



Evolutionary theory and criminal behaviour

Vernon L. Quinsey*

Queen's University at Kingston, Ontario, Canada

Purpose. To provide an introduction to evolutionary psychology by describing some of its applications in the literature on the psychology of criminal and antisocial behaviour.

Argument. Selectionist thinking is applied to five areas: the relationship of age and sex to crime, the inverse correlation between degree of kinship and homicide, paedophilia, persistent antisociality, and sexual coercion. In each of these areas, ultimate causes of behaviour are distinguished from proximal causes. Ultimate causes are produced by selective forces in ancestral environments and are responsible for species typical characteristics. Proximal causes, in contrast, are contemporaneous developmental, genetic, and environmental determinants of behaviour.

Conclusions. The interplay between ultimate and proximal causation provides new ways of understanding old problems and is a fruitful source of research hypotheses. Evolutionary psychology can provide a powerful integrative perspective on criminal and antisocial behaviour.

Evolutionary theories seek explanations of criminal behaviour involving ultimate causes of species typical characteristics. Ultimate causes are the features of ancestral environments that selected particular characteristics observable in present populations through their historical relationship with differential reproductive success and are distinguished from proximal causes, the mechanisms that produce the characteristic in the present environment. Ultimate causes address 'why' questions, whereas proximal causes address 'how' questions.

Evolutionary theories are environmental and selectionist in orientation because past environments are posited to have selected characteristics of organisms by acting at the level of individual genes—specifically, causing genes associated with reproductive success to increase in frequency over generations (Crawford & Anderson, 1989). Notwithstanding the fact that the effects of ultimate causes are mediated genetically, evolutionary theories are also environmental in a more proximal sense because genes frequently cause organisms to act differently in different environmental contexts. Behaviours that are determined by the proximal environment are termed *facultative*, as opposed to *obligate* behaviours that develop to a large degree independently of variations in environmental context.

Characteristics of organisms that are produced by natural selection are adaptations. Adaptations, following Williams (1992), are identified by their functional design, their

Invited paper.

*Requests for reprints should be addressed to V. L. Quinsey, Psychology Department, Queen's University, Kingston, ON, Canada K7L 3N6 (e-mail: quinsey@psyc.queensu.ca).

plausible relation to reproductive success (fitness), their species typicality, and by the failure to account for them more parsimoniously with alternative explanations. Evolutionary psychology studies mental adaptations as reflected in behaviour. Because of their historical origin, adaptations are easier to imagine than their existence is to prove, necessitating a careful empirical, and complex conceptual approach to hypothesis testing (Holcomb, 1998).

A concrete example may facilitate an understanding of the approach of evolutionary psychology. Consider a man in an ancestral environment who preferred trees as sexual partners. We can surmise that this man is very unlikely to be among our ancestors if his tree preference was caused by genes, because these genes would decrease in frequency over generations relative to genes that focused male sexual behaviour on characteristics correlated with human female reproductive capacity. This difference in relative reproductive success would cause the evolution of a male psychology involving sexual preferences for correlates of female fertility and likely number of future offspring. The resulting set of preferences would be a genetically caused mental adaptation present in males and not females. Note that, even though the characteristic is genetically caused, it would be unlikely to be evident in traditional behaviour genetic investigations because these are designed to identify the degree to which *differences* among people are attributable to genetic influence, not to identify species-typical genetically caused traits. More technically, behaviour genetic studies yield heritability estimates, defined as the variance in a population characteristic attributable to genetic variation.

Note that, although this putative sexual preference adaptation in our example evolved because of its relationship to reproductive success, it need not directly cause men to desire having children. Rather, the adaptation could cause men simply to desire sexual activity with fertile women, reproductive physiology taking care of the rest. More generally, evolution has designed people so that they desire things and experience emotions that increased the reproductive success of people in ancestral environments, not necessarily that they consciously pursue fitness *per se*. This point is aptly summarized by the observation that people are 'adaptation executors' rather than 'fitness maximizers' (Buss, 1995; Tooby & Cosmides, 1990). As Daly and Wilson (1988, p. 10) put it: 'Our perceptions of self-interest have evolved as proximal tokens of expected gains and losses of fitness.'

There are very many excellent recent books and articles that can serve as introductions to evolutionary psychology. References can be found at the website of the Human Behavior and Evolution Society (<http://www.hbes.com>). A more detailed treatment of evolutionary theories of criminal behaviour can be found in Quinsey, Skilling, Lalumière, and Craig (in press).

Although relatively recent in its application to human behaviour, Darwinian selectionist thinking has been particularly fruitful in understanding people's motives for various actions, including criminal actions. In this article I briefly describe applications of selectionist evolutionary thinking to sex differences in criminality, sexual coercion, sexual deviance, kinship and crime, and persistent antisocial conduct. This is by no means an exhaustive list of topics in criminology that have received an evolutionary analysis but will serve to illustrate the breadth of applications of this approach. Topics of potential interest to criminologists which have been omitted include decision-making (Cosmides & Tooby, 1997; Gigerenzer & Hoffrage, 1995; Gigerenzer & Hug, 1992), spousal assault (Daly & Wilson, 1988), within-family genetic conflict (Haig, 1999), and cultural variations in interpersonal violence (Cohen, 1998; 2001).

Sex differences in criminality

The number of an ancestral woman's offspring was limited by pregnancy, lactation, and menopause. The number of an ancestral man's offspring, on the other hand, was limited mainly by the number of fertile women with whom he could mate. The number of *surviving* offspring of either sex was further limited by the resources available to raise them.

Because the principal effective limitation on a man's relative reproductive success was the number of his fertile female partners, men competed among each other for mating opportunities. The observed greater variance in male as opposed to female reproductive success indicates greater competition among men than among women. Thus, relative to women, men have been engaged in a riskier reproductive enterprise because some men have very many offspring and others none. One important way that men could compete among themselves, therefore, was in the acquisition of status and wealth. Powerful, wealthy men, having more resources to commit, would be more attractive to women. Cross-cultural evidence suggests that men who succeed in competition for resources and/or status tend to increase their number of mates and to have greater reproductive success. Understandably in this context, women prefer mates who are ambitious, industrious, and of relatively high socio-economic status (Buss, 1989; Buss & Schmitt, 1993). This remains true in contemporary industrial societies, for example, Pérusse (1993) found that unmarried men who scored high on measures of income, prestige, and power also scored high on a measure combining frequency of intercourse and number of sexual partners.

Because there is greater variance in male reproductive success than in female reproductive success and because males compete with each other for the principal limiting resource on their reproductive success, we expect men to be less risk-averse than women and particularly to be less risk-averse during that part of their lives when competition for mateships is most intense. These observations can explain the 'young male syndrome' of competitiveness, risk taking, and violence (Wilson & Daly, 1985). More precisely, these theoretical observations explain why males commit many more times the number of crimes than females and why the peak for the commission of crimes is in late adolescence for both sexes (female mating effort, although less intense than that of males, also peaks in adolescence; see Campbell, 1995). The relationship between age, sex, and crime was first observed by the 19th-century Belgian astronomer, Quetelet, and has been so commonly found as to be termed the 'fundamental data of criminology' (Ellis & Walsh, 2000). The decline in criminal behaviour associated with increasing age in adulthood is not a senescence curve but does resemble a testosterone output curve, as well as a curve representing mating effort and competition for mateships. The repeated observation that crimes of violence are most frequently committed by males against other males and that homicides are often committed by young men of poor socio-economic prospects engaged in verbal jousting in front of their peers, further supports an interpretation that crime is fundamentally related to inter-male competition that has its ultimate roots in reproductive rivalry (Daly & Wilson, 1988; Wilson & Daly, 1985).

The idea that the behaviours involved in delinquency are a manifestation of mating effort and inter-male competition is supported by the positive correlation between degree of delinquency and the likelihood of fathering children at a young age. For example, Stouthamer-Loeber and Wei (1998) found in a longitudinal study of inner city public schools in Pittsburgh that 12% of 506 males fathered a child before the age of 19. These men were more than 200% more likely than other men in the sample to have committed serious criminal acts. Delinquency did not decrease after fatherhood.

Sexual coercion

Evolutionary approaches to explanations of male sexual coercion can be found in Malamuth and Heilmann (1998), Lalumière, Quinsey, Harris, and Rice (in press), Thornhill and Palmer (2000), and Thornhill and Thornhill (1983). An evolutionary view of heterosexual relationships suggests that men and women both compete and compromise with each other because their reproductive interests are not always the same. The divergence of the reproductive interests of men and women is best shown by male sexual coercion, which circumvents female choice by definition.

Sexual coercion appears to be cross-culturally and historically universal, although its frequency varies over societies (Palmer, 1989). Rape is more common where there is frequent warfare (often for the purpose of acquiring women), where men are organized in fraternal interest groups, and where women have low status. Rape remains common in modern wars. In contrast to other types of crime, victims of rape are differentially likely to be females of reproductive age (for a review of the ethnographic and historical literature, see Lalumière *et al.*, in press).

Mating effort is defined as energy spent in locating, courting, and having sex with members of the preferred sex and age. In contrast, *parental effort* is investment in one's mate and offspring. Of course, mating effort is not always followed by parental investment. Men expend more mating effort than women, but there are important individual differences among men. Men who score high on questionnaire measures of mating effort also report higher sensation-seeking, more antisocial characteristics, more adversarial sexual beliefs, and greater past frequency and future likelihood of engaging in coercive sexual behaviours than men who score low on mating effort (e.g., Malamuth & Malamuth, 1999). Sexually coercive men have more extensive histories of uncommitted sexual relationships and greater preference for partner variety and uncommitted sex (Lalumière & Quinsey, 1996). Arrested rapists are often criminally versatile and of lower socio-economic status.

Men who repeatedly commit sexual offences are increasingly likely over offences to have intercourse with their victims (Walker, 1997). Compared to other men, predatory rapists show a relatively greater sexual interest in depictions of brutal sexual coercion than in consensual sexual activities (Harris, Rice, Quinsey, Chaplin, & Earls, 1992; Lalumière & Quinsey, 1993; 1994). Among institutionalized sex offenders, the interaction of psychopathy, as measured by the Revised Psychopathy Checklist (Hare, 1991) and phallometrically measured sexual deviance is a potent predictor of the commission of new sexual offences (Rice & Harris, 1997).

From an evolutionary viewpoint, men would be expected to be indifferent to female mating preferences when the costs of doing so are very low (as, for example, among soliders occupying conquered territory), when women are perceived as adversaries, when men are too intoxicated to calculate possible delayed costs of sexual aggression in dating situations, and when men can attract many partners and are correspondingly unconcerned about their future relationship with a particular woman (Lalumière, Chalmers, Quinsey, & Seto, 1996; Lalumière & Quinsey, 1999). Similarly, men who exhibit antisocial characteristics, such as callousness, are more likely to employ sexual coercion because these characteristics lower the perceived costs of coercion (Lalumière & Quinsey, 1996; Rice, Chaplin, Harris, & Coutts, 1994). Lastly, men who are preferentially aroused by coercive sex are expected to be more likely to rape because its benefits are perceived as higher relative to its costs.

Sexual deviance

The idea of sexual deviance itself is implicitly Darwinian. Sexual interests that focus on reproductively irrelevant features of partners, such as feet, or partners that are not reproductively appropriate because they are too young, dead, the same sex, or the wrong species are most likely to be considered sexually deviant or anomalous. As would be expected from a Darwinian account, sexual preference for members of non-human species is extremely rare (as opposed to sexual behaviours directed toward non-human species which are not all that uncommon).

The Institute for Sex Research at Indiana University, founded by Alfred C. Kinsey, was asked to submit a case . . . of Zoophilia, a specific Paraphilia Not Otherwise Specified that is recognized by DSM-IV. A computer search of their extensive files of thousands of people interviewed between 1938 and 1963 revealed 96 cases involving intensive sexual activity with animals, but in not a single case was the animal contact or the fantasy of contact with animals the preferred source of achieving sexual excitement. Unlike the other Paraphilias, sexual activity with animals may always be a second choice . . . Apparently there are no cases in which the idea of sexual activity with an animal is more exciting than the idea of sexual activity with a human (Spitzer, Gibbon, Skodol, Williams, & First, 1994, p. 253).

Although men are less choosy than women in short-term mating contexts, male sexual preferences are nevertheless tuned to the reproductively relevant characteristics of potential partners. Heterosexual men show a strong preference for young adult females, whether measured by ratings of sexual attractiveness, covertly measured viewing time, or penile plethysmography (Quinsey, Earls, Ketsetzis, & Karamanoukian, 1996; Quinsey, Rice, Harris, & Reid, 1993). Heterosexual men prefer average weight female figures with prototypical female hip to waist ratios (e.g., Singh, 1993). Strong age preferences are evident: men, regardless of their own age, prefer women in their early to late twenties. This age preference is thought to represent a compromise between maximal female reproductive potential (relevant to a long-term mating approach) and maximum fertility (relevant to a short-term mating approach). There is also strong inter-rater agreement on female attractiveness, even within the preferred sex and age category (e.g., Landolt, Lalumière, & Quinsey, 1995). Average faces with a mixture of neotenous (immature) and sex typical adult facial features are preferred (Johnson, 1999). However, heterosexual males are not totally unresponsive to female cues among non-reproductively viable females: their penile responses to prepubertal females, although much lower than to postpubertal females, are higher than their responses to prepubertal boys and to neutral stimuli (e.g., Quinsey, Steinman, Bergersen, & Holmes, 1975).

This direction of male sexual interest to signs of female reproductive capability strongly suggests that it is an adaptation. It is, therefore, puzzling that some males prefer prepubertal children as sexual 'partners'. This anomalous sexual age preference (paedophilia) is not apparent in ranking tasks, but shows clearly in phallometric assessments and in covertly measured viewing time (Quinsey *et al.*, 1975; Harris, Rice, Quinsey, & Chaplin, 1996). Of course, not all males who become sexually involved with children prefer them as sexual partners. Sexual behaviour and preference must be distinguished in this context; sexual behaviour is often an inaccurate reflection of sexual preference because of environmental constraints affecting access to partners. Sexual *behaviour* directed towards children is more easily explainable than sexual *preference* for children.

Male homosexuals' preference for adult male partners at first seems difficult to reconcile with an evolutionary viewpoint. In fact, anomalous gender preferences are more easily explained than anomalous age preferences because homosexuals may simply develop the sexual preferences of females due to a failure of the hormonal mechanism that ordinarily masculinizes the brain *in utero* (Ellis & Ames, 1987; Collaer & Hines, 1995). The clearest evidence for the failure of the *in utero* hormonal mechanism involves the fraternal birth order effect in which the likelihood of a male becoming a homosexual adult rises with each of his elder brothers born to the same mother (Blanchard, 1997). Differences between heterosexual and homosexual men in brain structure (LeVay, 1991), handedness (Lalumière, Blanchard, & Zucker, 2000), and dermatoglyphic asymmetry (Hall & Kimura, 1994) suggest that the most likely explanation for this repeated finding is that the mother's immune system becomes sensitized to the presence of a male fetus by prior male fetuses and, because it is designed to reject foreign material, interferes with the masculinization of the male fetal brain (Blanchard & Klassen, 1997). The placenta screens the foreign genome (paternally derived DNA) from the mother's immune system more successfully with female than male fetuses (Gualtieri & Hicks, 1985; Munn *et al.*, 1998). The aspect of the male fetus that sensitizes the mother's immune system has not yet been identified but could well be the human leucocyte antigen, which is present on the surface of all male cells with the exception of placental cells (Blanchard & Klassen, 1997). As expected, there is no birth order effect on women's sexual preferences (Bogaert, 1997).

Because a specific sexual preference for non-reproductively capable children would be negatively associated with reproductive success in either sex, how could such a preference arise, even as pathology? Quinsey and Lalumière (1996) have argued that the male sexual preference system comprises modules individually tuned to particular ancestral reproductive problems in partner selection and courtship. For example, homosexual males have the sexual partner preferences of females but the typically male courtship pattern associated with a relatively greater interest in partner novelty (Symons, 1979). From this account, we expect modules designed for detecting and appreciating, among other things, gender, youthfulness, body shape, and health. Independent malfunctioning of these modules could explain the observed individual differences in male sexual preferences. The bimodality of heterosexual and homosexual preferences among men suggests that there is a binary gender preference mechanism. Both comparative and human evidence (e.g., Bakker & Slob, 1997; Ellis, 1997; Grober, 1997) suggests that this switch is set via hormonal influence: in mammals, this occurs *in utero* and the default is a preference for a male body shape. When the switch malfunctions, the reverse preference is observed.

Quinsey and Lalumière (1995) hypothesized that a malfunctioning set of body shape detector/appreciators can lead to paedophilia. When these detectors malfunction, the youth detectors are left unconstrained, rendering prepubertal individuals the most attractive. Because the body shape detector/appreciators are based on adult body shape, their malfunction leads to the well documented increase in homosexual and bisexual preferences among paedophiles, and the smaller ratio of heterosexual to homosexual paedophiles compared to the ratio of heterosexual to homosexual non-paedophiles.

Lalumière, Harris, Quinsey, and Rice (1998) found preliminary evidence for the fraternal birth order effect in phallometric deviant indices for homosexual child-molesters, predatory rapists, and heterosexual child-molesters. The larger the number of older brothers, the more deviant the phallometric index. More recent phallometric

research has confirmed the fraternal birth order effect in preference for male partners among child-molesters but has not found the fraternal birth order effect in sexual age preferences (Blanchard & Bogaert, 1998; Bogaert, Bezeau, Kuban, & Blanchard, 1997; Côté, Earls, & Lalumière, 2001). Côté *et al.* also confirmed the relationship between hyperdominant sexual interests (as found among predatory rapists) and the number of older brothers. The fraternal birth order effect thus appears to be linked to some sexual preference anomalies (male preference and hyperdominance) but not paedophilic preferences. A maternal immunological explanation for paedophilic preferences does not, therefore, appear to be viable, necessitating a search for other (most probably neurodevelopmental) mechanisms.

Kinship and crime

Hamilton (1964) proposed that an individual's fitness is both individual, in the form of personal reproductive success, and indirect, through the reproductive success of others to the extent that they share that individual's genes. This concept of inclusive fitness has had a profound influence on evolutionary theory. In accord with Hamilton's gene-centred selectionist theory, altruistic behaviour in non-human animals has often been found to be nepotistic. Animals act not only to increase their own reproductive success (their individual fitness) but also those with whom they share polymorphic genes by common descent (their relatives).

Because crimes of theft and violence represent courses of action in which the interests of victim and perpetrator are in conflict, we expect nepotistic variation in crimes. Committing crimes against relatives is, in a sense, the opposite of nepotism. However, because the human condition has always been social, involving alliances and conflict among kin and non-kin, we should expect that notions of kinship are not dependent upon the actors involved being one's own relatives in that kinship would be expected to be important in one's judgments of the actions of non-relatives as well. Other group-living primates, such as vervets, are aware of which other individuals are related to each other and use this information in interacting with non-kin (Cheney & Seyfarth, 1990). One might think of kinship as an implicit premise of social contracts (Cosmides & Tooby, 1992) in which people have behavioural expectations of those connected by these contracts. People should thus be sensitive to differences in the genetic relatedness of others and expect kinship-based variations in nepotistic behaviour among them.

Two predictions concerning perceived crime severity can be derived from evolutionary theory. The first, arising from Hamilton's theory of inclusive fitness, is that crimes in general should be viewed as more serious to the degree that the victim is genetically related to the perpetrator. The second, arising from the deleterious effects of inbreeding depression, is that heterosexual sexual coercion should be perceived as more serious the closer the genetic relationship of victim and perpetrator, particularly when the victim is a female of fertile age. Perceptions of the severity of particular crimes, therefore, may be related not only to the nature of the crime but also to the genetic relationship of the victim and perpetrator.

Perceived seriousness is one of a number of elements determining societal responses to a particular crime, other determinants include the offender's previous criminal history, the degree to which the offender lacks criminal intent, and so forth. There is a surprising degree of consensus among people from different social classes and societies on the relative severity of different crimes (e.g., Wolfgang, Figlio, Tracy, &

Singer, 1985). Quinsey, Lalumière, Querée, and McNaughton (1999) asked 230 university students to estimate the magnitude of the severity of brief crime descriptions in three separate studies. In the first two, the genetic relatedness of victim and perpetrator was varied and in the third, the hypothetical genetic relatedness of the respondent and the fictitious victim was varied. All three studies found the linear relationships between genetic relatedness and perceived crime severity predicted by the inclusive fitness theory of altruism.

Perceptions are one thing but how about real crimes? Is the pattern of the most reliably recorded crime, homicide, in accord with the theory of inclusive fitness? Daly and Wilson (1988) have shown that murder among blood (as opposed to marital or in-law) relatives is relatively rare across societies and historical eras, particularly given the opportunity for such murders. People who act against their own fitness interests by killing consanguineous kin are likely to be perceived by others as mentally ill. Daly and Wilson's most compelling finding in support of this idea is that children are much more likely to be killed by step-parents than by natural parents. Stepchild status is the biggest risk factor for being a murder victim ever identified among children under 5 years old.

Persistent antisocial conduct

As reviewed earlier, most criminal offenders begin their criminal careers in mid-adolescence and desist by their mid-twenties. There are, however, a few individuals who exhibit serious antisocial behaviour in childhood, persist in their criminal behaviour in adulthood, and are responsible for a greatly disproportionate amount of criminal activity (Moffitt, 1993*a*). In accord with the findings from longitudinal studies, there is strong evidence from taxometric analyses that there is a discrete natural class of persistently antisocial adult male offenders identifiable from measures of adolescent antisocial conduct, psychopathy, and antisocial personality disorder (Harris, Rice, & Quinsey, 1994; Skilling, Harris, Rice, & Quinsey, in press). Similar analyses have identified a discrete class of antisocial youth from the self reported antisocial behaviours of an unselected sample of 11–14-year-old elementary school boys (Skilling, Quinsey, & Craig, 2001).

Findings from twin (e.g., Slutske *et al.*, 1997) and adoption studies indicate that genes exert an important influence on variations in antisocial conduct (for a review see Carey & Goldman, 1997). Shared environment effects, such as being raised in a particular family or neighbourhood, appear to be less important (Caspi, Taylor, Moffitt, & Plomin, 2000). Neuropathology, whether caused by genes or environment, exerts more important effects on criminality and aggressiveness (Brennan, Mednick, & Mednick, 1993; Gualtieri & Hicks, 1985; Moffitt, 1993*b*).

Evolutionary theorists (Frank, 1988; Mealey, 1995) have suggested that genes responsible for the class of persistently antisocial individuals are maintained in the population by frequency-dependent selection. Frequency-dependent selection means that the genes confer a reproductive or survival benefit at low frequencies in the population but not at higher frequencies. For example, genes associated with an exploitative and nonreciprocating approach to social exchange might prosper in a population of cooperative social strategists but would not be of any great advantage in a population already composed primarily of cheaters.

These considerations have led evolutionary theorists to propose typologies of offenders. For example, Mealey (1995) has suggested that adolescent-limited

delinquency is a facultative response to competitive disadvantage, whereas lifelong persistent antisocial conduct is a genetically caused obligate strategy. If Mealey's theory is correct, then lifelong persistent antisociality is not a result of pathology. Fluctuating asymmetry, randomly occurring deviations from left-right symmetry in measurements of various body parts, is a measure of developmental instability or perturbations. In accord with the view that persistent antisociality is an obligate life-history strategy and not the result of some sort of pathology, Lalumière, Harris, and Rice (2001) found that offenders who were rated as highly psychopathic on the Revised Psychopathy Checklist (Hare, 1991) were not distinguishable from community-recruited subjects on measures of fluctuating asymmetry, whereas less psychopathic offenders exhibited greater fluctuating asymmetry. Harris, Rice, and Lalumière (2001) found two separate paths to violent offending in a large sample of offenders from a maximum-security psychiatric institution: one involving psychopathy and another associated with neurodevelopmental insults.

Although a good deal more work remains to be done, the picture that is emerging from this line of research on individual differences in antisociality can be summarized as follows. First, there are delinquents who tend to start antisocial behaviour late and quit early. Their behaviour appears to be a manifestation of mating effort and intermale competition in response to competitive disadvantage (cf. Quinsey, Book, & Lalumière, 2001). A subset of these individuals are somewhat more persistent and exhibit significant neurodevelopmental anomalies. A much smaller group starts antisocial conduct much earlier and is more persistent. These individuals appear to form a qualitatively different discrete class. It appears likely, but has not yet been shown, that membership in this class is genetically caused.

Conclusions

Applications of selectionist thinking to understanding criminal behaviour have supplied answers to fundamental problems that have previously eluded explanation, such as the relationship of age and sex to crime and the inverse relationship between degree of kinship and homicide, have set interesting and provocative agendas for future research, as in the aetiology of paedophilia and persistent antisociality, and have organized a mass of observations with a few theoretical principles, as in the area of sexual coercion.

More important, however, is the shift in conceptual focus provided by Darwinian selectionist thinking. The study of criminal behaviour, like the study of behaviour in general, would no doubt profit from the integration with the life sciences that is encouraged by Darwinian theory. However, evolutionary psychology itself must adapt to changing circumstances. Given the heritability of criminal behaviour and the acceleration of its molecular explication, evolutionary theory must be made to incorporate behaviour genetic findings of individual differences into its traditional focus on species typical characteristics. The goal of evolutionary psychology is to provide an explanation of criminal behaviour that is consistent with the unifying theory of the life sciences. This goal is integrative, not imperialistic or cannibalistic. As we have seen, evolutionary thinking embraces ultimate and proximal causes, the latter including developmental, genetic, and environmental influences.

Acknowledgements

Preparation of the article was facilitated by an Ontario Mental Health Foundation Senior Research Fellowship and a research contract with the Providence Continuing Care Centre of

Kingston, Ontario. Small parts of the manuscript were adapted from Lalumière and Quinsey (1999) and Quinsey *et al.* (1999). I wish to thank J. Atkinson and T. Volk for comments on an earlier draft of this paper.

References

- Bakker, J., & Slob, A. K. (1997). Sexual differentiation of the brain and partner preference in the male rat: Behavioral, neuroanatomical, and neuroimmunocytochemical studies. In L. Ellis & L. Ebertz (Eds.), *Sexual orientation: Toward biological understanding* (pp. 91-106). Westport, CT: Praeger.
- Blanchard, R. (1997). Birth order and sibling sex ratio in homosexual versus heterosexual males and females. *Annual Review of Sex Research*, *8*, 27-67.
- Blanchard, R., & Bogaert, A. F. (1998). Birth order in homosexual versus heterosexual sex offenders against children, pubescents, and adults. *Archives of Sexual Behavior*, *27*, 595-603.
- Blanchard, R., & Klassen, P. (1997). H-Y antigen and homosexuality in men. *Journal of Theoretical Biology*, *187*, 373-378.
- Bogaert, A. F. (1997). Birth order and sexual orientation in women. *Behavioral Neuroscience*, *111*, 1395-1397.
- Bogaert, A. F., Bezeau, S., Kuban, M., & Blanchard, R. (1997). Pedophilia, sexual orientation, and birth order. *Journal of Abnormal Psychology*, *106*, 331-335.
- Brennan, P. A., Mednick, B. R., & Mednick, S. A. (1993). Parental psychopathology, congenital factors, and violence. In S. Hodgins (Ed.), *Mental disorder and crime* (pp. 244-262). Newbury Park, CA: Sage.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1-49.
- Buss, D. M. (1995). Psychological sex differences: Origins through sexual selection. *American Psychologist*, *50*, 164-168.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204-232.
- Campbell, A. (1995). A few good men: Evolutionary psychology and female adolescent aggression. *Ethology and Sociobiology*, *16*, 99-123.
- Carey, G., & Goldman, D. (1997). The genetics of antisocial behavior. In D. M. Stoff, J. Breiling, & J. D. Maser (Eds.), *Handbook of antisocial behavior* (pp. 243-254). New York: Wiley.
- Caspi, A., Taylor, A., Moffitt, T. E., & Plomin, R. (2000). Neighborhood deprivation affects children's mental health: Environmental risks identified in a genetic design. *Psychological Science*, *11*, 338-342.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University Press.
- Cohen, D. (1998). Culture, social organization, and patterns of violence. *Journal of Personality and Social Psychology*, *75*, 408-419.
- Cohen, D. (2001). Cultural variation: Considerations and implications. *Psychological Bulletin*, *127*, 451-471.
- Collaer, M. L., & Hines, M. (1995). Human behavioral sex differences: A role for gonadal hormones during early development? *Psychological Bulletin*, *118*, 55-107.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 163-228). New York: Oxford University Press.
- Cosmides, L., & Tooby, J. (1997). Dissecting the computational architecture of social inference mechanisms. In G. R. Bock & G. Cardew (Eds.), *Characterizing human psychological adaptations* (pp. 132-155). Chichester: Wiley.
- Côté, K., Earls, C. M., & Lalumière, M. L. (in press). Birth order, birth interval, and deviant sexual preferences among sex offenders. *Sexual Abuse*.

- Crawford, C. B., & Anderson, J. L. (1989). Sociobiology: An environmentalist discipline? *American Psychologist*, *44*, 1449-1459.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine.
- Ellis, L. (1997). Perinatal influences on behavior and health, with special emphasis on sexual orientation and other sex-linked behavior. In L. Ellis & L. Ebertz (Eds.), *Sexual orientation: Toward biological understanding* (pp. 71-88). Westport, CT: Praeger.
- Ellis, L., & Ames, M. A. (1987). Neurohormonal functioning and sexual orientation: A theory of homosexuality-heterosexuality. *Psychological Bulletin*, *101*, 233-258.
- Ellis, L., & Walsh, A. (2000). *Criminology: A global perspective*. Toronto: Allyn and Bacon.
- Frank, R. H. (1988). *Passions with reason: The strategic role of the emotions*. New York: Norton.
- Gigerenzer, G., & Hoffrage, U. (1995). How to improve Bayesian reasoning without instruction: Frequency formats. *Psychological Review*, *102*, 684-704.
- Gigerenzer, G., & Hug, K. (1992). Domain-specific reasoning: Social contracts, cheating, and perspective change. *Cognition*, *43*, 127-171.
- Grober, M. S. (1997). Neuroendocrine foundations of diverse sexual phenotypes in fish. In L. Ellis & L. Ebertz (Eds.), *Sexual orientation: Toward biological understanding* (pp. 3-20). Westport, CT: Praeger.
- Gualtieri, T., & Hicks, R. E. (1985). An immunoreactive theory of selective male affliction. *The Behavioral and Brain Sciences*, *8*, 427-441.
- Haig, D. (1999). Asymmetric relations: Internal conflicts and the horror of incest. *Evolution and Human Behavior*, *20*, 83-98.
- Hall, J. A. Y., & Kimura, D. (1994). Dermatoglyphic asymmetry and sexual orientation in men. *Behavioral Neuroscience*, *108*, 1203-1206.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, *7*, 1-52.
- Hare, R. D. (1991). *The Hare Psychopathy Checklist-Revised*. Toronto, Ontario: Multi-Health Systems.
- Harris, G. T., Rice, M. E., & Lalumière, M. L. (2001). Criminal violence: The roles of psychopathy, neurodevelopmental insults, and antisocial parenting. *Criminal Justice and Behavior*, *28*, 402-426.
- Harris, G. T., Rice, M. E., & Quinsey, V. L. (1994). Psychopathy as a taxon: Evidence that psychopaths are a discrete class. *Journal of Consulting and Clinical Psychology*, *62*, 387-397.
- Harris, G. T., Rice, M. E., Quinsey, V. L., & Chaplin, T. C. (1996). Viewing time as a measure of sexual interest among child molesters and normal heterosexual men. *Behaviour Research and Therapy*, *34*, 389-394.
- Harris, G. T., Rice, M. E., Quinsey, V. L., Chaplin, T. C., & Earls, C. (1992). Maximizing the discriminant validity of phallometric data. *Psychological Assessment*, *4*, 502-511.
- Holcomb, H. R. (1998). Testing evolutionary hypotheses. In C. Crawford & D. L. Krebs (Eds.), *Handbook of evolutionary psychology* (pp. 303-334). London: Erlbaum.
- Johnston, V. S. (1999). *Why we feel: The science of human emotions*. Reading, MA: Perseus.
- Lalumière, M. L., Blanchard, R., & Zucker, K. J. (2000). Sexual orientation and handedness in men and women: A meta-analysis. *Psychological Bulletin*, *126*, 575-592.
- Lalumière, M. L., Chalmers, L. J., Quinsey, V. L., & Seto, M. C. (1996). A test of the mate deprivation hypothesis of sexual coercion. *Ethology and Sociobiology*, *17*, 299-318.
- Lalumière, M. L., Harris, G. T., & Rice, M. E. (2001). Psychopathy and developmental instability. *Evolution and Human Behavior*, *22*, 75-92.
- Lalumière, M. L., Harris, G. T., Quinsey, V. L., & Rice, M. E. (1998). Sexual deviance and number of older brothers among sexual offenders. *Sexual Abuse*, *10*, 5-15.
- Lalumière, M. L., & Quinsey, V. L. (1993). The sensitivity of phallometric measures with rapists. *Annals of Sex Research*, *6*, 123-138.

- Lalumière, M. L., & Quinsey, V. L. (1994). The discriminability of rapists from non-sex offenders using phallometric measures: A meta-analysis. *Criminal Justice and Behavior*, *21*, 150-175.
- Lalumière, M. L., & Quinsey, V. L. (1996). Sexual deviance, antisociality, mating effort, and the use of sexually coercive behaviors. *Personality and Individual Differences*, *21*, 33-48.
- Lalumière, M. L., & Quinsey, V. L. (1999). A Darwinian interpretation of individual differences in male propensity for sexual aggression. *Jurimetrics*, *39*, 201-216.
- Lalumière, M. L., Quinsey, V. L., Harris, G. T., & Rice, M. E. (in press). *The causes of rape*. Washington, DC: American Psychological Association.
- Landolt, M. A., Lalumière, M. L., & Quinsey, V. L. (1995). Sex differences and intra-sex variations in human mating tactics: An evolutionary approach. *Ethology and Sociobiology*, *16*, 3-23.
- LeVay, S. (1991). A difference in hypothalamic structure between heterosexual and homosexual men. *Science*, *253*, 1034-1037.
- Malamuth, N. M., & Heilmann, M. F. (1998). Evolutionary psychology and sexual aggression. In C. Crawford & D. L. Krebs (Eds.), *Handbook of evolutionary psychology* (pp. 515-542). Mahwah, NJ: Erlbaum.
- Malamuth, N. M., & Malamuth, E. Z. (1999). Integrating multiple levels of scientific analysis and the confluence model of sexual coercers. *Jurimetrics*, *39*, 157-179.
- Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *Behavioral and Brain Sciences*, *18*, 523-599.
- Moffitt, T. E. (1993a). Adolescence-limited and life-course-persistent antisocial behavior: A developmental taxonomy. *Psychological Review*, *100*, 674-701.
- Moffitt, T. E. (1993b). The neuropsychology of conduct disorder. *Development and Psychopathology*, *5*, 135-151.
- Munn, D. H., Zhou, M., Attwood, J. T., Bondarev, I., Conway, S. J., Marshall, B., Brown, C., & Mellor, A. L. (1998). Prevention of allogeneic fetal rejection by tryptophan catabolism. *Science*, *281*, 1191-1193.
- Palmer, C. T. (1989). Is rape a cultural universal? A re-examination of the ethnographic evidence. *Ethnology*, *28*, 1-16.
- Pérusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, *16*, 267-283.
- Quinsey, V. L., Book, A. S., & Lalumière, M. L. (2001). A factor analysis of traits related to individual differences in antisocial behavior. *Criminal Justice and Behavior*, *28*, 522-536.
- Quinsey, V. L., Earls, C., Ketsetzis, M., & Karamanoukian, A. (1996). Viewing time as a measure of sexual interest. *Ethology and Sociobiology*, *17*, 341-354.
- Quinsey, V. L., & Lalumière, M. L. (1995). Evolutionary perspectives on sexual offending. *Sexual Abuse*, *7*, 301-315.
- Quinsey, V. L., Lalumière, M. L., Querée, M., & McNaughton, J. K. (1999). Perceived crime severity and biological kinship. *Human Nature*, *10*, 399-414.
- Quinsey, V. L., Skilling, T. A., Lalumière, M. L., & Craig, W. (in press). *Juvenile delinquency: Understanding individual differences in antisociality*. Washington, DC: American Psychological Association.
- Quinsey, V. L., Steinman, C. M., Bergersen, S. G., & Holmes, T. F. (1975). Penile circumference, skin conductance, and ranking responses of child molesters and 'normals' to sexual and nonsexual visual stimuli. *Behavior Therapy*, *6*, 213-219.
- Quinsey, V. L., Rice, M. E., Harris, G. T., & Reid, K. S. (1993). Conceptual and measurement issues in the phylogenetic and ontogenetic development of sexual age preferences in males. In H. E. Barbaree, W. L. Marshall, & S. M. Hudson (Eds.), *The juvenile sex offender* (pp. 143-163). New York: Guilford.
- Rice, M. E., Chaplin, T. C., Harris, G. T., & Coutts, J. (1994). Empathy for the victim and sexual assault among rapists and nonrapists. *Journal of Interpersonal Violence*, *10*, 435-449.
- Rice, M. E., & Harris, G. T. (1997). Cross validation and extension of the Violence Risk Appraisal Guide for child molesters and rapists. *Law and Human Behavior*, *21*, 231-241.

- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, *65*, 293–307.
- Skilling, T. A., Harris, G. T., Rice, M. E., & Quinsey, V. L. (in press). Identifying persistently antisocial offenders using the Hare Psychopathy Checklist and DSM Antisocial Personality Disorder criteria. *Journal of Consulting and Clinical Psychology: Assessment*.
- Skilling, T. A., Quinsey, V. L., & Craig, W. (2001). Evidence of a taxon underlying serious antisocial behavior in boys. *Criminal Justice and Behavior*, *28*, 450–470.
- Slutske, W. S., Heath, A. C., Dinwiddie, S. H., Madden, P. A. F., Bucholz, K. K., Dunne, M. P., Statham, D. J., & Martin, N. G. (1997). Modeling genetic and environmental influences in the etiology of conduct disorder: A study of 2682 adult twin pairs. *Journal of Abnormal Psychology*, *106*, 266–279.
- Spitzer, R. L., Gibbon, M., Skodol, A. E., Williams, J. B. W., & First, M. B. (Eds.) (1994). *DSM-IV casebook: A learning companion to the Diagnostic and Statistical Manual of Mental Disorders—4th ed.* Washington, DC: American Psychiatric Press.
- Stouthamer-Loeber, M., & Wei, E. H. (1998). The precursors of young fatherhood and its effect on delinquency of teenage males. *Journal of Adolescent Health*, *22*, 56–65.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Thornhill, R., & Palmer, C. T. (2000). *A natural history of rape: Biological bases of sexual coercion*. Cambridge, MA: MIT Press.
- Thornhill, R., & Thornhill, N. W. (1983). Human rape: An evolutionary analysis. *Ethology and Sociobiology*, *4*, 137–173.
- Tooby, J. L., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, *11*, 375–424.
- Walker, W. D. (1997). *Patterns in sexual offending*. PhD thesis, Queen's University, Kingston, ON, Canada.
- Williams, G. C. (1992). *Natural selection*. Oxford: Oxford University Press.
- Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology*, *6*, 59–73.
- Wolfgang, M. E., Figlio, R. M., Tracy, P. E., & Singer, S. I. (1985). *The National Survey of Crime Severity*. Washington, DC: US Department of Justice, Bureau of Justice Statistics.

Received 10 August 2001; revised version received 24 August 2001