the learning of these shifts.

The cheater theory does not assert that males will be either a cad or a dad across the entire lifespan. In some species in which the cad and the dad strategies are exhibited by different males, one finds many young cads gradually switching to a dad strategy as they age.

As cad males move beyond their reproductive prime, more and more cads shift toward territorial, paternal-oriented strategies (Boness et al., 1993; Paul, 1993:58; Smith and Arcese, 1989). In various fish species, for example, males enter their reproductive years as "sneakers" but later ontogenically shift toward becoming territorial males and thereby they come to attract voluntary sex partners (Gross, 1984). In other species, whether a male becomes a sneaker or a territorial male depends upon ecological conditions (Gross, 1996).

Fish that are sneakers do not court, defend territories, or build nests to attract females (Bass, 1996:353). Instead, they inseminate eggs laid by females in the nest of a territorial male by quickly darting in between a mating couple and ejaculating over the freshly laid eggs before the territorial male is able to chase them off. Additionally, among at least one species of song sparrows, cad reproductive tactics are exhibited almost entirely by yearling males, particularly in areas where sparrow populations are the densest (Smith and Arcese, 1989:839). In this species, nearly all males eventually come to exhibit a dad strategy as they mature, but during the early reproductive years a substantial proportion are cads.

The cad strategy may offer greater reproductive payoff for young males than for older males in many species, including humans, presumably because young males do not have access to the sort of resources needed to attract stable sex partners. Consequently, they specialize in opportunistic matings and the sort of risky, devious tactics that make such matings successful. As they accumulate resources in later life, many males would be expected to shift to a more dad-oriented reproductive strategy.

The above reasoning would offer an evolutionary explanation for what
has been called burnout among criminals and psychopaths. Burnout refers to the well-documented tendency for criminals and psychopaths to gradually relinquish their antisocial tendencies as they enter middle age (see Ellis, 1988:534; Hirschi and Gottfredson, 1983, 1987; Mealey, 1995; Wilson and Herrnstein, 1985:126). If the cheater theory is applicable to the study of criminality, burnout should be essentially a universal phenomenon. No strictly environmental theory would make such a broad-ranging prediction.

Hypothesis 5: The cheater strategy should be more prevalent in the lower than in the upper social strata. As already noted, two fairly distinct subpopulations of males have evolved in many species. One subpopulation provides mates and offspring with resources, the other has few resources to offer and resorts to alternative strategies for securing mates (Dixson, 1993:563; Grahn et al., 1993:93; Hews et al., 1994:96; Katano, 1990). In these species, females are most attracted to the males who have resources and who engage in elaborate courtship and form long-term cooperative relationships (Grahn et al., 1993; Katano, 1990; Trivers, 1985:408), males controlling fewer resources are more inclined to mate opportunistically (sometimes forcefully) and to avoid parental investment (Hews et al., 1994:96; Jones, 1959).

Some evolutionary theorists have argued that significant proportions of human males, particularly those of low social status, will be genetically inclined to readily learn a cad strategy (Harpending and Draper, 1988; Harpending and Sobus, 1987; Raine, 1993:40). As one proponent recently stated, males "who are the least likely to out compete other males in a status hierarchy . . . are the ones most likely to adopt a cheating strategy" (Mealey, 1995:527). It is important to emphasize that evolutionary theory is not positing that social status is itself necessarily genetically determined. It simply asserts that males who find themselves lacking in resources, for whatever reason, will be more likely than high-status males to adopt a cheater strategy to obtain copulation opportunities.

The cheater theory, of course, is not the only theory to hypothesize that criminal behavior would be inversely correlated with social status. This prediction is also central to several strictly environmental theories, such as strain theory and conflict theory, and peripheral to others, such as Gottfredson and Hirschi's (1990) self-control theory.

In the late 1970s, a major reanalysis of studies pertaining to criminal behavior and social status called the relationship into question (Tittle et al., 1978), although in a more recent review the relationship was upheld except in the case of self-reported offenses (Ellis, 1988). In the latter review, nearly 200 publications were identified that had addressed the crime-status relationship. Of the 143 of these studies that were based on
self-reports or limited to minor offenses, 35 found no significant relationship between crime/delinquency and social status; the remainder found a significant inverse relationship. In the case of the 46 studies that focused on officially recorded serious offenses, all found significant inverse correlations. This latter review suggested that only studies based on self-reports and/or largely confined to trivial offending have failed to consistently find an inverse correlation between criminality and social status (also see Elliott, 1994). Thus, hypothesis 5 seems to be supported.

**Hypothesis 6: Physical features may distinguish cads from dads.** Because the cheater strategy is usually associated with more rapid development to reproductive maturity, in many species, cheater males tend to be smaller as adults than honest males (Gross, 1996:92; Wikelski, et al., 1996:581), although there are exceptions (Hews and Moore, 1996).

Orangutans appear to be extreme in this regard. About half of all male orangutans grow to a size that is more than twice that of the average adult female, while the other half of males stop growing when they are only slightly larger than adult females. Females exhibit a strong mating preference for the larger males. Presumably to compensate, sexual assaults (also called forced copulations or coercive sex) are common among orangutans, with nearly all of the perpetrators being the smaller males (Wrangham and Peterson, 1996:136) — one of whom even sexually assaulted a human female (Wrangham and Peterson, 1996:137).

If the cheater theory of criminal and antisocial behavior is true, it would not be surprising to find some physical features distinguishing criminal/psychopathic males from other males. Among the possibilities worthy of research attention would be differences in stature and musculature. Already, considerable research suggests that criminals on average exceed the average male in mesomorphy, a body type linked to muscular development (Hartl et al., 1982).

**THE r/K THEORY OF CRIMINAL AND ANTISOCIAL BEHAVIOR**

The concept of an r/K continuum has been widely used in evolutionary biology for the past 20 years to describe a theoretical continuum along which all organisms are postulated to exist (e.g., Daly and Wilson, 1983:199; MacArthur and Wilson, 1967; Pianka, 1970). Organisms near the r end of the continuum reproduce rapidly and prolifically whenever environmental opportunities allow, but they do so without investing much time or energy in their offspring. Organisms near the K end reproduce slowly and cautiously even when environmental opportunities would allow them to be considerably more prolific, and they invest great amounts of time and energy in each of the few offspring they have. Theoretically, r
strategists will usually begin reproducing at an earlier stage of development, will have numerous offspring per pregnancy as well as over the life course, and will spend less time gestating, protecting, feeding, and training each offspring relative to K strategists (Chisholm, 1988:81; Relethford, 1990:498). Several r/K theorists assume that there is both intra- and interspecies variability along the r/K continuum (Bereczkei, 1993; Ellis, 1987; Gadgil and Solbrig, 1972; Jolly, 1985:42; Menge, 1974:84; Rushton, 1995).

Basically, r/K theory is similar to proposals that both quantitative (r) and qualitative (K) approaches to reproduction can be successful and that trade-offs are inherent in both strategies (Kaplan, 1994; Smith and Fretwell, 1974). Another way of making the same distinction is to stipulate that reproductive potential can be realized by emphasizing either mating (r) or parenting (K) (Lalumiere and Quinsey, 1996:33; Rowe, 1996:270). Theoretically, the trade-offs between mating effort versus parenting effort will manifest themselves in various ways, both behaviorally and physiologically. Organisms reproducing in large numbers, for example, cannot spend as much time caring for their offspring as organisms reproducing in small numbers. Traits useful in the pursuit of a K strategy would include kin-directed altruism and long-term nurturing of young; traits useful to the r strategy would include aggressive competitiveness and a strong sex drive.

Those who have applied the r/K concept to the study of criminal and antisocial behavior have contended that antisocial behavior is favored most among r strategists. This is partly because deceptive/victimizing approaches to reproduction would frustrate the cooperation among parents required for intense, long-term parental investments. Stated another way, because K strategists must invest extensive time and energy in each offspring, they are favored for evolving long-term cooperative, altruistic relationships between parents. Ultimately, parental cooperation leads to the evolution of cooperation among extended relatives and within communities of even more distantly related group members as a result of general inclusive fitness forces. Criminal and antisocial behavior would be contrary to such long-term cooperation arrangements.

Proponents of r/K theory have repeatedly noted that males should be more prone toward the r approach to reproduction than females (Ellis, 1989/90; Gould, 1982:459; Gross, 1992:246; Masters, 1983). This deduction follows from noting that males have a higher reproductive potential without the necessity of making as much parental investment as females must make.

The r/K theory is unique in terms of the sheer number of hypotheses that it generates. We have consolidated a number of these hypotheses for brevity.

_Hypothesis 1: Criminality and psychopathy should be more prevalent_
among men than among women. As with the cheater theory, the r/K theory is very explicit in hypothesizing that men will be more criminal and antisocial than women. If just one society could be found where more females than males commit serious victimful offenses, both evolutionary theories would be cast into serious doubt. In this sense, the cheater theory and the r/K theory are more vulnerable to disproof than are the strictly environmental theories of criminality, since the latter would be able to explain any exceptions by asserting that the gender roles in some societies may compel females toward greater criminality than males.

Hypothesis 2: Persons with the greatest tendencies toward criminal and antisocial behavior should exhibit at least most of the physiological traits associated with an r strategy, such as low birth weights, high rates of premature birthing, births in fairly rapid succession, and frequent twinning. While the evidence is still sketchy, it generally supports this hypothesis. Specifically, compared to persons in general, criminals are more likely to have been born prematurely and of low birth weight (reviewed by Ellis, 1987:156). No evidence specifically pertaining to twinning or short birth spacing in relationship to criminality was located. This set of hypotheses is important not only because it lies at the heart of r/K theory, but also because to our knowledge, no environmental theory has ever predicted that these sorts of variables would be associated with criminality.

Hypothesis 3: Parents of criminals and psychopaths should begin having children earlier in life and should have larger numbers of children than parents in general. Studies have consistently found a positive correlation between criminality in offspring and the size of the family in which they were reared (Ellis, 1988:520; West, 1969:73). While this is consistent with r/K theory, it is also readily explainable in terms of some strictly environmental theories, such as self-control theory (Gottfredson and Hirschi, 1995:36).

The r/K theory specifically predicts that after controlling for periods of imprisonment and other artificial restrictions on reproduction, a positive relationship should exist between histories of serious criminality and the number of children people have in their lifetime and the children's birth weights. No evidence was located specifically bearing on this hypothesis.

Regarding some aspects of this hypothesis, the evidence is not supportive. For example, certain religious groups that traditionally have large families (e.g., the Amish and the Mormons in the United States) are reputed to have unusually low crime rates. In the absence of extenuating circumstances, the r/K theory would predict that their crime rates would be unusually high. There is evidence that religiosity per se is associated with lower involvement in crime (Ellis and Peterson, 1996). If so, perhaps religious involvement is sometimes able to override the links between fertility and criminality predicted by r/K theory.
Hypothesis 4: Biological parents of criminals and psychopaths should themselves be criminal and psychopathic. Since the r/K theory assumes that genetic factors underlie tendencies to learn deceptive/victimizing behavior, the biological parent of persons who exhibit high rates of criminal and antisocial behavior should themselves exhibit such behavior. The evidence supporting this deduction is substantial (Nagin and Farrington, 1992; Raine, 1993:245; Robins et al., 1975; Rutter and Giller, 1984:182; West and Farrington, 1973:125).

While there are certainly environmental explanations for why criminality runs in families (e.g., bad example, poor supervision), environmental theories would not predict that the tendency would be any different for genetically intact compared to adoptive families. The r/K theory would predict that intergenerational links in criminal tendencies would be substantially reduced in the case of adoptive families. One study was located that seemed to bear directly on this hypothesis; it found a lower intergenerational correlation for criminality in adoptive families than in genetically intact families (Hutchings and Mednick, 1977:130).

Hypothesis 5: To the extent that racial/ethnic differences exist regarding the r/K continuum, r/K differences should parallel race/ethnic differences in criminality and psychopathy. That is, if one racial/ethnic group exhibits r traits more than another, it should also exhibit criminal and antisocial behavior to a greater degree. The most controversial aspect of the r/K theory has been its implication that there may be an evolutionary foundation for racial/ethnic differences in criminal and antisocial behavior. Several evolutionary theorists have suggested that among the three most widely recognized racial/ethnic groups, blacks exhibit r-strategy traits the most, Asians the least, and whites to an intermediate degree (Ellis, 1987, 1989a:92, 1993:166; Miller, 1994; Rushton and Bogaert, 1988; Walsh, 1995a:147). In other words, compared to whites, blacks have higher birth rates, higher rates of prematurity, lower birth weights, higher twinning rates, larger family sizes, earlier onset of sexual activity, and higher rates of child abuse and neglect (Ellis, 1987; Rushton, 1988).

While recognizing that measuring both criminality and race is very imprecise, evidence still suggests that wherever two or more different racial groups exist in significant numbers, blacks exhibit higher average rates of crime than do whites, and whites in turn have higher rates than Asians (Ellis, 1988:532; Walsh, 1995a:188). The racial differences are especially distinct in the case of serious and persistent aggressive criminality. Currently, little evidence exists regarding racial or ethnic differences in psychopathy.

If one attributes these obviously sensitive empirical findings to various forms of racism on the part of whites (who predominate in most of the countries in which the research on race and crime has been conducted),
one would be obliged to explain why Asian groups would be less criminal than whites in white-dominated societies.

The r/K theory is currently the only criminological theory that offers a specific explanation for why white crime rates would be intermediate to those of blacks and Asians and that at the same time predicts the ordering of these three racial groups in terms of such reproductive traits as birth weights, birth rates, twinning rates, and age of onset of sexual activity, both within and between races and ethnic groups (see Ellis, 1987). To test the theory further as it pertains to race and criminality, there is a need to extend comparisons beyond the three main racial groups to include other racial categories and numerous ethnic subcategories.

**Hypothesis 6:** *Whichever social class (or stratum) exhibits the most r-strategist traits should also exhibit the greatest degree of criminal and antisocial behavior.* The cheater theory and many social environmental theories specifically predict an inverse correlation between social status and criminality. In contrast, the r/K theory, especially as formulated by Ellis (1993:164), predicts that it is mainly the lower social stratum in which criminality will be unusually high and that there will be little difference between the middle and upper strata. To the degree middle- and upper-strata differences do exist, the Ellis version of the r/K theory actually predicts that crime rates will be slightly higher for the upper stratum than for the middle. While the evidence linking low social status with high criminality is fairly well established (Elliott, 1994; Ellis, 1988; for a contrary view see Tittle et al., 1978), no evidence was located specifically bearing on the hypothesis that crime rates will be slightly higher in the upper than in the middle strata.

**Hypothesis 7:** *Populations with low sex ratios (more women than men) should gradually shift toward an r strategy and have higher crime rates than populations with high or balanced sex ratios.* The r/K theory has recently led to a hypothesis about how sex ratios within human populations might be linked to crime rates (Walsh, 1995a:193; also see Lykken, 1995:219). To explain the reasoning underlying this hypothesis, we note that Guttentag and Secord (1983) published an informative review of evidence linking declining sex ratios with increases in out-of-wedlock births (also see Pedersen, 1991; South and Trent, 1988). They explain this association with a "gender (or dyadic) power" theory, which essentially asserts that whichever sex is in short supply will be able to dictate the nature of the mating environment. And, because males prefer more promiscuous mating patterns than do females, lowering a population's sex ratio will drive the population away from long-term marital relationships.

Guttentag and Secord's theory has a major shortcoming: It does not explain why males are more inclined than females to mate promiscuously; it simply assumes that this gender difference exists as a well-entrenched
cultural tradition. The \( r/K \) theory has no difficulty explaining gender differences in promiscuous preferences, since it is couched in modern evolutionary theory. As already noted, the tendency for males to prefer promiscuous mating more than females is theoretically due to the fact that they can reproduce more successfully this way than females can.

There are other differences between the \( r/K \) theory and the Guttentag-Secord theory regarding sex ratios and promiscuous mating. For example, the \( r/K \) theory suggests that low sex ratios will not only be associated with promiscuous mating patterns and out-of-wedlock births, but also with overall high birth rates, low birth weights, and high twinning rates, hypotheses to which the Guttentag-Secord theory is silent.

Further, \( r/K \) theory is not limited to the human species. In this regard, Krebs and Davies (1993:226) have shown that in various nonhuman species, low sex ratios are linked to promiscuous (nonpair bonding) mating patterns (also see Kvarnemo et al., 1995). As noted earlier in discussing child abuse and neglect, evolutionary theory would also lead one to expect to find a positive correlation between child abuse and neglect and rates of unstable bonding patterns.

Turning to how sex ratios should be linked to a broad range of criminal and antisocial behavior, a basic assumption of the \( r/K \) theory is that antisocial behavior is an evolved complement to an \( r \) reproductive strategy. If so, and if low proportions of males in a population drive a population toward \( r \) forms of reproduction, the theory predicts that criminal and antisocial behavior will increase in populations as the sex ratio drops and will gradually decrease whenever the sex ratio approximates equality or even becomes male biased (Walsh, 1995a:193). Without linking their analysis in any way to evolutionary theory, Messner and Sampson (1991) provided evidence that is fairly consistent with these predictions. On the other hand, an ethnographic comparison of homicide rates in six preliterate societies brought Hewlett (1991:26) to conclude that “those societies with high homicide rates also have male-biased juvenile sex ratios.” This is directly contrary to the \( r/K \) theory. Hypothesis 7 is also contrary to reasoning by Rowe (1996:300). Working from an evolutionary proposal as well, Rowe concluded that a relative abundance of males will drive males toward greater competition for sex partners, and thereby higher crime rates.

Overall, the \( r/K \) theory leads to numerous specific hypotheses about how reproductive traits should be correlated with criminal behavior. How well most of these hypotheses hold up under empirical scrutiny remains to be determined.

**DISCUSSION AND CONCLUSIONS**

Evolutionary theories have experienced a renaissance in criminology in the past two decades. Besides the theories described in this article, other
evolutionary theories of criminality have also been proposed, ones that do not explicitly stipulate genetic variability in human propensities to learn criminal behavior (e.g., Cohen and Machalek, 1988; Vila, 1994).

All of the modern evolutionary theories share only a faint resemblance to the first evolutionary theory in criminology proposed over a century ago by Lombroso. The dissimilarities are understandable in part because Lombroso knew nothing of the concept of genetics, nor did he have the benefit of the vast store of research on evolutionary principles developed over the past century or a modern understanding of how brain functioning controls behavior, including learned behavior. As a result, nothing resembling the concept of *atavism* is found in modern evolutionary theories of criminal behavior. In fact, rather than considering criminals throw backs to some primitive human form, most modern evolutionary theories of criminality imply the opposite: that criminal behavior may mark a special adaptation to life in large impersonal societies. If so, criminal and antisocial behavior may have only been adaptive over roughly the past 10,000 years at most, and only then primarily in urbanized environments.

**THE FIVE EVOLUTIONARY THEORIES OF CRIMINALITY**

We will summarize each of the five identified gene-based criminological theories that have been presented before discussing them collectively. They all share the assumptions that genetic factors predispose people to varying degrees toward victimizing criminal behavior and that natural selection has operated on human populations and subpopulations to favor varying tendencies toward criminal and antisocial behavior.

**Rape**

The evolutionary theory of rape (or sexual assault) asserts that men who are at least pushy with respect to seeking to copulate with multiple partners will typically have a reproductive edge over men who are not. Thereby, any genes promoting pushiness in males should spread throughout most populations, at least until significant countervailing forces are instituted. Because of their involvement in the gestation process, women have been favored by natural selection for being more cautious in mating and for attempting to confine their mating to men who appear willing and able to make long-term parental investments. These gender differences in optimal approaches to reproduction create tension between the sexes. According to the evolutionary theory of rape, one result of this tension is that a substantial proportion of males in most populations readily employ forceful copulatory tactics, especially when the prospects of being punished for doing so are low.
Spousal Assault

The evolutionary theory of spousal (and dating) assault contends that most instances of these crimes will in one way or another be associated with maintaining exclusive copulatory access. In other words, when either sex senses that a sexual relationship is in jeopardy, one of the fairly desperate response options will be to direct physical violence toward the spouse and/or the rival. From an evolutionary perspective, men should be more prone to employ such desperate tactics because they run the risk of cuckoldry, that is, inadvertently directing their parental investment toward someone else's offspring. Theoretically, spousal assaults should be most common in populations in which infidelity is most common.

Child Abuse and Neglect

The evolutionary theory developed to explain child abuse and neglect focuses on conditions that might sometimes give a reproductive edge to abusive parents. According to this theory, child abuse and neglect will be most probable among parents under the following four conditions: (1) Abusive and neglectful parents should tend to have more offspring than they can rear; thus, abuse and neglect should be associated with poverty and/or with large family size. (2) Victims of abuse and neglect should be children who are minimally viable from a reproductive standpoint; thus, physical and mental disabilities in children should be associated with abusive and neglectful behavior by parents. (3) When one parent shirks his or her parental responsibilities, the other should be inclined to do likewise; thus, child abuse and neglect should be associated with parental divorce and child abandonment. (4) If the genetic relationship between parent and child is low (or in doubt), child abuse and neglect should be relatively high; thus, abuse and neglect should be associated with adoption, stepparenthood, and infidelity by either of the parents.

We examined two general evolutionary theories of criminal and antisocial behavior: the cheater (or cad) theory and the $r/K$ theory. While both focus on the reproductive consequences of a criminal and antisocial lifestyle, they emphasize different aspects of those reproductive consequences. Whereas the cheater theory emphasizes how a significant proportion of mainly males should develop deceptive and victimizing behavior, and thereby bring about complex social measures to curtail such behavior, the $r/K$ theory concentrates on how criminality may have evolved to complement certain aspects of reproductive physiology and behavior.

The Cheater Theory

According to the cheater theory, males have been naturally selected to
make lower parental investment than women. This is partly because males can be more easily cuckolded into caring for unrelated offspring, and partly because they can sire far more offspring than females can possibly bear. At the same time, women have been naturally selected for choosing mates who will make high parental investments. According to cheater theory, one result of these competing natural selection forces has been to split males into two subpopulations. One subpopulation more or less complies with female preferences for males who make high parental investments (although still not as high as most women might prefer). The other (the cheaters or cads) merely mimic high-investing males and use devious tactics to opportunistically secure numerous sex partners. According to the cheater theory, these devious tactics often include the use of violence, chronic deception, and get-rich-quick tactics that can be extremely hurtful to others. The result is males who assault and thieve at unusually high rates.

**The r/K Theory**

The r/K theory of criminal and antisocial behavior asserts that criminals and psychopaths are at one end of an evolutionary continuum in terms of how they approach reproduction. At the \( K \) end are persons who proliferate their genes by investing inordinate time and energy in caring for a small number of offspring, and at the \( r \) end are persons who reproduce prolifically and provide minimal care for offspring.

As far as humans are concerned, criminals and psychopaths are hypothesized to exhibit traits associated with an \( r \) strategy. If this is so, several physiological/reproductive traits should help to distinguish criminals and noncriminals, on average. In particular, criminals should have somewhat lower birth weights, shorter gestation periods, and be more often the product of multiple births (e.g., twinning). Theoretically, they should also begin sexual activity relatively early (as should their parents), should come from large families, and should have more than an average number of children themselves.

The r/K theory is the only evolutionary theory of criminality that has ventured into the controversial realm of racial differences in criminal and antisocial behavior. As with social status, the theory does not predict which race or social status will have the highest rates of crime and psychopathy. Rather, it simply asserts that whichever racial/ethnic groups or social strata exhibit \( r \)-related traits to the greatest degree will also exhibit high rates of crime and psychopathy.

As this review has shown, numerous hypotheses may be derived from each of the five evolutionary theories of criminal behavior discussed. While several of these hypotheses are identical (or almost so) to ones
derived from strictly environmental criminological theories, several others are quite unique to the evolutionary perspective. Since most of these hypotheses have not been fully tested, the evidence is currently inadequate for passing judgment on the overall merit of these relatively new theories.

POSSIBLE PROXIMATE MECHANISMS

Before bringing this review to a close, it is worth noting that evolutionary theorists often distinguish two categories of causal variables: ultimate causes and proximate causes (Browne, 1995:1003; Thornhill and Thornhill, 1983:137). Ultimate causes refer to the natural selection forces that have favored genes for various combinations of traits, both physical and behavioral. Proximate causes (or proximate mechanisms) pertain to the detailed physiological events that mediate any genetic effects, especially on behavior. Even though the focus of this article has been on possible ultimate causes, it is important to think of these two categories of variables as complementary, not contradictory. Accordingly, we briefly identify some of the possible proximate mechanisms that may affect the probability of criminal behavior.

As noted above, it is naive to believe that there are actual genes directly coding for criminality. Nevertheless, there could still be numerous genes that influence how the brain works in ways that increase (or decrease) the probability of criminal behavior under various environmental conditions. One promising lead in this respect involves the sex hormone testosterone and its effects on brain functioning. Studies of various animal species have shown that the combination of high perinatal testosterone and high postpubertal testosterone increases the probability of aggression (especially dominance-related aggression) (reviewed by Ellis and Coontz, 1990). This high testosterone regimen is typical of male mammals, as opposed to female mammals (Ellis and Coontz, 1990). Thereby, genes functioning on the Y chromosome as well as on the autosomes early in fetal development may eventually help to explain sex differences in criminal behavior (especially violent criminal behavior) (Sluyter et al., 1996; Walsh, 1995b). Consistent with this reasoning are studies indicating modest correlations among males between circulating testosterone and persistent involvement in criminality (Christiansen and Knussmann, 1987; Dabbs and Morris, 1990; Mazur, 1995; Thiessen, 1990; Windle and Windle, 1995) and other forms of socially disruptive activities (Dabbs et al., 1996; Scerbo and Kolko, 1994).

Another promising lead for elucidating the genetic foundation for criminality involves an enzyme that is active in the brain, monoamine oxidase (MAO). This enzyme, which comes in two forms (MAO-A and MAO-B), helps regulate the chemical breakdown of various neurotransmitters, most
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notably serotonin and dopamine (Zuckerman, 1994:295) and its activity is almost entirely under genetic control (Ellis, 1991a:230; Zuckerman, 1994:297). Again, among the genes that are involved in regulating MAO activity are those on the Y chromosome that help control the formation of testes and thereby the production of testosterone during fetal development (and consequently later in life).

When testosterone levels are high, MAO enzyme activity is depressed (Ellis, 1991b:231), which is the basic reason males have lower MAO activity than females, especially following the onset of puberty. Within each sex (but especially among males), studies have found MAO activity to be low for individuals with histories of serious antisocial behavior and with problems of alcoholism and drug abuse (reviewed by Ellis, 1991a:235; Zuckerman, 1994:299).

Research still needs to determine why low MAO enzyme activity contributes to antisocial (and related) behavior, but it is not unreasonable to suspect that various neurotransmitters (especially serotonin) are involved. Supporting this view is evidence that low serotonin brain activity has been associated with impulsive, and sometimes violent combative, behavior—both in humans (Virkkunen et al., 1989) and in other animals (Kostowski et al., 1984; Vergnes et al., 1988).

Something that is particularly interesting about the link between serotonin and aggression is that this neurotransmitter has also been found to be affected by the positions animals assume in social hierarchies—serotonin levels generally are positively linked to high rank (Brammer et al., 1994; Yeh et al., 1996). Criminologists should explore the possibility that serotonin may be one of the proximate mechanisms whereby genes influence the relationship between criminality and social status.

Yet another way genes could be affecting criminality is through their effects on alcoholism. This would coincide with evidence that genes are responsible for much of the variation in susceptibility to alcohol abuse (reviewed by Koopmans and Boomsma, 1996) and that alcohol abuse is a major behavioral correlate of criminality and antisocial behavior (Greenfield and Weisner, 1995).

The main point being made with this brief coverage of some proximate physiological mechanisms (see Fishbein, 1990, for a more extensive review) is that evolutionary theories are in no way in opposition to the idea that other variables, both biological and social, contribute to criminal behavior. In the final analysis, the explanations for criminal behavior are likely to involve complex interplays among learning and genetic, hormonal, and neurochemical factors, all operating within a complex evolved social system.
IN CLOSING

In bringing this review to a close, we wish to emphasize that there is no fundamental difference between gene-based evolutionary theories and strictly environmental theories of criminal behavior on whether learning is responsible for variations in criminal behavior. For both theories, learning is important. The main difference is that gene-based evolutionary theories assume that learning is ultimately a neurological process highly influenced by genes, an assumption environmental theories do not make. If evolutionary (and other biosocial) theorists are correct on this point, criminologists in the future must not only know how the environment impacts the learning of criminal tendencies, but also how genes, the brain, and other biological factors interact with the environment to affect such learning. This article suggests that these interactions get played out in a time-worn evolutionary theater that may have had, and may continue to have, reproductive consequences.

Many believe that evolutionary theorizing in criminology is a thing of the past, all but abandoned in the early part of this century. This article shows that evolutionary theories of criminal and antisocial behavior have in fact reemerged during the past two decades in forms that the 19th Century theorists would scarcely recognize. These new theories show promise in offering new explanations for established observations as well as for generating new hypotheses. Decades of careful empirical testing will be required to assess the merit of many of these hypotheses.

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Zuckerman, Marvin

Zuravin, Susan J.

Lee Ellis is Professor of Sociology at Minot State University, Minot, North Dakota. His research interests cover a wide range of criminological and sociological topics. He recently edited and contributed six chapters to a two volume book series entitled Social Stratification and Socioeconomic Inequality (Praeger, 1993 and 1994).

Anthony Walsh is currently Professor of Criminal Justice at Boise State University, Idaho. His primary interest is the biosocial bases of behavior, particularly criminal behavior. His latest book is Biosociology: An Emerging Paradigm (Praeger, 1995). He is currently involved in writing a criminology textbook with Dr. Ellis to be published by Allyn & Bacon.