Criminal offending as part of an alternative reproductive strategy: investigating evolutionary hypotheses using Swedish total population data

Shuyang Yao a, Niklas Långström a, Hans Temrin b, Hasse Walum a,c,*

a Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Box 281, S-171 77 Stockholm, Sweden
b Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden
c Center for Translational Social Neuroscience, Yerkes National Primate Research Center, Emory University, 954 Gatewood Rd., Atlanta, GA 30329, United States

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A B S T R A C T

Criminality is highly costly to victims and their relatives, but often also to offenders. From an evolutionary viewpoint, criminal behavior may persist despite adverse consequences by providing offenders with fitness benefits as part of a successful alternative mating strategy. Specifically, criminal behavior may have evolved as a reproductive strategy based on low parental investment reflected in low commitment in reproductive relationships. We linked data from nationwide total population registers in Sweden to test if criminality is associated with reproductive success. Further, we used several different measures related to monogamy to determine the relation between criminal behavior and alternative mating tactics. Convicted criminal offenders had more children than individuals never convicted of a criminal offense. Criminal offenders also had more reproductive partners, were less often married, more likely to get remarried if ever married, and had more often contracted a sexually transmitted disease than non-offenders. Importantly, the increased reproductive success of criminals was explained by a fertility increase from having children with several different partners. We conclude that criminality appears to be adaptive in a contemporary industrialized country, and that this association can be explained by antisocial behavior being part of an adaptive alternative reproductive strategy.

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1. Introduction

Criminality is clearly costly to victims, their relatives and to societies. However, antisocial behavior can also often be costly to offenders. Consequences of a criminal life-style, such as incarceration and increased exposure to violence, can have negative effects on mating opportunities and survival. Still, criminal behavior may remain in the population despite the risk of adverse consequences if also associated with increased reproductive success as part of an alternative mating strategy. It has been suggested that criminal behavior evolved as a result of a reproductive strategy based on low parental investment reflected in low commitment in reproductive relationships. Rowe, for instance, argued that “crime results from an evolved behavioral strategy that maximizes mating effort and minimizes parenting effort” (Rowe, 1996). This idea rests on the fact that among mammals in general, males in contrast to females have substantial potential to increase their reproductive success by mating with multiple partners (Clutton-Brock, 1991). In humans, the minimal parental investment needed for a male can be perceived as no more than the effort necessary for a successful impregnation. Conversely, since human reproduction requires internal gestation and usually breastfeeding, prolonged maternal care has been essential for offspring survival throughout evolution. This difference in parental investment suggests that securing assistance from males, ideally the father(s), over longer periods of time to increase paternal provisioning is central to the female strategy to increase reproductive success (Clutton-Brock, 1991). The asymmetry between female and male strategies also implies that women will be choosier about whom they mate with than men are (Clutton-Brock, 1991).

Males can respond to females’ typical mate preference by complying with the female inclination and invest in offspring, or adopt an alternative reproductive strategy by trying to maximize the number of children along with minimizing parental effort in any of their offspring. Thus, it is possible for males to increase their reproductive success without paying the cost of parental investment either by dishonestly mimicking the courtship behavior of other males that do invest highly in offspring and therefore get to mate, or by forcing females to mate with them (Gross, 1996). This deceitful tactic is often referred to as a “cheater” strategy. According to the cheater theory of criminality, antisocial behavior is a consequence of the human version of a low parental investment reproductive strategy.
(Ellis & Walsh, 1997). The central notion is that variation in brain functioning that facilitates lifelong rule-breaking behavior is adaptive primarily because of the reproductive fitness advantages these traits have in comparison to reproductive strategies based on high parental investment.

If persistent criminal behavior reflected a reproductive cheater strategy, we would expect male criminals, compared to non-criminals, to invest less in committed relationships and engage more in casual sex. Further, this theory suggests that men committing non-sexual crimes will be more likely to commit sexual offences than individuals not adopting the cheater strategy. Previous studies have shown criminality to be linked to a promiscuous mating style, unstable marriages and lower levels of childcare and supervision (Ellis & Walsh, 2000). More specifically, in a review of the literature Ellis and Walsh found that 50 out of 51 studies investigating associations between mating behavior and criminality reported a positive relationship between criminal behavior and number of sex partners (Ellis & Walsh, 1997). Beaver, Wright, and Walsh (2008) used a gene-based approach and showed an association between number of sex partners and violent criminal behavior through a common genetic pathway engaging the dopamine transporter gene (DAT1) (Beaver et al., 2008). Another study, comprising 674 men, found that carriers of two copies of the same DAT1 polymorphism have significantly more sex partners, as well as significantly higher delinquency scores, than men who had one or no copies (Guo, Tong, & Cai, 2008). This particular gene variant is typically found among “people who need high levels of excitement and stimulation to activate their reward system in the same capacity as those with normally functioning reward systems” (DeLisi, 2009). Further, a British cohort study found that the 10% most antisocial men fathered 27% of the children (Jaffe, Moffitt, Caspi, & Taylor, 2003).

We investigated whether there was an association between criminality and outcomes related to the cheater theory (Ellis & Walsh, 1997) in a Swedish total population sample. First, we examined if criminal offenders had a relatively high reproductive success (number of biological children), which is a prerequisite for the cheater theory. Second, we hypothesized that male criminal offenders would be involved more often in short-term mating, less likely to engage in pair-bonded relationships and less productively monogamous than male non-offenders. Third, we posited that males convicted of other crimes would commit a majority of all sexual assaults, reflecting the idea that the cheater strategy is associated with forced mating. We investigated these hypotheses in both men and women, to elucidate sex differences in criminality from an evolutionary viewpoint.

2. Materials and methods

2.1. Dataset and study population

Using the unique personal identification number provided to all citizens and immigrants upon arrival to Sweden as key, we linked a series of longitudinal Swedish population registers. These were the total population, multi-generation, crime, national patient, prescribed drug, migration and cause of death registers and two sociodemographic databases; the National Censuses (1970, 1980, and 1990) and longitudinal integration database for health insurance and labor market studies (LISA by Swedish acronym, 1990-2009).

The total population register includes information about birth date and place, and the multi-generation register provided data on parents to index individuals born in Sweden after 1931 and living there after 1961, or to immigrants to Sweden before age 18. The crime register covers all convictions in lower court since 1973. We used conviction data since the Swedish Penal Code determines that offenders are convicted as guilty regardless of mental disorder or other medical conditions. Hence, non-custodial sentences or those that involve forensic psychiatric treatment due to medico-legal insanity are all included (Frisell, Lichtenstein, & Langstrom, 2011; Frisell, Pawitan, & Langstrom, 2012). Additionally, plea-bargaining is prohibited so conviction data accurately reflect the officially resolved criminality. Finally, the age of criminal responsibility in Sweden is 15 years and, hence, the crime register only includes individuals convicted at this age or later. The migration register provided information on dates and places for immigration/emigration. The cause of death, national patient and prescribed drug registers supplied data on death, medical diagnoses and prescribed and dispensed medications, respectively. Socio-economic information was obtained from the National Censuses (1970, 1980 and 1990).

Since crimes committed before age 15 were not recorded, we defined the study population as individuals born 1958–1994 and excluded individuals who died or emigrated from Sweden before age 15, thus enabling identification of all criminal convictions in the crime register (1973–2009). These criteria yielded a total study population of 4,849,478 individuals (2,483,243 males and 2,366,235 females). For this cohort, the multi-generation, crime, migration and cause of death registers have excellent coverage (Frisell, 2012).

2.2. Measures

2.2.1. Criminality

We assessed persistent criminality with an ordinal 4-category variable: without any criminal conviction, 1 conviction, 2 criminal convictions and 3+ criminal convictions, respectively. We also specifically examined the two major offence types among all criminal convictions: theft (22% of all registered criminal convictions) and non-sexual violent offences (8%). Violent offences were defined in accordance with previous studies (Frisell et al., 2011) and included homicide, assault, robbery, threats and violence against an officer, gross violation of a person’s integrity, unlawful coercion, unlawful threat, kidnapping, illegal confinement, arson, and intimidation. Attempted and aggravated versions of these offences were included wherever applicable. Both theft and violent offences were assessed by a binary variable (ever had a conviction or not).

2.2.2. Reproductive success

Following previous work investigating evolutionary hypotheses in contemporary human populations (Stearns, Byars, Govindaraju, & Ewbank, 2010), we selected fertility (number of biological offspring) to assess reproductive success. The multi-generation register provided data on number of children linked to each parent. Importantly, a recent study utilizing Swedish population data, found the genetic correlation between number of children and grandchildren to be 1.0 (Zietsch, Kuja-Halkola, Walum, & Verweij, 2014). Therefore, in contemporary Sweden, the number of biological children is equally accurate as a measure of fitness compared to the number of grandchildren.

2.2.3. Pair bonding

To test the relationship between persistent criminality and pair-bonding behavior, we compared marriage patterns of criminals and non-criminals. Two variables were created from LISA data; the first indicated if subjects had ever been married or not (“ever married”) and the other the likelihood of getting remarried (also implicating divorce) if once married (“number of marriages”).

2.2.4. Short-term mating

We used a proxy for short-term mating or casual sexual behavior; a binary variable indicating if a subject had ever been prescribed podophyllotoxin, the major medication for genital warts (Condyloma acuminiata). Podophyllotoxin was chosen because it is the only medication for a sexually transmitted infection (STI) in the prescribed drug register (data currently available for 2005–2009).
A recent study with the same population found dispensed podophyllotoxin a useful measure of the incidence of genital warts (Leval et al., 2012). Since genital warts are sexually transmitted, and the risk of STIs increases with number of sexual partners (Langstrom & Hanson, 2006; Wen, Escourt, Simpson, & Mindel, 1999), podophyllotoxin prescriptions could be regarded as a proxy for short-term mating/casual sexual behaviors.

2.2.5. Reproductive monogamy

Reproductive monogamy was measured by number of reproductive partners (Reichard & Boesche, 2003). We used multi-generation register data to identify with how many different partners subjects had biological children.

2.2.6. Sexual assault

As suggested by Ellis and Walsh (Ellis & Walsh, 1997), criminal offenders should be more likely to adopt a forceful copulatory tactic, the extreme manifestation of which is rape and sexual coercion. We acquired this information from the national crime register.

2.2.7. Covariates

We included variables potentially associated with both criminal and reproductive behavior as covariates. The year of birth (obtained from the total population register) could clearly influence the risk of committing a crime; based on that most offences are committed between ages 15–25 years and possible secular or cohort trends. This could hold also for fertility, number of sexual partners, number of reproductive partners and marriage patterns. Immigrant status has been associated with both rule breaking, primarily through associations with other familial and socioeconomic risk markers (Moehling & Piehl, 2009), and adherence to cultural norms influencing fertility and monogamy-related outcomes (Coleman, 2006). The migration register provided information on immigrant status defined as being born in Sweden or not. Previous studies suggest that both childhood socioeconomic position (Frisell et al., 2011; Tuvblad, Grann, & Lichtenstein, 2006) and number of siblings (Fischer, 1984; Kosova, Abney, & Ober, 2010; van den Oord, Boomsma, & Verhulst, 1994) are involved in the link between criminality and reproduction. We defined childhood socio-economic position as the highest occupation of either of the biological parents when the individual was between ages 5 and 15 years (data from National Censuses for those born 1970–1990). Socio-economic position was categorized as low (skilled and unskilled workers), medium (low- and intermediate-position white-collar workers) or high (high-position white-collar workers and self-employed professionals and entrepreneurs) (Frisell et al., 2011). We defined as total number of siblings (full- and half-siblings) all individuals who shared at least one parent with the index individual according to the multi-generation register. Those who lacked data for either parent were excluded from the analysis.

Research suggests that substance misuse is associated with increased risk for criminal behavior (Grann & Fazel, 2004) and decreased fertility (Power et al., 2013) also in the Swedish population. Further, mental disorders including schizophrenia, bipolar disorder, personality disorder and attention-deficit/hyperactivity disorder (ADHD), albeit often related to concomitant substance misuse, are related to both criminal behavior and fertility (Barkley, 2002; Del Giudice, 2010; Fazel, Langstrom, Hjern, Grann, & Lichtenstein, 2009; Fazel, Lichtenstein, Grann, Goodwin, & Langstrom, 2010; Mordre, Groholt, Kjelsberg, Sandstad, & Myhre, 2011; Richard-Devantoy, Olie, & Gourevest, 2009).

Data on substance misuse and mental disorders were obtained from the national patient register (inpatient care 1973–2009; non-GP specialist physician outpatient care 2001–2009) according to the 8th, 9th and 10th editions of the ICD. Included disorders were substance misuse (alcohol abuse or dependence [ICD-8: code 303; ICD-9: codes 303, 305.1; ICD-10: code F10, except x.5] and drug abuse or dependence [ICD-8: 304; ICD-9: 304, 305.9; ICD-10: F11-F19, except x.5]), schizophrenia (ICD8/-9 code: 295; ICD10: F20), bipolar disorder (ICD8: 296.1, 296.3 or 296.8; ICD9: 296A, C, D, E or W; ICD10: F30-F31), personality disorder (ICD8/-9: 301; ICD10: F60-F62) (Del Giudice, 2010; Fazel et al., 2009, 2010; Richard-Devantoy et al., 2009) and ADHD (ICD9: 314; ICD10: F90) (Larsson et al., 2013). ADHD caseness was also ascertained from the prescribed drug register based on ADHD-specific medications (methylphenidate [ATC code: N06BA04]; atomoxetine [N06BA09]; amphetamine [N06BA01]; and dexamphetamine [N06BA02]) (Zetterqvist, Asherson, Hallidner, Langstrom, & Larsson, 2013).

Finally, we considered impulsivity as a potential confounder affecting both criminality and outcomes in mating situations. Impulsivity is a stable individual characteristic reflected in risk-taking, lack of planning, and quick decision-making (Niv, Tuvblad, Raine, Wang, & Baker, 2012). Previous studies suggest differences in impulsivity between children likely to be involved in accidents and those less accident-prone (Manheimer & Mellinger, 1967). To tap impulsivity, we used a binary variable of any individual experiences of accidents requiring inpatient/outpatient care (external cause of injury, ICD-10 codes ‘V’, ‘W’ and ‘X0-XX’, data extracted from NPR).

2.3. Statistical analysis

We used Poisson regression to examine the association between all outcome variables considered counts (i.e., fertility, number of marriages, and number of reproductive partners) and criminal offending (predictor variable). Logistic regression was employed for binary outcome variables (i.e., ever married and genital warts infection). All statistical analyses were performed using SAS version 9.3 (SAS Institute Inc., USA).

3. Results

Table 1 shows the prevalence of criminal offending in our study cohort. A total of 27.8% of the males and 9.1% of females had been convicted at least once, whereas 7.7% of males and 1.0% of females had three or more criminal convictions. We present characteristics of convicted criminal offenders and non-offenders in Table 2. Compared to non-offenders, offenders had higher mean fertility, more reproductive partners and more marriages. Expectedly, higher prevalences of substance misuse, mental disorder and accidents were also found among offenders.

3.1. Criminality and reproductive success

To test the hypothesis that criminality is related to reproductive fitness, we modeled the relationships between criminal history and reproductive success, we found moderately strong (e.g., d = 0.39 and d = 0.26 for any conviction in men and women respectively), significant associations between criminality and fertility (p < 0.0001) in both men and women.
Table 3. Accounting for potential sociodemographic and psychiatric confounders attenuated the associations between criminal offending and fertility although they all remained significant. This suggests that criminals are more reproductively successful than non-criminals and sociodemographic and psychiatric confounders are unlikely to explain this association.

3.2. Criminality and pair bonding

Next, we investigated if our data supported the cheater theory. This theory, based on the notion that there are significant sex differences in variability in reproductive success, is inarguably more applicable to male criminality. Nonetheless, we included both men...
Table 3


<table>
<thead>
<tr>
<th>Definition of crime</th>
<th>Men</th>
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<th>Women</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crudea</td>
<td>Adjustedb</td>
<td>Poisson regression coefficient</td>
<td>Wald chi-square</td>
<td>Crudea</td>
<td>Adjustedb</td>
<td>Poisson regression coefficient</td>
<td>Wald chi-square</td>
</tr>
<tr>
<td>1 conviction</td>
<td>0.132*</td>
<td>0.046*</td>
<td>5588.59</td>
<td>509.63</td>
<td>0.104*</td>
<td>0.041*</td>
<td>2206.51</td>
<td>242.23</td>
</tr>
<tr>
<td>2 convictions</td>
<td>0.156*</td>
<td>0.048*</td>
<td>3583.35</td>
<td>246.92</td>
<td>0.143*</td>
<td>0.058*</td>
<td>867.01</td>
<td>91.02</td>
</tr>
<tr>
<td>3 + convictions</td>
<td>0.144*</td>
<td>0.044*</td>
<td>4409.86</td>
<td>249.10</td>
<td>0.116*</td>
<td>0.023</td>
<td>499.05</td>
<td>10.93</td>
</tr>
<tr>
<td>Any theft conviction</td>
<td>0.068*</td>
<td>0.016*</td>
<td>1096.22</td>
<td>42.97</td>
<td>0.110*</td>
<td>0.031*</td>
<td>1456.42</td>
<td>72.23</td>
</tr>
<tr>
<td>Any violent crime conviction</td>
<td>0.138*</td>
<td>0.086*</td>
<td>3259.89</td>
<td>763.81</td>
<td>0.186*</td>
<td>0.117*</td>
<td>1073.32</td>
<td>261.47</td>
</tr>
</tbody>
</table>

Note: a) Regression coefficients were calculated from Poisson regression models adjusting for birth year. b) Coefficients were calculated as in crude models but also adjusting for immigrant status, childhood socioeconomic position, number of siblings (full and half-siblings), psychiatric disorder (schizophrenia, bipolar disorder, personality disorder, ADHD and substance misuse) and accidents requiring inpatient care.

and women but stratified all analyses by sex. First, when addressing if criminality was linked to less committed pair bonding, criminal offenders were less likely to marry than were non-criminals irrespective of the definition of persistence of criminality (Table 4.1). Further, if ever married, additional marriages were more common among criminal offenders (Table 4.2). We observed no notable difference between males and females regarding criminality and marriage patterns.

3.3. Criminality and short-term mating

To examine the association between criminality and short-term mating, dispensed podophyllotoxin prescriptions were used as a proxy measure of higher numbers of sexual partners. Criminality was related to genital warts medication across strata of criminality persistence in both men and women (only significantly so in the first two strata for women), as well as for theft and violent crime (Table 5).

3.4. Criminality and reproductive monogamy

The link between criminal behavior and reproductive monogamy was assessed with the number of mating partners with whom each index individual had children (Table 6). Associations were overall moderately strong, positive and significant across sexes with a tendency towards more robust associations for individuals with more persistent and violent criminal careers. This suggested that criminal offending is clearly associated with reproductively non-monogamous mating.

3.5. Criminality and sexual assault

To investigate directly if general criminality is related to rule-breaking behavior in a mating context we computed the proportion of all sexual criminal offenders with convictions for any other type of criminal act. Overall, 2637 of 3358 (79%) male offenders of rape or sexual coercion against adults (largely women) had one or more convictions (other than rape or sexual coercion).

3.6. The mediating effect of reproductive monogamy

To more directly test if our data is in line with the theoretical we investigated if variation in monogamous behavior had a mediating effect on the association between criminality and reproductive success. Therefore, we controlled for number of reproductive partners in the Poisson regression model (Table 7). This indicator of alternative

Table 4.1


<table>
<thead>
<tr>
<th>Definition of crime</th>
<th>Crudea</th>
<th>Adjustedb</th>
<th>Poisson regression coefficient</th>
<th>Wald chi-square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Men</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 conviction</td>
<td>0.102*</td>
<td>0.021*</td>
<td>43.96</td>
<td>16.96</td>
</tr>
<tr>
<td>2 convictions</td>
<td>0.041*</td>
<td>0.078*</td>
<td>75.69</td>
<td>29.75</td>
</tr>
<tr>
<td>3 + convictions</td>
<td>0.078*</td>
<td>0.113*</td>
<td>375.66</td>
<td>104.92</td>
</tr>
<tr>
<td>Any theft conviction</td>
<td>0.047*</td>
<td>0.037*</td>
<td>156.90</td>
<td>36.36</td>
</tr>
<tr>
<td>Any violent crime conviction</td>
<td>0.073*</td>
<td>0.046*</td>
<td>253.20</td>
<td>60.49</td>
</tr>
<tr>
<td>Women</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>1 conviction</td>
<td>0.054*</td>
<td>0.030*</td>
<td>184.48</td>
<td>68.84</td>
</tr>
<tr>
<td>2 convictions</td>
<td>0.113*</td>
<td>0.030*</td>
<td>167.74</td>
<td>52.71</td>
</tr>
<tr>
<td>3 + convictions</td>
<td>0.194*</td>
<td>0.078*</td>
<td>458.14</td>
<td>117.84</td>
</tr>
<tr>
<td>Any theft conviction</td>
<td>0.088*</td>
<td>0.051*</td>
<td>317.60</td>
<td>63.04</td>
</tr>
<tr>
<td>Any violent crime conviction</td>
<td>0.151*</td>
<td>0.101*</td>
<td>208.25</td>
<td>56.45</td>
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</table>

Note: OR: odds ratio, CI: confidence interval. a) Odds ratios were obtained with logistic regression models adjusting for birth year. b) Odds ratios were calculated as in crude models but also adjusted for immigration status, childhood SEI, number of siblings (full and half-siblings), psychiatric disorder (schizophrenia, bipolar disorder, substance misuse, ADHD and personality disorder) and accidents requiring inpatient care.

* p < 0.0001.
reproductive strategies was the one available for the total population that simultaneously had high coverage. Importantly, when adjusting for number of reproductive partners, the association between criminality and fertility expressed in number of offspring changed drastically from positive to negative values. In other words, criminal offenders had fewer children with each partner but increased their fertility above that of non-offenders by mating and conceiving children with more partners.

Finally, we observed overall trends that associations between criminality and all reproduction-related variables appeared stronger for increasing number of criminal convictions (1, 2 versus 3+) in men, and for most of the reproduction related measures in women.

4. Discussion

First, using criminal conviction data for all 4.8 million men and women in the total Swedish population born in 1958–1995, we showed that criminal offending is indeed associated with increased reproductive success compared to a non-criminal lifestyle. We used a sample much larger than that used in the only prior study that directly focused the relationship between number of children and reproductive success compared to a non-criminal lifestyle. We showed that criminal behavior could be a by-product of a successful alternative mating strategy. We show an association between criminality and reproductive success, but it should be noted that the reproductive advantage hypothesis is not mutually exclusive with current individual-oriented psychological theories on the development and persistence of criminal behavior (Andrews & Bonta, 2010). The cognitive distortions, affective instability, impulsivity and risk-taking that characterize criminal offenders could mediate at least part of the reproductive advantage of anti-social behavior. Several of these traits are known to be substantially heritable (Frisell et al., 2011; Larsson, Anckarsater, Rastam, Chang, & Lichtenstein, 2012; Larsson, Andershed, & Lichtenstein, 2006) and could therefore have an evolutionarily nontrivial effect on the associations between criminal offending and reproductive outcomes. We addressed this issue by including individual psychopathology diagnosed as schizophrenia, bipolar disorder, ADHD, personality disorder, substance misuse as more reproductive partners. Hence, on average, offenders have fewer children with each partner than non-offenders but raise their fertility beyond the general population average by having children with multiple partners. Stronger support, particularly in men, was suggested the more persistent the criminality pattern appeared to be.

Fertility (the number of live-born children in this study) is a reliable measure of reproductive fitness in the current population. It reflects both successful offspring survival and the passing of genes down to the next generation (Zietsch et al., 2014). Although prior research has suggested that criminal behavior is associated with larger family size (Ellis, 1988; Fischer, 1984; van den Oord et al., 1994); a potential indicator of higher fertility (Kosova et al., 2010), possible mechanisms behind the relationship between criminality and number of children have not been directly addressed.

Our results are in line with the idea based on evolutionary theory that criminal behavior could be a by-product of a successful alternative mating strategy. We show an association between criminality and reproductive success, but it should be noted that the reproductive advantage hypothesis is not mutually exclusive with current individual-oriented psychological theories on the development and persistence of criminal behavior (Andrews & Bonta, 2010). The cognitive distortions, affective instability, impulsivity and risk-taking that characterize criminal offenders could mediate at least part of the reproductive advantage of anti-social behavior. Several of these traits are known to be substantially heritable (Frisell et al., 2011; Larsson, Anckarsater, Rastam, Chang, & Lichtenstein, 2012; Larsson, Andershed, & Lichtenstein, 2006) and could therefore have an evolutionarily nontrivial effect on the associations between criminal offending and reproductive outcomes. We addressed this issue by including individual psychopathology diagnosed as schizophrenia, bipolar disorder, ADHD, personality disorder, substance misuse as
well as impulsivity as covariates in our analyses. These variables did not fully explain the reproductive outcomes — criminality association. Although it is likely that we failed to capture the full variation in pertinent traits, our analyses provided convincing evidence of a persistent association between criminality and reproductive fitness when controlling also for other known risk factors.

Predictions about future evolutionary change can be done by combining information regarding selection strength and quantitative genetics (Lande & Arnold, 1983). The fact that previous studies using the same Swedish data found criminal behavior to be moderately to highly heritable (Frisell et al., 2011; Kendler, Patrick, Larson, Gardner, & Lichtenstein, 2013), together with our results that offenders have higher fertility than non-offenders, may suggest an increase in criminal behavior in Sweden over coming generations. Naturally, if this was the case, our results could be seen as both surprising and alarming. However, more sophisticated statistical modeling is needed to determine what positive regression model coefficients could possibly tell us about future evolutionary change (Stearns et al., 2010). That is beyond the scope of the present study, but future research using Swedish total population data could be informative in that task.

The marriage patterns of the parents of criminal offenders (Ellis, 1988; Ellis & Walsh, 1997) and the association between criminality and marriage in offenders themselves (van Schellen, Apel, & Nieuwbeerta, 2012) have attracted substantial attention. Our result suggesting that convicted offenders are less likely to marry agrees with other recent research (van Schellen et al., 2012). In contrast, the finding that married criminals are more likely to remarry is novel. Altogether, this could suggest that criminal individuals are less likely to pair bond; that is, neither likely to enter married life nor to remain in such a committed relationship. Conversely, this agrees with other studies finding that monogamy could reduce crime rates (Bacon, Child, & Barry, 1963; Henrich, Boyd, & Richerson, 2012). However, especially violent criminal behavior peak in late adolescence and emerging adulthood in Sweden and many other industrialized countries (Frisell et al., 2011; Greenberg, 1985; Krug, Dahlberg, Mercy, Zwi, & Lozano, 2002) while marriage usually occurs later (for the first time in Sweden at 25–35 years of age). Therefore, our design can be considered largely longitudinal, suggesting that the association between marriage and criminality cannot be explained more than marginally by a marriage effect on criminality.

The higher number of reproductive partners among criminals is also worth highlighting. The nontrivial and significant coefficients suggested a correlation between this measure and criminality in men and women alike. Moreover, the striking mediating effect on the association between criminality and fertility is intriguing. It suggests that criminals have fewer children with each reproductive partner and display decreased commitment in reproductive dyads which, hypothetically, could also reflect lower parental investment.

The cheater theory aims at explaining criminal behavior from an evolutionary perspective, with focus on men. However, in our analyses the patterns remained largely the same in women, suggesting that criminality in both sexes is associated with an alternative mating strategy. This lack of sex specificity can at first glance seem to contradict the cheater theory since women cannot gain the same reproductive benefits from a non-monogamous mating style as men can. However, from a genetic perspective, when selection pressures are low, individuals on one sex both males and females often display the evolved trait due to high genetic correlation between sexes (Lande, 1980). Hence, it is possible that even if the selection pressures forming a cheater mating strategy, and consequently criminal behavior, acted primarily on men these traits can be displayed by women as well as long as they do not come with a substantial fitness cost in this sex. The genetic correlation between the sexes is for most complex traits positive and very strong (Vink et al., 2012). However, it is likely that women having short and unstable relations will face a fitness cost since this will to a large extent imply that they will care for their offspring by themselves. Alternatively, the association between criminality and fertility could be moderated by a personality type characterized by impulsivity and affective instability. We acknowledge that the measure used to assess impulsivity in this study do not capture all of the variance in the Swedish population and it is therefore possible that impulsive behavior could explain more of the fertility—criminality association than shown in our analyses. If the moderating effect of impulsivity is similar in men and women, no substantial sex differences in the association between criminality and fertility are expected.

A considerable strength of the present study is that we linked longitudinal national registers and, therefore, were able to follow a huge total population sample over several decades. Similarly, recall or reporting biases were avoided since we did not use self-reports. However, there are also limitations. Underreporting (Swedish National Council for Crime Prevention, 2008) and misclassification of criminal behavior are general problems with criminality research based on register data (Frisell et al., 2011). Misreporting rates of fathers’ identities (by mothers at the birth of each child) in the multi-generation register are unknown, but a review of international studies suggested an average rate of 3.7% (Belli, Hughes, Hughes, & Ashton, 2005; Frisell et al., 2011). Assuming that criminal men were under-reported as fathers, such a reporting bias would underestimate fertility differences between criminals and non-criminals. Another weakness is that we did not consider adoptations, but since inter-country adoption rates in Sweden are low, this is unlikely to have affected our results substantially. A low coverage of data for some variables led to large numbers of missing values and might have led to misclassifications. As mentioned in Methods, unrecorded cases were regarded as non-cases for diagnoses and prescribed drugs (mental

Table 7


<table>
<thead>
<tr>
<th>Definition of criminality</th>
<th>Men</th>
<th>Women</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adjusted</td>
<td>Adjusted</td>
</tr>
<tr>
<td></td>
<td>Poisson</td>
<td>Poisson</td>
</tr>
<tr>
<td></td>
<td>regression</td>
<td>regression</td>
</tr>
<tr>
<td></td>
<td>coefficient</td>
<td>Wald chi-square</td>
</tr>
<tr>
<td>1 conviction</td>
<td>0.046⁎</td>
<td>509.63</td>
</tr>
<tr>
<td>2 convictions</td>
<td>0.048⁎</td>
<td>246.92</td>
</tr>
<tr>
<td>3 + convictions</td>
<td>0.044⁎</td>
<td>249.10</td>
</tr>
<tr>
<td>Any theft conviction</td>
<td>0.016⁎</td>
<td>42.97</td>
</tr>
<tr>
<td>Any violent crime conviction</td>
<td>0.086⁎</td>
<td>763.81</td>
</tr>
</tbody>
</table>

Note: a) Poisson regression coefficients were calculated adjusting for birth year, immigration status, childhood SEI, number of siblings (full and half-siblings), psychiatric disorder (schizophrenia, bipolar disorder, substance misuse, ADHD and personality disorder) and accidents requiring inpatient care. b) Adjusted for number of reproductive partners.

⁎ p < 0.0001.
disorders, externally caused injuries and prescribed podophyllotoxin). Participants with missing values on any variable, except for marriage, childhood SEI and the number of siblings, were regarded as "non-exposed". Further, marriage data from before 1990 were not available. However, we believe that lack of information was largely independent of criminality so that misclassification did not substantially bias the results.

In summary, we found substantial support for the idea that criminality is associated with an evolutionary strategy that emphasizes mating effort over long-term reproductive partner investment. Indeed, despite strong negative societal feedback on criminal behavior, such a reproductive strategy appears successful also in the current Swedish population. Further studies are warranted to determine if our results are widely generalizable and to provide a more comprehensive picture of how evolutionary theory could explain the persistency of criminality in the population.

Acknowledgments

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References


