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Sexual Offending

Sexual behavior towards non-consenting individuals is a challenging topic for theoretical and empirical inquiry because there are many related terms that are inconsistently used. Generally, sexual offending is the broadest term that refers to a sexual act that may cause unwanted physical or psychological harm to the victim. Sexual aggression and sexual assault typically refer to physical and more severe forms of sexual offending. Sexual coercion is also a broad term but refers to forceful or manipulative tactics people use to obtain sex from a reluctant person that may result in either psychological or physical harm (Camilleri, Quinsey, & Tapscott, 2009). Some terms specify the relationship between perpetrator and victim, such as child molestation, incest, and partner sexual coercion. These distinctions are important because different types of sexual offending require different explanations (see Camilleri, 2012). Among non-human animals, analogous behaviors are referred to as forced copulation, resisted mating, and sexual coercion, or sometimes are discussed as a lack of female control over fertilization (see Box 2.1). Our review will involve a typology of sexual offending that allows for theoretical consistency

across these varieties of sexual offending. We will refrain from using the term “rape” more generally because (1) it is legally defined, which changes across times and jurisdictions, and (2) it is a severe form of sexual offending. Thus, our discussion will follow Camilleri’s (2012) typology to understand various types of sexual offending behavior by considering how they could function as an adaptation.

Throughout this chapter, we will also draw parallels from research on nonhuman animals, particularly examining work that involves sexual conflict over reproduction. Behavior of nonhuman animals is often studied using life history theory: the idea that natural selection has shaped the schedule and duration of key events in an animal’s life (e.g., age at first reproduction, investment in care for offspring) so as to maximize reproductive success (Stearns, 1992). Examination of behavior from a life history perspective often involves consideration of the flexibility (plasticity) of behavioral investment; for example, are animals fixed or flexible in their reproductive behaviors once they are set upon a particular life history trajectory? Also considered is the mechanism underlying development along a particular trajectory (e.g., the role of genetic and environmental factors on the development of adult reproductive behavior). Note that members of a species may differ in their life histories depending on variation in these factors. Here, we focus primarily on male alternative reproductive tactics (discrete variation in reproductive behavior; Boxes 2.1–2.3) and additionally discuss disordered sexual behavior among

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animals (Box 2.4) and examples of alternative reproductive tactics and sexual aggression among primates (Box 2.5).

Box 2.1: Introduction to Forced Copulation and Fertilization Among Nonhuman

Animals: Alternative Reproductive Tactics

Among animals, there are clear examples of sexual violence and aggression, particularly directed at females from males, and in some cases, this behavior can take extreme forms, involving direct male coercion and control of female reproduction and even forced copulation (see Muller, Kahlenberg, & Wrangham, 2009a; Palmer, 1989). As outlined in the discussion of variation in the behavior of human males, forcible copulation may be the result of selection as a mating tactic or an exaptation or by-product resulting from prior selection for increased male dominance and aggression. In some species, forced copulation is the standard form of mating (e.g., in some species of waterfowl; McKinney, Derrickson, & Mineau, 1983). Additionally, intra-male cooperation may also be involved in female-directed aggression and forced copulation, as when groups of males act collaboratively with one another to control or coerce a female (e.g., dolphin male alliances; see Connor & Vollmer, 2009). When females are at risk of forced matings, they may evolve counteradaptations to minimize harm and decrease the chance of fertilization resulting (e.g., cryptic female choice; Eberhard, 1996). Thus, the existence of male attempts to control female mating, and paternity of young results in a situation of sexual conflict between males and females.

However, in some species, coercive or forced sex is only carried out by some males in the population, while others engage in courtship and access mating only through female choice (Boxes 2.2–2.5). Therefore, there are differences in the degree to which males and females have differing preferences over fertilization (and therefore in the role male control and of female

counteradaptations) in any specific mating event. Some of the clearest examples of conflict over mating and fertilization between females and some males are in species that show discrete variation in male reproductive behavior, a phenomenon that is termed alternative reproductive tactics (Oliveira, Taborsky, & Brockmann, 2008). Alternative reproductive tactics are observed in many taxa and are defined by discrete variation in reproductive phenotype (behavior and often also morphology and physiology; see Oliveira et al., 2008 for recent review). Research has primarily focused on these tactics in males: while females also appear to show discrete variation in reproductive behaviors, it is unclear whether alternative female tactics are a rarer phenomenon or simply a less-examined one (see Henson & Warner, 1997; Neff & Svensson, 2013). For this reason and in the interests of drawing parallels with human variation, we focus here on examples from males, treating individual species as case studies that highlight the variation in reproductive conflict between males and females.

When examining alternative reproductive tactics, one important question that arises is whether tactics are flexible: that is, once reproductively mature, are individuals restricted to only one or a few of the potential tactics within a species or do they maintain the potential to engage in any of the tactics, given the correct situation? Alternative reproductive tactics may reflect fixed alternative life histories (see Box 2.2) that may result from a genetic polymorphism (obligate tactic) or be developmentally facultative (e.g., arising through epigenetic changes among individuals that share a common genome). The result of this fixed life history pathway is that individuals are, by the point of reproductive maturity, excluded from engaging in one or more of the tactics that exist in a species. Alternatively, tactics

(continued)

Box 2.1 (continued)

may show developmental flexibility, across the lifespan of the individual, such that individuals can switch between tactics facultatively on a long-term (e.g., based on growth) or short-term (e.g., based social environment) basis (see Box 2.3). While it can be debated whether these latter cases of short-term flexibility truly represent alternative reproductive tactics (as they may not demonstrate the discrete variation that typically defines alternative tactics; see Taborsky, Oliveira, & Brockmann, 2008), we nonetheless include such examples from nonhuman animals here, due to the parallels to the possible underlying mechanisms of rape and coercive sexual behavior in humans.

Among animals, the issues of coercive or forced sexual encounters can become challenging in terms of definition. First, there is an issue of external fertilization. While this eliminates the potential for unwanted copulation, females in many species may experience unwanted fertilization. Perhaps the clearest such examples come from fishes: in several species, some males engage in a sneaking tactic where they join in a spawning event and add their gametes to those of the actively spawning male and female (see Taborsky, 1994, 1998, 2001; note that in such species, sneaker males tend to be more successful when they are of a smaller size or engage in female mimicry and therefore decrease their likelihood of being noticed by the dominant male and spawning female). Although females in these species may not risk physical harm from sneaker males, there is the experience of conflict arising from these alternative male reproductive tactics, as females are unable to control fertilization of their eggs. When considering here the similarities between alternative mating strategies among human males and among animal species, we take a broad approach in

the animal examples, discussing general variations in reproductive phenotype associated with conflict over fertilization. Below we identify specific examples from nonhuman animals that generally involve male and female conflict, highlighting cases where such conflict also involves potential harm to females (see particularly Box 2.5 for specific examination of control and forcible copulation among primates).

Finally, a note on the mechanisms and physiological correlates of alternative reproductive tactics. While a popular topic of discussion in the examination of the underlying mechanisms and associated physiology, we do not go into detail on this point here. Rather, we note known and potential mechanisms when appropriate and direct curious readers to read more extensive examinations of these topics (see Oliveira et al., 2008). It is clear that as our understanding of variation in human reproductive behavior increases, drawing these specific parallels to similar animal behaviors will be of importance, and we encourage readers to consider the value of understanding mechanisms when examining the potential evolutionary basis of behavioral variation.

Psychological and Behavioral Adaptations

The adaptationist program in evolutionary psychology identifies how psychological phenotypes (i.e., thoughts, feelings, or behaviors) could have been naturally or sexually selected to overcome barriers to fitness. Generally, a trait is adaptive if it has specialized design features that function to increase the organism's fitness and if they are complex, precise, efficient, reliable, and economical (Williams, 1966). Fitness benefits can be tested by observing how variations in the trait are related to variations in reproductive success. Investigating psychological adaptations with humans poses unique challenges because there are obvious limits

to manipulating traits and in measuring fitness. This does not mean adaptationist approaches to human psychology are impossible—it just means the methods need to be more comprehensive.

Evidentiary standards for adaptations have been elaborated in great detail. Schmitt and Pilcher (2004) reviewed how evidence for adaptations requires both theoretical and empirical support, and because psychologists study constructs that are not always directly observable and are noisy, they look for convergent evidence from theoretical, psychological, medical, physiological, genetic, phylogenetic, anthropological, and cross-cultural research. Andrews, Gangestad, and Matthews (2002) identified six standards for identifying adaptations: comparative evidence, fitness maximization, benefits in ancestral environments, optimization models, tight fit between design features and its function, and inferring a trait's function from its form. Our review of the literature on sexual coercion will review evidence for these standards in varying degrees by considering the fit between theory and research data that support such hypotheses and by looking to other species for analogous behaviors to understand how sexual coercion could have evolved among humans.

Early Adaptive Explanations

The earliest evolutionary explanations focused on rape more generally by treating it as a homogenous behavior with a single ultimate explanation. Symons (1979) provided one of the first evolutionary accounts of rape by suggesting that due to a male mating psychology that is oriented towards high frequency mating, force is used with a non-consenting person when the costs of engaging in such behavior are low. The concept of costs and benefits was elaborated by Shields and Shields (1983), who suggested that because of differences in sexual strategies, deceitful and manipulative courtship, in addition to forcible rape, could have evolved.

A popular hypothesis, the mate deprivation hypothesis, has been proposed in different forms for over 30 years (Alexander & Noonan, 1979;

Lalumière, Chalmers, Quinsey, & Seto, 1996; Thornhill, 1980; Thornhill & Thornhill, 1983). This hypothesis posits that men are more likely to engage in sexually coercive behavior when the probability of mating through consensual means is low. Consistent with such an evolutionary approach were data indicating this behavior was mostly committed by younger men (since reproductive success is more strongly related to mate number among men) and is associated with lower socioeconomic status (Perkins & Klaus, 1996; Thornhill & Thornhill, 1983) and higher rates of pregnancy resulting from rape than from consenting sex (Gottschall & Gottschall, 2003). Also, analogous behaviors are found in nonhuman species, including other primates (Box 2.5). Another condition for adaptation is that the behavior must be universal—indeed, sexual offending is certainly found in all documented cultures and times (Brown, 1991; Lalumière et al., 2005), and evolutionary-minded researchers are also studying variability in rape prevalence rates across nations (e.g., Barber, 2000).

Accumulation of empirical tests of evolutionary hypotheses indicated more complexity in explaining sexual offending. In a non-forensic sample, Lalumière, Chalmers, Quinsey, and Seto (1996) found that sexually coercive men were not different from men who were not sexually coercive in terms of self-perceived mating sexual success and reported more instances of sexual experiences. These results were at odds with the mate deprivation model, and so Lalumière et al. proposed the micro-mate deprivation hypothesis—that men who are typically successful at mating resort to coercive sex when faced with refusal. Also in this time, individual difference characteristics were being associated with sexual offending, such as sexual preference for coercive sex (e.g., Lalumière & Quinsey, 1996), and conditions where sexual coercion could not have resulted in reproductive success emerged as counterarguments to evolutionary explanations, such as sexual offending against children (Coyne, 2003). More sophisticated evolutionary explanations were forwarded to account for these other types of offending behavior (Quinsey & Lalumière, 1995).

Table 2.1 Evolutionary typology of sexual offending

	Adaptation (Boxes 2.1 and 2.5)	By-product (Box 2.4)	Disorder (Box 2.4)
Obligate (Box 2.2)	Psychopathy	Sexual homicide	Developmentally disabled; incest
Facultative—developmentally fixed (Box 2.2)	Competitively disadvantaged	Sexual homicide	Paraphilias (pedophilia, zoophilia, gerontophilia) ^a
Facultative—developmentally flexible (Boxes 2.3 and 2.5)	Young male syndrome	Sexual homicide	Paraphilias (exhibitionism, voyeurism, toucherism, frotteurism)
	Cuckoldry risk		Pathological jealousy
	Sexual bullying		

See appropriate boxes where noted for analogous examples from nonhuman animals

^aThis type was included as an obligate disorder in Camilleri (2012), but considering the organizational effects of hormones on sexual preferences, these paraphilias can be thought of as disorders of developmentally fixed traits

Evolutionary Typology

Camilleri (2012) extended Lalumière et al.'s (2005) application of obligate and facultative adaptations towards sexual offending to account for differences in sexual offender types. This typology recognizes that any behavior can fall into one of nine categories by considering two dimensions: adaptive-maladaptive traits (adaptation, by-product, disorder) and obligate-facultative behavioral patterns (obligate and facultative developmentally fixed, which can be considered to be associated with fixed life history trajectories, and facultative developmentally flexible, which shows greater plasticity within individuals; see Table 2.1). This typology provides a theoretically meaningful way to categorize sexual offenders by suggesting etiological paths to sexual offending represents different types. Similar behavioral patterns are seen across nonhuman animals (see Box 2.1). Previous attempts at sexual offender typologies have treated traits or mechanisms as separate types. This is problematic because these traits or mechanisms may be descriptive of many sexual offender types, not diagnostic of any particular one (see Camilleri, 2012 for a review). Also, most typologies of sexual offenders lack theoretical reasons for including some traits and not others, as is found in the Massachusetts Treatment Center Rapist Typology (Knight, 1999). The types as presented here are based on our current understanding of the phenomena but can change depending on theoretical and research developments.

Obligate

Obligate traits, unlike facultative ones, are due to genetic differences between organisms, and so differences in behavioral patterns can be attributed to differences in genes. Although most psychological traits are considered facultative, there are some characteristics of people that may be considered obligate (i.e., heritable alternative strategy)—a likely candidate is personality (Buss, 1991). By definition, personality refers to individual differences in patterns of thoughts, feelings, and behaviors. Genes appear to account for stability in personality traits (McGue, Bacon, & Lykken, 1993) because particular genes may lead to decreased plasticity in personality development.¹

One path to sexual offending that may be obligate in its structure is *psychopathy* (Kinner, 2003; Mealey, 1995). Characteristics of psychopaths, such as leading a parasitic lifestyle and being manipulative, suggest their behavior is oriented towards exploiting others. Psychopaths are well known in forensic settings because they comprise approximately 15 % of prison populations (reviewed in Ogloff, 2006). Although there is substantial literature on psychopathy assessments, types, characteristics, and consequences (see Patrick, 2008), there is little agreement on the etiology of psychopathy. Understanding the causes of

¹ Although the explanation is more nuanced than simply “genes cause personality” (see Caspi, Roberts, & Shiner, 2005).

psychopathy is important for research on sexual offending because coercive sexuality appears to be a core factor (Harris, Rice, Hilton, Lalumière, & Quinsey, 2007), and there is a positive relationship between psychopathy and sexual arousal to non-consenting sexual scenarios (as cited in Harris, Lalumière, Seto, Rice, & Chaplin, 2012). Men who sexually molested children had significantly lower psychopathy scores than rapists and a combined group rapists who also molested children (Porter et al., 2000).

Evolutionary-derived explanations have suggested that psychopaths are a discrete class of individuals and that psychopathy as an obligate trait is maintained through frequency-dependent selection (Mealey, 1995)—particular trait or traits are optimal only when they exist as a certain percentage in a population. Selection favors the traits when they are rare and disfavors them when they are common. There are several lines of research that address this hypothesis, including taxometric analyses and behavioral genetics.

Psychopathy and taxometric analyses. Taxometric analyses are used to identify whether one or more discrete groups underlie a continuously measured construct (see Boxes 2.1–2.3 and 2.5 for discussion of an analogous phenomenon in animals—alternative reproductive tactics that show discrete variation in reproductive behavior). This method is useful to identify whether there are categorical differences between psychopaths and nonpsychopaths, because measurements on this construct vary on a continuous scale. Evidence of a taxon is consistent with viewing psychopathy as an obligate trait because taxa represent different types of people. To date, there are many studies that have looked at the taxometric structure of psychopathy: although early studies found support for a taxon (Harris et al., 2007; Harris, Rice, & Quinsey, 1994; Skilling, Quinsey, & Craig, 2001; Vasey, Kotov, Frick, & Loney, 2005), a larger number of studies are now indicating psychopathy varies on a dimensional scale (e.g., Edens, Marcus, Lilienfeld, & Poythress, 2006; Guay, Ruscio, Knight, & Hare, 2007; Marcus, John, & Edens, 2004; Walters, Brinkley, Magaletta, & Diamond, 2008). Explanations for these conflicting findings include methodological differences and the

suggestion that current measures of psychopathy are confounded because they include antisocial traits of nonpsychopathic criminals. Harris et al. (2007) identified a third factor of psychopathy, labeled coercive and precocious sexuality, and found that it also clustered into a taxon. This result was not replicated by Walters et al. (2011); however, their methods differed in that they did not run taxometric analyses on the precocious/coercive sex factor alone, but included those items in the PCL-R before running the analysis. Thus, this analysis included items that would appear among both psychopathic and nonpsychopathic offenders, making it difficult to discriminate between the two.

Finally, an important consideration when sampling from non-forensic populations is that there may not be a sufficient number of true psychopaths in the sample to detect a taxon because it is estimated they comprise only 3 % of the population. Because true base rates are unknown, we are unsure how long psychopaths may escape detection by the justice system; if the majority of psychopaths are identified and therefore typically incarcerated, this decreases our ability to sample them among a purportedly normal population.

Psychopathy and genetics. The most convincing evidence in support of psychopathy as an obligate trait is the extensive research on genetic contributions to psychopathy. If psychopathy is an obligate trait sustained through frequency-dependent selection, then genetic differences should account for a substantial proportion of variation in psychopathy. There have been several studies looking at the behavior genetics of both psychopathy and a related construct—antisocial personality. Not only have studies generally found robust genetic contributions to these constructs (Burt, 2009; Ferguson, 2010); a study found a strong genetic contribution to variation in psychopathic traits among 7-year-olds (callous, unemotional, and antisocial), with no effects of shared environmental effects (Viding, Blair, Moffitt, & Plomin, 2005). Longitudinal research also shows that early signs of psychopathy in adolescence are related to psychopathy later in life (Lynam, Caspi, Moffitt, Loeber, & Stouthamer-Loeber, 2007).

There are some suggestions that a common factor underlies psychopathy and antisocial

personality disorder (e.g., Skilling, Harris, Rice, & Quinsey, 2002). Larsson et al. (2007) found that a common genetic factor was related to both psychopathy and antisocial personality disorder and that a common shared environment was related to only antisocial personality disorder. Similar findings showed weaker genetic effects, compared to environmental effects, when considering antisocial behavior (Rhee & Waldman, 2002). These results are intriguing because they suggest greater environmental influence on nonpsychopathic offenders and greater genetic influence on psychopathic offenders. Similar to nonhuman species, it is difficult to tease apart different etiologies when the phenotypes are the same (see Boxes 2.1 and 2.2).

With genetic contributions to psychopathy established, researchers are now focusing their attention to exactly which genes may be associated with this disposition. Although no single gene has emerged as a primary candidate, investigations are now piecing together the complex impact genes, metabolic pathways, transporters, and neural receptors have on both antisocial behavior and psychopathy (reviewed in Gunter, Vaughn, & Philibert, 2010).

These results do not mean experiences have no impact on the development of psychopathy—epigenetics show some early promise (Gunter et al., 2010), and there are some early development factors that might impact psychopathy (Marshall & Cooke, 1999). The complexity of obligate traits suggests that changes in tactics are still possible (see Box 2.2), that a life history that is fixed does not mean that all behaviors associated with it are unchanging. Longitudinal research is still needed to get a better sense of the developmental trajectory of psychopathy. Not surprisingly, Blonigen, Hicks, Krueger, Patrick, and Iacono (2006) found stronger genetic contributions to stability of psychopathy traits over time and greater non-shared environment effects on psychopathic traits that changed over time. Interestingly, Harris, Rice, and Lalumière (2001) found the independent effects of psychopathy and neurodevelopment (i.e., environmental impact early in development) on criminality.

Considering the extent to which there are variable findings on psychopaths, the nature and

etiology of psychopathy have yet to be confirmed. Research that includes criminal and noncriminal populations using improved measures of psychopathy that include items only relevant to their diagnosis may help. Still, consistent with psychopathy as an obligate strategy, there are considerable data to suggest strong genetic contributions to its expression. If further confirmatory findings emerge, then implications for treatment suggest supervision and management may work best (Camilleri, 2012; Quinsey, Harris, Rice, & Cormier, 2006). Future research should consider the reproductive costs and benefits of psychopathy—data and models are needed to see whether psychopathy is reproductively viable and is indeed preserved through frequency-dependent selection.

Facultative: Developmentally Fixed

Behavioral phenotypes that are facultative but developmentally fixed mean the probability of its expression is consistently high across the lifespan once the mechanism is activated (which can also be conceptualized as fixed alternative life history pathways; see Box 2.2). These responses are still considered facultative because their expression depends on responses to certain environments. These mechanisms assist with explaining the smaller proportion of men who start their antisocial behavior at an early age, including sexual offending, and fail to desist. There are many examples where reproductive behaviors appear to change in response to environmental conditions early in development. As an example, precocious sexuality is related to poorer social conditions, such as socioeconomic status, life expectancy, neighborhood resources, and absence of a father, suggesting early-onset sexuality is a facultative reproductive response to lower probability of survival and mating success (reviewed in Thornhill & Palmer, 2004). Competitively disadvantaged men appear to fit this category.

In addition to finding that offenders clustered into adolescent-limited offenders (see “Young Male Syndrome”), Moffitt (1993) found another cluster they identified as life-course persistent—antisocial behavior starts early in development and

persists. The evolutionary typology proposed suggests that life-course persistent offenders could result either from a developmentally fixed path or an obligate path. One type, labeled the *competitively disadvantaged*, falls within the developmentally fixed path. According to Lalumière et al. (2005), this path includes men who experience either social or neural adversity early in development, resulting in lowered embodied capital whereby the benefits of adopting a high mating effort, risk taking, and antisocial reproductive strategies outweigh their costs. Theoretically, the reason why such a response becomes fixed is because poor environmental conditions early in development reliably signal poor mating opportunities later in life. We see such phenotypic adjustments in other species (see Box 2.2). In humans, there are many early social and neurodevelopmental correlates of crime that are consistent with this explanation.

Competitive disadvantage and social adversity. Much research has demonstrated a link between poverty and crime more generally and with rape more specifically. Variables associated with poor living conditions appear to be a fairly robust correlate of crime, such as income inequality (Daly, Wilson, & Vasdev 2001), antisocial parenting (Harris et al., 2001), and abuse victimization (Jespersen, Lalumière, & Seto, 2009). Interestingly, Ingoldsby and Shaw (2002), studying the effects of early environments on antisocial behaviors, found that middle of childhood may be a critical period where such environmental experiences might have longer-term consequences. SES has been linked to crime in general and sexual offending as well. In a meta-analysis, poverty was related to rape with a moderate effect size of 0.38 (Hsieh & Pugh, 1993). Although income inequality was not significantly related to rape in this meta-analysis, the effect size was strong and it was based on only two studies. A more recent study found that the Gini coefficient was related to rape, not other violent crimes (Choe, 2008).² These results suggest that conditions

indicative of competition, such as poverty or larger income disparity, are related to higher rates of sexual violence.

An assumption of each path to sexual offending being proposed here is that it is sex-specific—that is, the paths should be more strongly related to sexual offending among men than among women. Because sexual coercion promotes reproduction by increasing mate number, this strategy would not increase fitness among women. Tittle and Meier's (1990) review found that, more often than not, the relationship between SES and crime was more pronounced among men than women. The problem with this study was that it was a narrative review of the literature—meta-analytic reviews are therefore still needed. Another setback is that these studies focused on delinquency as the dependent variable. It is also possible that SES may have more similar impacts on the sexes for crime in general but greater effects on men for sexual offending.

The exact mechanisms through which poor conditions impact behavior are not well understood. There is emerging evidence, however, that social adversity experienced in childhood, such as socioeconomic status, affects regions of the brain that are related to social information processing (Noble, Houston, Kan, & Sowell, 2012), but it should be noted that links between neural processes and behavior, such as risk taking, require further work (Steinberg, 2007).

The timing of early experiences appears to be important to consider. In their review, Ingoldsby and Shaw (2002) argued that exposure to neighborhood stressors by middle childhood, such as economic disadvantage, violence, and deviant peer groups, may impact the trajectory of early-onset antisociality. Subsequent research were consistent with this model whereby some support was found for early childhood exposure to parent-child conflict and neighborhood problems were related to early signs of antisocial behavior, and that antisocial peer groups later in childhood seems to maintain antisocial behaviors (Ingoldsby et al., 2006). Still, there were a group of children who had these early exposures yet their antisocial behavior declined with age, so there may be other factors that contribute to

² How poor regions within a location are clustered does not appear to matter. Poverty clustering was not found to be related to rape (Stretesky, Schuck, & Hogan, 2004).

life-course persistent antisociality. For example, there appears to be additive effects of early risk factors on adolescent antisocial behavior, and peer relationships might mediate the relationship between early experiences and antisociality in adolescence (Criss, Shaw, Moilanen, Hitchings, & Ingoldsby, 2009). It also appears that the *amount* of exposure to poverty, such as time in poverty and percent of youth spent in poverty, is related to delinquent behavior—being poor in the short term was not related to delinquency (Jarjoura, Triplett, & Brinker, 2002). They also found that exposure to poverty in the first 5 years of life was related to delinquency—after controlling for the effects of poverty from ages 0 to 5, poverty from ages 6 to 10 was unrelated to delinquency. Each of these results suggests not just temporal sensitivity to social adversity, but the amount and timing are important in determining the risk of antisocial behavior, which are consistent with the competitive disadvantage hypothesis.

Competitive disadvantage and neurodevelopment. In addition to social adversity, neurodevelopmental incidents may also lead to competitive disadvantage, resulting in sexually coercive behaviors as a facultative-fixed response. For example, Rylands et al. (2012) found that not only were men who were different in impulsive aggression, a trait associated with sexual offending, showed differences in terms of childhood adversity, they were also different in terms of brainstem serotonin transporter (SERT). Interestingly, brainstem SERT was strongly related to experiencing childhood trauma ($r = 0.76$).

One method for investigating neural adversity early in development is to consider physical perturbations that are indicative of such experiences. Arseneault, Tremblay, Boulerice, Séguin, and Saucier (2000) found that minor physical anomalies were predictive of violent behavior in adolescence after controlling for family adversity in childhood. This is important because it suggests that physical or neurological variables could be independent from childhood environmental effects. Specific to sexual offending, atypical early neurological development, such as that related to prenatal alcohol

exposure, is related to sexual offenses (reviewed in Baumbach, 2002). Psychometric research is therefore needed for early assessment of competitive disadvantage and for factor analyses to determine whether neural and social adversity are independent paths.

Another work has suggested that early experiences may have consequences to adult social development by revealing how phenotypic markers of developmental stressors relate to violent criminal behavior. Lalumière, Harris, and Rice (2001) found that nonpsychopathic offenders (including rapists and non-rapists) had higher fluctuating asymmetry than non-offenders (higher fluctuating asymmetry indicates developmental incidents). Similarly, nonpsychopathic offenders scored higher than psychopathic offenders on obstetrical problems, indicating complications in early development and suggesting a possible role of such complications in the development of antisocial behavior in adults.

Although we can think of social and neural adversity as being separate factors that trigger competitive disadvantage, there may be additive or interaction effects between them. Raine's review of the literature suggests that experiencing both biological and social risk factors exponentially increased the risk of antisocial and violent behavior, and Arseneault et al. (2002) found that obstetrical problems had an impact on adolescent violent behavior only if they had grown up in adverse social environments.

Box 2.2: Alternative Tactics as Fixed Alternative Life Histories (Analogue to "Obligate" and "Facultative Developmentally Fixed")

In contrast to the facultative developmentally flexible tactics described in Box 2.3, some alternative reproductive tactics are associated with fixed alternative life histories. Variation in life history may result from genetic polymorphisms underlying the alternative phenotypes (resulting in so-called "obligate" tactics) or to

(continued)

Box 2.2 (continued)

differences in early development among individuals that share a common genome, leading to a phenotype that is facultative but developmentally fixed by reproductive age (see Emlen, 2008). These two potential origins of fixed alternative tactics can be difficult to distinguish from one another by simply examining phenotype, as both can result in certain tactics being unavailable to certain males once their life history course is set (see below). As discussed in Box 2.1, determining the organizational mechanisms underlying these set of life history pathways can be challenging, and they are therefore often best considered to be the likely result of some gene by environment interactions (e.g., as when early growth is a determining factor: early growth can be influenced both by genes and by environmental factors such as resource availability at time of birth).

One clear example of a genetically based alternative tactics that vary in degree of conflict over fertilization is found in the pygmy swordtail *Xiphophorus nigrensis*, an internally fertilizing fish with female pregnancy (Zimmerer & Kallman, 1989). Males in this species show Y-linked variation (the *P*-locus) with four alleles that result in size and color variation. This variation in male size and color results in discrete variation in male reproductive behavior: specifically, small males show a broader range of reproductive behavior than the other male types (Zimmerer & Kallman, 1989). Of particular interest to us, small males are the only ones that perform “sneak-chases,” which involve darting towards the female and a gonopodial thrust and copulation attempts (Zimmerer & Kallman, 1989). Thus, this single-gene variant is associated with the level of conflict over fertilization between males and females.

Salmon shows male variation in reproductive tactic which is fixed across the timespan on the basis of both condition (early growth) and frequency dependence (i.e., the relative frequency of each tactic in the environment; Gross, 1985). The large dominant “hooknose” males show slower early growth and take longer to reach reproductive maturity but are the only morph females will spontaneously spawn with. The “jack” or “sneaker” morph develops more quickly and has frequency-dependent reproductive success (high success when jacks is rare in the population due to decreased hooknose vigilance; Gross, 1985) based on their ability to get close to spawning females. This period of early growth determines the lifetime tactic of a male salmon: once matured as a jack, the “hooknose” pathway is no longer available to him (Gross, 1985).

However, tactics based on alternative life histories do not preclude changes in tactic across the lifespan. Male ocellated wrasse (*Symphodus ocellatus*, a fish species native to the Mediterranean) engage in three different reproductive tactics. Dominant territorial “nesting males” are the largest and most colorful males and are the only male phenotype that females choose to spawn with and that perform parental care (Taborsky, Hudde, & Wirtz, 1987; Warner & Lejeune, 1985). The other two male phenotypes “satellite” and “sneaker males” are the medium and smallest of the reproductive males and are respectively the moderately and least dominant and colorful (Taborsky et al., 1987; Warner & Lejeune, 1985). Sneakers and satellites spawn parasitically at the nests of nesting males and are not preferred by females; thus, their spawning is a form of reproductive conflict in this species (Alonzo & Warner, 2000; van den Berghe, Wernerus, & Warner, 1989). The three male ocellated wrasse types are the product of three alternative life history pathways

(continued)

Box 2.2 (continued)

that relate to the amount of pre-reproductive growth (although the ultimate mechanism of differentiation remains unknown; see Alonzo, Taborsky, & Wirtz, 2000). All possible male life histories involve a change in reproductive phenotype between their first and second reproductive year (sneaker to satellite, satellite to nesting male, or nonreproductive to nesting male; Alonzo et al., 2000). Therefore, some males spend their entire lives in reproductive conflict with females (never becoming the preferred phenotype), while others experience this conflict only in their first reproductive year, or not at all (Alonzo et al., 2000). Similar change in reproductive tactic occurs in other fish species, although these may not involve a change in conflict over fertilization with females. For example, bluegill sunfish (*Lepomis macrochirus*) shows fixed life histories that can involve a change in reproductive tactics (Gross & Charnov, 1980), but individual bluegill males either always breed as a phenotype that is preferred by females (nesting males) or they never do (sneakers who become satellites).

Facultative: Developmentally Flexible

Facultative psychological mechanisms are defined as traits that are responsive to environmental conditions and would have evolved in response to unpredictable environments (Alcock, 2001). Most psychological traits are considered to be facultative, but little attention has considered the ontogeny of these mechanisms. Some mechanisms are flexible, meaning its occurrence is not permanent, but responds to both the presence and absence of a particular condition. For example, being hungry depends on how satiated an organism is—hunger subsides after eating. Other responses are fixed, meaning its occurrence persists once turned on. An example of

this is the organizational effects hormones have on sex-typical behavior (see Quinsey, 2003). There are many examples of sexually coercive behaviors in nonhuman species that are facultative (Box 2.3). What is common among facultative adaptations is that their expression depends on variations in environmental conditions. Several paths to sexual offending may fall into either of these categories.

Box 2.3: Long- and Short-Term Flexible Alternative Tactics (Analogue to “Developmentally Flexible”)

In some species, investment in particularly reproductive tactics is facultative and developmentally flexible: individuals of reproductive age can engage in any of the possible tactics, provided the proper context (see also Box 2.4 for more such examples from primates). Often, the major factor involved in the reproductive tactic used is an individual's social status, such as when the most dominant male has controlled access to females. In these situations, subordinate males may resort to a tactic of forced copulation of unguarded females (see Box 2.4). Individual dominance can vary over the long term (such as when the alpha male in a group has a distinctly different morphology, e.g., elephant seals, described below) or short term (when tactic is based on a specific relative characteristic, such as size, e.g., garter snakes and water dragons, described below). Other social factors may play a role in tactic determination: for example, relative sex ratio of reproductive individuals in the population (the operational or adult sex ratio; see Kokko & Jennions, 2008) can change reproductive behavior specifically with regard to conflict over fertilization (and can also lead to other forms of male–female reproductive conflict, such as overinvestment in parental care; see also Apicella & Marlowe, 2007; Kokko & Jennions, 2008).

(continued)

Box 2.3 (continued)

In elephant seals, large dominant “beachmasters” guard and attempt to control the reproduction of female seals, while smaller, subordinate “satellite” males attempt to sneak copulation (Hoelzel, LeBoeuf, Reiter, & Campagna, 1999; Le Boeuf, 1974); reproductive success of males generally correlates with their copulation success (Hoelzel et al., 1999). Females are generally more receptive to males who are more dominant (Cox, 1981). Variation male aggressive behavior during mating results in females experiencing greater risk of injury or mortality from satellite than they do from beachmasters (Mesnick & Le Boeuf, 1991). Thus, females attempt to evade copulation with subordinate males, although they decrease potential costs of mating by showing increased receptivity when they are unable to evade satellites (Mesnick & Le Boeuf, 1991). As male dominance is based on physical ability, and therefore on size, all males have the potential to achieve dominance provided they survive for long enough (Le Boeuf, 1974).

Clear examples of the role of short-term variability in reproductive strategy can be seen in garter snakes (Shine, Langkilde, & Mason, 2003) and eastern Australian water dragons (Baird, Baird, & Shine, 2012). Garter snakes show variation in reproductive behavior based on body size (larger males show more courtship behavior; Shine et al., 2003). They also change relative investment in reproductive behaviors based on the number of male competitors present (shifting investment from inducing female receptivity to increasing the likelihood of mating when more male competitors are present; Shine et al., 2003). Eastern Australian water dragons also show alternative tactics that are moderated by social context and thus can

show high short-term plasticity: larger dominant males are territorial, while smaller males act as opportunistic satellite males (Baird et al., 2012). An experimental removal of territorial males confirmed that when a territory vacancy arises, satellite males quickly move up in status and adopt the strategy of a dominant territorial male (Baird et al., 2012).

Cuckoldry risk. Sexual offending in relationships has recently been given considerable attention by evolutionists. Traditional evolutionary explanations that rape evolved in response to limited mating opportunities do not apply in this context because presumably the person is (or at least was) in a mutually consensual mating relationship. An alternative explanation was posed to suggest that partner sexual coercion overcomes a fitness barrier posed by cuckoldry risk. That is, a way men could have minimized cuckoldry risk was by forcing copulation when faced with a reluctant sexual partner who had engaged in an extra-pair mating within the last reproductive cycle (Buss, 2003; Camilleri & Quinsey, 2009a; Goetz & Shackelford, 2006; Lalumière et al., 2005; Thornhill & Palmer, 2000; Wilson & Daly, 1992).

Camilleri and Quinsey (2012) embedded this idea in the context of sexual conflict, which is when a trait is adaptive in one sex while posing fitness costs to the other sex. First, there may be fitness benefits of extra-pair copulations among women, including mating with males with better genes, gaining resources from an extra-pair partner, paternity confusion leading to greater investment in offspring, status enhancement, diversifying genes, and potentially “trading up” to a better quality mate (reviewed in Mulder & Rauch, 2009; Wilson & Daly, 1992). Being cuckolded certainly poses reproductive costs to men, and so we would expect adaptations to identify and minimize this risk. Sexually coercing one’s partner was hypothesized to function by minimizing cuckoldry risk. Sexual conflict is a powerful middle-level theory because

in addition to accounting for partner sexual coercion, it may account for a wide variety of aggressive behaviors in sexual relationships, including harassment, intimidation, social isolation, punishment, and infanticide. For partner sexual coercion to be considered a cause or consequence of sexual conflict, harm in one sex must be adaptive in the other sex, harm must not be a by-product of the trait, called *collateral harm* or *collateral cost*, and indirect benefits to the harmed sex must be ruled out, such as having sexually coercive sons. Addressing these criteria is difficult with humans because coevolutionary trajectories are methodologically difficult to ascertain—since genetic and fitness experimental designs are not possible, alternative methods have been proposed to answer some of the questions posed by the sexual conflict theory (see Camilleri & Quinsey, 2012, for a more detailed review of this topic).

The relationship between cuckoldry risk and partner sexual coercion appears to be a robust finding. Goetz and Shackelford (2006) found a significant relationship between infidelity and partner sexual coercion, as reported by both perpetrators and victims. Starratt, Goetz, Shackelford, McKibbin, and Stewart-Williams (2008) found that more insults of partner infidelity were related to more instances of partner sexual coercion. Goetz and Shackelford (2009) replicated these effects in another sample. Reanalyzing Camilleri and Quinsey's (2009a) data, there was a significant correlation between cues to partner infidelity and self-reported propensity for partner sexual coercion among men, $r(140) = 0.30, p < 0.001$, not among women, $r(142) = 0.12, p = 0.16$ (i.e., women did not show a greater propensity for partner sexual coercion when their partner had an increased risk of infidelity). Across these six studies, effect sizes narrowly ranged from 0.23 to 0.32 ($M = 0.28$, $SD = 0.04$, 95 % CI 0.24–0.31), suggesting cuckoldry risk has a moderate impact on partner sexual coercion and that other factors contribute to this behavior, such as psychopathy (Camilleri & Quinsey, 2009b). Using a forensic sample, Camilleri and Quinsey (2009) found that among incarcerated partner rapists, 27 % suspected, knew, or were threatened with infidelity prior to committing their offense. Considering these results

have been replicated across students, communities, forensic samples, potential perpetrators, and victims using multiple operationalizations, these data suggest a robust relationship between cuckoldry risk and partner sexual coercion.

These relationships indicate partner sexual coercion may be in response to partner infidelity, but they do not identify whether such a facultative response is developmentally flexible or fixed. There is some preliminary evidence that cuckoldry risk is developmentally flexible. In a non-forensic sample, Camilleri and Quinsey (2009a) found that the relationship between partner sexual coercion and cuckoldry risk was strongest when risk events took place recently. As the average time since cuckoldry risk events took place increased, the relationship between cuckoldry risk and partner sexual coercion weakened. The response, as predicted, also appears to be sex-specific because these effects were found only among men.

Also, Camilleri and Quinsey (2009a) did not find a relationship between an indirect proxy of cuckoldry risk—proportion of time away from partner since last having intercourse—and propensity for partner sexual coercion. They argued that more direct cues to infidelity are needed for someone to take the risks associated with coercive behaviors. Interestingly, McKibbin, Starratt, Shackelford, and Goetz (2011) found that proportion of time was related to partner sexual coercion but only when men's suspicion of partner infidelity was higher. Methodologically, these studies have setbacks because they are correlational and self-report. Thus, further work using experimental designs and research with forensic samples and the use of mathematical models would assist with providing a more comprehensive understanding of how cuckoldry risk is facultatively related to partner sexual coercion. For example, it is possible that one instance of infidelity might permanently increase a partner's sensitivity to cuckoldry risk.

The young male syndrome. Two of the most robust predictors of antisocial behavior, including sexual offending, are age and sex. Known as the fundamental data of criminology, a large proportion of crimes are committed by younger males (reviewed in Quinsey, Skilling, Lalumière, & Craig, 2004). Evolutionary explanations account

for these data by suggesting that younger males are more willing to tolerate risks due to higher fitness variance, and thus higher competition, for establishing mateships (Wilson & Daly, 1985). Selection would have favored traits associated with taking risks for resources, status, and mateships during this developmental period of high competition. Lalumière et al. (2005) proposed that these risky behaviors, which include sexual coercion, subside as men age because they eventually form long-term mateships and switch to parental investment, making such risky behaviors too costly. Consistent with this view is that marriage is a protective factor for violent recidivism (reviewed in Laub & Sampson, 2001). This path to sexual offending would therefore be considered a *developmentally flexible facultative mechanism*, because conditions turn these behaviors on and off.

This path to sexually coercive behavior in humans might account for a large proportion of both sexual and nonsexual crimes (Lalumière et al., 2005). Data patterns show an increase in the frequency of sexual crimes committed by males into young adulthood then a decline as men age. A similar curve is found among women, but the frequency does not peak to the same extent as men. Using US data, both forcible rape and all sexual offenses follow this pattern (higher rates among women are due to including prostitution; FBI Uniform Crime Reports, 1993–2001).

Moffitt's longitudinal research on criminal populations identified *adolescent-limited* offenders as a discrete category and is consistent with the Young Male Syndrome. That is, unlike life-course-persistent offenders, men who fall into the adolescent-limited category are not characterized by unfavorable traits to the same degree, including certain personality traits, psychopathology, interpersonal/familial conflict, and neurocognitive deficits, among others (Moffitt, 1993; Moffitt, Caspi, Harrington, & Milne, 2002).

Despite the pervasiveness of the age-sex-crime curve, not all young men commit sexual offenses. There are still individual differences in one's likelihood to engage in such behavior. To account for this, Lalumière et al. (2005) suggested there are younger men whose environmental conditions increase the benefits of risk behaviors, including

living in areas where competition is high as indicated by higher homicide rates. Moffitt et al.'s adolescent-limited group, although generally better off than life-course-persistent offenders, scored lower on economic life variables than other antisocial men (Moffitt et al., 2002). So, younger men who face environments or conditions that promote competition might have a more temporary response because the conditions may not be as entrenched or severe as those experienced by LCP.

Individual differences in young male syndrome are consistent with Wilson and Daly's (1998) hypothesis that men's sexual proprietariness and violence should correlate with higher intrasexual competition. Some evidence in support of this idea is that domestic violence is positively related to higher male-to-female sex ratio (D'Alessio & Stolzenberg, 2010); however, not all studies find such a clear relationship. Barber (2000) found a *negative* correlation between male-to-female sex ratio and rape rates across nations, but only among 15–64-year-olds (no relationship was found among 15–19-year-olds), suggesting that in regions where there is high competition, measured by more men relative to women, there are fewer rates of sexual violence. An issue with these data is that regions where there are more women relative to men could be a consequence of high competition (due to male-male homicide), not a cause of it. Sex ratio is an important variable in determining competition (see Box 2.3), but future work in this area will need to control for life expectancy and homicide rates to provide a more accurate understanding of its relationship to sexual violence in humans.

Although younger males account for a large proportion of sexual crimes, and are likely to desist as they age, there is a smaller number of sexual offenders who start earlier in development and persist well into adulthood. These offenders may fall into either the facultative fixed or obligate categories described above.

By-Products and Disorders

By-Products. Although this volume is focused on adaptive explanations of behavior, there may be either unintended outcomes of these adaptations,

known as by-products, or these adaptations may not be functioning in the way they were designed, known as disorders. The typology of sexual offenders outlined by Camilleri (2012) also recognizes that sexual offending could also be understood in these ways. Rape has been considered a by-product of men's sexual interest in impersonal sex (Symons, 1979) or arousal to visual stimuli, sex drive, and sexual variety (Palmer, 1991). There are several considerations, however, with by-product explanations. The first is that because by-products come from adaptations, it is not clear exactly which of the cited traits are adaptive. Arousal to visual stimuli, for example, certainly seems to correlate with men's sexual psychology, but its adaptive function has not been established. This is not to say these characteristics are not adaptations, but if sexual offending is indeed their by-products, researchers need to establish the adaptive function of those initial traits, then empirically link those traits to sexual offending.

There has not been a systematic method to test the links between sexual offending as a by-product and their associated adaptations. Camilleri (2012) proposed a way to test for this link with the assumption that the degree to which sexes differ on adaptations should match the degree to which the sexes differ on their by-products. Effect size differences between the sexes varied from 0.3 to 1.2 in terms of partners desired, sexual consent after knowing someone for a month, and interest in short-term mating (Schmitt et al., 2003), whereas the effect size for rape was 15.2—a massive effect size that does not match the range of sexual psychological traits. If by-product hypotheses are true, then they need to explain why such a discrepancy exists. Another way to match by-products with adaptations is to see if patterns of sexual homicide correspond with patterns of sexual offending that does not result in homicide. Two studies found that sexual homicide matches the age-sex-crime curve found in general sexual offending (Shackelford, 2002; Wilson, Daly, & Scheib, 1997). These methods represent a starting point for more direct and thorough tests of by-product hypotheses for sexual offending.

Furthermore, we would expect, following Camilleri's (2012) typology, that sexual homicide offenders cluster into adaptive types (i.e., since there are five types of sexual offenders listed under adaptations, we expect sexual homicide to cluster into the same five categories). Although this approach is not a direct test of by-products, it does suggest that sexual homicide is not a homogenous behavior with one etiological path. Further support for the notion that sexual homicide is a by-product of adaptive paths to sexual offending comes from Sewall, Krupp, and Lalumière's (2013) cluster analysis—they found sexual homicide perpetrators clustered into sadistic, competitively disadvantaged, and slashers (i.e., mutilates victim's body). However, one category that did not emerge was psychopathic offenders. Their results may not be generalizable to all sexual offenders because they included serial sexual homicide perpetrators, and a thorough assessment of constructs was not always possible (e.g., PCL-R). Further work following their approach would assist with understanding the etiology of sexual homicide.

Providing support for by-product hypotheses involves more than just ruling out adaptation predictions. More systematic investigations of the adaptations from which rape is hypothesized to be a by-product from, in addition to better ways to empirically test for by-products, are needed. That is, by-product explanations need to be held to the same standards that are used to establish adaptations.

Disorders. The disordered path to sexual offending is different from men who are competitively disadvantaged—competitive disadvantage suggests adopting a coercive reproductive strategy as an adaptive response to atypical development that poses a barrier to reproduction. Disorders are gross abnormalities to one's psychology and behavior that impair adaptive sexual behaviors. Despite such explanations being around for quite some time (e.g., Palmer, 1991; Quinsey & Lalumière, 1995), very few studies have tested them. Similar to by-products, a disorder needs to be linked to particular psychological adaptations, and theoretical and empirical evidence needs to be accrued to suggest that the adaptation is not functioning in the way it was

designed. Candidates for disordered forms of sexual offending include developmentally disabled offenders, paraphilias, and pathological jealousy (see Box 2.4 for similar disorder among nonhuman animals).

Initial evidence that sexual offending by developmentally disabled men is more likely a result of a disordered psychology, as opposed to being a form of competitive disadvantage, comes from finding that these men are more likely to sexually prefer nonreproductive stimuli (Rice, Harris, Lang, & Chaplin, 2008). It is not clear which mechanisms are malfunctioning, but cognitive decision making (i.e., ability to weigh costs and benefits) is a likely candidate. Some offender groups, such as incest offenders, may have a malfunctioning kin recognition mechanism, although some may also result from deviant sexual interests (Seto, Lalumière, & Kuban, 1999).

Some paraphilias could be a disorder of possibly developmentally fixed mechanisms: disordered age preferences could result in pedophilia or gerontophilia and disordered species recognition could result in zoophilia. Other paraphilias might result from flexible mechanisms: disorders of the courtship process might result in voyeurism, exhibitionism, frotteurism, and toucherism (Freund, Scher, & Hucker, 1983). Although very little research currently exists for paraphilias generally, pedophilia has been given considerable attention, particularly its link to various neurological impairments in offenders (Seto, 2008). Lastly, pathological jealousy might result from disordered mechanisms associated with minimizing cuckoldry risk, since these men are persistently jealous, even without any indication that a partner has been unfaithful.

Similar to by-product explanations, more extensive research on the initial adaptations are needed, with appropriate methodologies to identify which mechanism is malfunctioning. There are many studies that link sexual offending with other disorders or neuropsychological impairments, such as the fraternal birth order effect (Lalumière, Harris, Quinsey, & Rice, 1998), handedness (Bogaert, 2001), comorbid psychiatric disorders (Långström et al., 2004), and brain injury (Blanchard et al., 2002), but

how these factors lead to specific sexual offending types is still unknown.

Box 2.4: Evidence of By-Product and Disorder in Animal Reproductive Behavior

As in humans, animals can show a striking breadth of reproductive responding, including behaviors that could be considered errors, as they would result in nonproductive sexual behavior, such as mating with the wrong species or inanimate objects or with killing a sexual partner.

Low selectivity of sexual response of males has been documented in many species, and this erroneous behavior of males likely persists because the cost of such errors is sufficiently low as to “escape” selection pressure for high selectivity or as a by-product of selection for other sexual behaviors. For example, the head and neck of female birds, even if static in motion, are sufficient stimuli to elicit copulation by males (Domjan, Greene, & North, 1989; Schein & Hale, 1959). Similarly, there are several documented examples of male animals copulating with static (deceased) members of their species (termed “Davian behavior”; Dickerman, 1960; e.g., Costa et al., 2010; Moeliker, 2001; Russell, Sladen, & Ainley, 2012; Sinovas, 2009). Additionally, there are many anecdotal examples of males of many species copulating with objects that have even a passing similarity to females, be they other species or inanimate objects. In species where reproduction can involve male control of females and forcible copulation, females may occasionally be killed during sex (e.g., Le Boeuf & Mesnick, 1990).

Unlike research with humans, the etiology of disordered sexual behavior in nonhumans is often unknown, due to the complexity and difficulty of such research. As animal examples are often found serendipitously, researchers generally lack information about the parentage or developmental experiences of individuals displaying unusual

(continued)

Box 2.4 (continued)

behavior. There is, however, some indication that early experiences can play a role in shaping male response to focus on inappropriate targets. These typically arise in species where species recognition is based on early exposure: individuals, particularly those raised by other species, may misidentify accordingly when choosing reproductive partners (see reviews by Bolhuis, 1991; Irvin & Price, 1999), and experience can play a role in development of sexual response to objects (e.g., male turkey response to the human hand; Schein & Hale, 1959). Note that “reverse imprinting” has been suggested to play a role in human inbreeding avoidance (based on co-residency; Westermarck effect—Westermarck, 1891; Lieberman & Smith, 2012; and observation of association between own mother and other children; see Lieberman & Smith, 2012), and the role of imprinting in the development of paraphilias has been debated (for a recent review of learning and sexual response in humans and nonhuman animals, see Hoffmann (2012)).

Box 2.5: Primates and Sexual Aggression

Our closest genetic relatives, primates (particularly apes) show clear differences among males both within and among species in terms of reproductive behaviors (Smuts & Smuts, 1993). Differences in male reproductive tactics generally involve variation in degree of sexual aggression and coercion. While forced copulation is rare when looking across species, many primates show a bias in female-directed aggression by males, such that they more frequently target females when they are in estrus, suggesting that such aggression functions as sexual coercion and control (Smuts & Smuts, 1993). Infanticide is another form of aggression-based sexual

conflict often studied in primates (see Smuts & Smuts, 1993), but whether it should be considered a form of sexual coercion, due to the influence on female receptivity, has been debated (see discussion in Palombit, 2009). Although there are several examples of indirect coercion and control among primates (see Muller & Wrangham, 2009), we focus specifically on examples of forced copulation and direct coercion (aggression to overcome female mating resistance; Muller, Kahlenberg, & Wrangham, 2009a) and include only species for which there is clear information on these behaviors.

The examples outlined below largely fall into the category of short- and long-term facultative developmentally flexible tactics and, in some cases, mirror examples among humans (particularly “young male syndrome” and “cuckoldry risk”). This does not necessarily rule out the possibility of obligate or developmentally fixed tactics, although given the traits of the suggested examples of these tactics in humans (e.g., the rarity of psychopaths in the general population), detecting such patterns of behavior among primates would be challenging, given our decreased instances and duration of contact compared to our contact with our own species.

*Chimpanzees**Common chimpanzee (Pan troglodytes):*

Male aggression directed at females is rather frequently biased towards cycling females, and performance of such aggression is not isolated to males of a particular social status (Muller, 2007; Muller, Emery Thompson, & Wrangham, 2006). This male aggression represents high costs to females, who can suffer extreme damage during these interactions (Muller, Kahlenberg, & Wrangham, 2009b). However, the most extreme form of direct coercion, forced copulation, is relatively rare (Tutin, 1979). It has been suggested that this is because of

(continued)

Box 2.5 (continued)

the high levels of female promiscuity and low resistance to male courtship (Muller, Kahlenberg, & Wrangham, 2009b). The few instances of forced copulation recorded have generally been cases of brothers or sons forcing copulation on sister/mother (Goodall, 1986), suggesting that it may be used only when females resist males who they are averse to mating with (due to the potential costs of inbreeding; e.g., Ralls, Ballou, & Templeton, 1988).

Bonobo (*Pan paniscus*): In striking contrast to the common chimpanzee, there is a clear lack of male aggression towards females and little evidence of instances of indirect or direct coercion and forced copulation among bonobos. This reflects the general pattern of low aggression in this species (where sexual activity, rather than aggression, is used to resolve conflicts) and codominance between males and females. See Paoli (2009) for a full review of these points, and of bonobo sexual behavior.

Gorillas

Forced copulation by lowland gorillas has been observed in captivity, but only when the female could not escape (Smuts & Smuts, 1993), and forced copulation has been only rarely reported in wild-living gorillas (Robbins, 2009). Female-directed aggression among gorillas seems to act to control female group affiliation, as well being a form of sexual coercion, and females typically receive aggression only from dominant silverback males (Robbins, 2009). There is more female-directed aggression in multi-silverback groups that receive more aggression, but this is a result of the greater number of dominant males, rather than increased aggression by individual males (Robbins, 2009). Thus, mountain gorilla (*Gorilla beringei beringei*) females, which are more frequently in multi-male groups, generally receive more aggression than western

gorillas (*Gorilla gorilla gorilla*) females (Robbins, 2009). Sexual coercion through aggression is implied by mating patterns; for example, among mountain gorillas in multi-male groups, the male who directs more aggression towards a female also copulates more frequently with her (Robbins, 2009; Smuts & Smuts, 1993). Levels of aggression and harm to females are also often less than in other species (e.g., chimpanzees, Muller, Kahlenberg, & Wrangham, 2009b), and male gorilla aggression often takes the form of threats rather than direct physical contact (Robbins, 2009).

Orangutans

Forced copulation is common among orangutans (see extensive review in Knott, 2009), although these copulations generally result in less lasting physical damage to females, and male orangutans generally show lower levels of physical violence towards females relative to other primates such as chimpanzees (see Knott, 2009; Muller, Kahlenberg, & Wrangham, 2009b). Orangutans offer the clearest examples of alternative tactics among primates, as the propensity of males to engage in forcible copulation is associated with clear morphological variation in facial ornamentation (Knott, 2009). “Flanged” males are the older (and thus typically most dominant), preferred by females, and have prominent fleshy cheek ornamentations that more younger “unflanged” males lack. While both types engage in forced copulation, across sites, unflanged males are more likely to engage in forcible sex (see overview in Knott, 2009). The variation in rate of forced copulations by flanged males may reflect their dominance (or prime) status—the oldest flanged males which are past-prime and less preferred by females are also more likely to engage in forced copulation (Knott, 2009; Mitani, 1985). Thus, it

(continued)

Box 2.5 (continued)

seems that female preference correlates with likelihood of engaging in forced copulation and that it is in fact a strategy of non-preferred (and less dominant) male orangutans (Knott, 2009). In agreement with this idea, the size of unflanged males is generally predictive of their likelihood of forcing copulation, and those large unflanged males who are closest to becoming dominant (and therefore flanged) are less likely to force copulation, perhaps reflecting a female ability to assess status within male phenotypes (Utami Atmoko, 2000).

Baboons

Among baboon species, forced copulation does not appear to occur in the wild (Smuts, 1985/2007). There is interspecies variation in the level of male aggression and control of females, and such aggression can function as a form of coercion or control, although it also occurs outside of a sexual context (Smuts & Smuts, 1993). Chacma baboon (*Papio hamadryas griseipes*) males show a generally high level of female-directed aggression, which appears to be multimodal in function: it can serve as male coercion, but there is also a clear role of male-male competition (e.g., signaling to rivals; Kitchen et al., 2009). Aggression by dominant males hamadryas baboons (*Papio hamadryas*) appears to condition females to remain close to him, as it is particularly frequent during and immediately following a change in leadership (Swedell & Schreier, 2009).

Social coalitions as female counteradaptations to male aggression

In several baboon species, male–female interactions termed “friendships” appear to in part be a method of female defense against aggression from other males directed towards themselves and their offspring (Smuts, 1985/2007). Similar

preferences of females for particular males based on social benefits have been noted in several other species including gorillas, chimpanzees, and macaques (Smuts & Smuts, 1993). These positive associations may function as a female counteradaptation to male aggression and sexual conflict among primates, and even females in harem species show preferences for group membership based on the protection from aggression and infanticide that the dominant male provides (Smuts & Smuts, 1993).

Female-female interactions may also function to decrease the amount of aggression and reproductive control females experience from males. Bonds between female bonobos appear to strongly contribute to the notably low levels of aggression in this species generally (Paoli, 2009). Additionally, there is evidence that female coalitions among common chimpanzees may function to reduce exposure to male aggression (Newton-Fisher, 2006).

The selection pressure that rape places on human women is understudied relative to the potential selective benefits and mechanisms underlying male rape behavior. Rape presents considerable physical risk to women and can result in additional potential costs by decreasing her control over her reproduction decisions. Thus, it stands to reason that women may have evolved counteradaptations to mitigate these costs, both in terms of physiological mechanisms, and biases towards particular social interactions and behaviors. Increased attention to rape-avoidance behaviors, as well as mechanisms that may allow for rape-cost reduction in women would be valuable, in terms of better understanding both the fitness consequences of rape and the potential adaptive function of how women respond to rape and sexual control/coercion.

Conclusions

The purpose of this chapter was to review research and theory on sexual offending from an evolutionary framework. Evolutionary approaches towards behavior and psychology suggest the evolution of these traits could function as an adaptation, by-product of adaptations, or disordered adaptations. Although we focused on adaptive explanations, alternatives should be given equal empirical and theoretical attention. We also reviewed how in other species, forced copulation could function as either an obligate, facultative-fixed, or facultative flexible behavioral tactic. A larger puzzle is that humans appear to present multiple contexts, functions, and malfunctions under which sexual offending occurs. We could identify no other example of a species that shows such diversity in coercive/nonconsensual sexual behaviors or in any specific reproductive behavior. This contrast may be a product of insufficient research with nonhuman animals (e.g., lack of attention to or constraints on our ability observe such individual variation), a generally greater emphasis on these behaviors and their subtle variations in humans, or some unique feature of humans as a species that has lead to greater elaboration of the associated behaviors. Overall, we recognize that sexual offending is a complex act, occurring under different contexts, against different types of victims, and with different underlying motivations and potential fitness consequences to the perpetrator. Further research using this theoretical model as a guide might assist with untangling this complexity.

References

- Alcock, J. (2001). *Animal behavior: An evolutionary approach* (7th ed.). Sunderland, MA: Sinauer Associates.
- Alexander, R. D., & Noonan, K. M. (1979). Concealment of ovulation, parental care, and human social evolution. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 436–453). North Scituate, MA: Duxbury Press.
- Alonzo, S. H., Taborsky, M., & Wirtz, P. (2000). Male alternative reproductive behaviors in a Mediterranean wrasse, *Symphodus ocellatus*: Evidence from otoliths for separate life-history pathways. *Evolutionary Ecology Research*, 2, 997–1007.
- Alonzo, S. H., & Warner, R. R. (2000). Dynamic games and field experiments examining intra- and intersexual conflict: Explaining counter-intuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*. *Behavioral Ecology*, 11, 56–70.
- Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism—How to carry out an exaptationist program. *Behavioral and Brain Sciences*, 25, 489–504.
- Apicella, C. L., & Marlowe, F. W. (2007). Men's reproductive investment decisions: Mating, parenting and self-perceived mate value. *Human Nature*, 18, 22–34.
- Arseneault, L., Tremblay, R. E., Boulerice, B., Séguin, J. R., & Saucier, J. F. (2000). Minor physical anomalies and family adversity as risk factors for violent delinquency in adolescence. *The American Journal of Psychiatry*, 157(6), 917–923.
- Arseneault, L., Tremblay, R. E., Boulerice, B., & Saucier, J. F. (2002). Obstetrical complications and violent delinquency: Testing two developmental pathways. *Child Development*, 73(2), 496–508.
- Baird, T. A., Baird, T. D., & Shine, R. (2012). Aggressive transition between alternative male social tactics in a long-lived Australian dragon (*Physignathus lesueurii*) living at high density. *PLoS One*, 7(8), e418–e419.
- Barber, N. (2000). The sex ratio as a predictor of cross-national variation in violent crime. *Cross-Cultural Research*, 34, 264.
- Baumbach, J. (2002). Some implications of prenatal alcohol exposure for the treatment of adolescents with sexual offending behaviors. *Sexual Abuse: A Journal of Research and Treatment*, 14(4), 313–327.
- Blanchard, R., Christensen, B. K., Strong, S. M., Cantor, J. M., Kuban, M. E., Klassen, P., Dickey, R., & Blak, T. (2002). Retrospective self-reports of childhood accidents causing unconsciousness in phallometrically diagnosed pedophiles. *Archives of Sexual Behavior*, 31, 511–526.
- Blonigen, D. M., Hicks, B. M., Krueger, R. F., Patrick, C. J., & Iacono, W. G. (2006). Continuity and change in psychopathic traits as measured via normal-range personality: A longitudinal-biometric study. *Journal of Abnormal Psychology*, 115(1), 85–95.
- Bogaert, A. F. (2001). Handedness, criminality, and sexual offending. *Neuropsychologia*, 39(5), 465–469.
- Bolhuis, J. J. (1991). Mechanisms of avian imprinting: A review. *Biological Reviews of the Cambridge Philosophical Society*, 66, 303–345.
- Brown, D. E. (1991). *Human universals*. Boston: McGraw-Hill.
- Burt, S. A. (2009). Are there meaningful etiological differences within antisocial behavior? Results of a meta-analysis. *Clinical Psychology Review*, 29(2), 163–178.
- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42, 459–491.
- Buss, D. M. (2003). *The evolution of desire: Strategies of human mating* (2nd ed.). New York: Basic Books.
- Camilleri, J. A. (2012). Evolutionary psychological perspectives on sexual offending: From etiology to intervention. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *The Oxford handbook of*

- evolutionary perspectives on violence, homicide, and war* (pp. 173–196). New York: Oxford University Press.
- Camilleri, J. A., & Quinsey, V. L. (2009a). Testing the cuckoldry risk hypothesis of partner sexual coercion in community and forensic samples. *Evolutionary Psychology*, 7, 164–178.
- Camilleri, J. A., & Quinsey, V. L. (2009b). Individual differences in the propensity for partner sexual coercion. *Sexual Abuse: A Journal of Research and Treatment*, 21, 111–129.
- Camilleri, J. A., & Quinsey, V. L. (2012). Sexual conflict and partner rape. In A. T. Goetz & T. K. Shackelford (Eds.), *Oxford handbook of sexual conflict in humans* (pp. 257–268). New York: Oxford University Press.
- Camilleri, J. A., Quinsey, V. L., & Tapscott, J. L. (2009). Assessing the propensity for sexual coaxing and coercion in relationships: Factor structure, reliability, and validity of the tactics to obtain sex scale. *Archives of Sexual Behavior*, 38(6), 959–973. doi:10.1007/s10508-008-9377-2.
- Caspi, A., Roberts, B. W., & Shiner, R. L. (2005). Personality development: Stability and change. *Annual Review of Psychology*, 56, 453–484.
- Choe, J. (2008). Income inequality and crime in the United States. *Economics Letters*, 101(1), 31–33.
- Connor, R. C., & Vollmer, N. L. (2009). Sexual coercion in dolphin courtships: A comparison with chimpanzees. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 218–243). Cambridge, MA: Harvard University Press.
- Costa, H. C., da Silva, E. T., Campos, P. S., da Cunha Oliveira, M. P., Nunes, A. V., & da Silva Santos, P. (2010). The Corpse Bride: A case of Davian behaviour in the Green Ameiva (*Ameiva ameiva*) in southeastern Brazil. *Herpetology Notes*, 3, 79–83.
- Cox, C. R. (1981). Agonistic encounters among male elephant seals: Frequency, context, and the role of female preference. *American Zoologist*, 21, 197–209.
- Coyne, J. A. (2003). Of vice and men: A case study in evolutionary psychology. In S. B. Travis (Ed.), *Evolution, gender, and rape* (pp. 172–189). Cambridge, MA: MIT Press.
- Criss, M. M., Shaw, D. S., Moilanen, K. L., Hitchings, J. E., & Ingoldsby, E. M. (2009). Family, neighborhood, and peer characteristics as predictors of child adjustment: A longitudinal analysis of additive and mediation models. *Social Development*, 18(3), 511–535.
- Daly, M., Wilson, M., & Vasdev, S. (2001). Income inequality and homicide rates in Canada and the United States. *Canadian Journal of Criminology*, 43, 219–236.
- D'Alessio, S. J., & Stolzenberg, L. (2010). The sex ratio and male-on-female intimate partner violence. *Journal of Criminal Justice*, 38(4), 555–561.
- Dickerman, R. W. (1960). "Davian Behaviour Complex" in ground squirrels. *Journal of Mammalogy*, 41, 403.
- Domjan, M., Greene, P., & North, N. C. (1989). Contextual conditioning and the control of copulatory behavior by species-typical sign stimuli in male Japanese quail. *Journal of Experimental Psychology: Animal Behavior Processes*, 15, 147–153.
- Eberhard, W. G. (1996). *Female control: Sexual selection by cryptic female choice*. Princeton, NJ: Princeton University Press.
- Edens, J. F., Marcus, D. K., Lilienfeld, S. O., & Poythress, N. G. (2006). Psychopathic, not psychopath: Taxometric evidence for the dimensional structure of psychopathy. *Journal of Abnormal Psychology*, 115, 131–144.
- Emlen, D. J. (2008). The role of genes and the environment in the expression and evolution of animal alternative tactics. In R. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics: An integrative approach* (pp. 85–108). Cambridge, MA: Cambridge University Press.
- Ferguson, C. J. (2010). Genetic contributions to antisocial personality and behavior: A meta-analytic review from an evolutionary perspective. *The Journal of Social Psychology*, 150, 160–180.
- Freund, K., Scher, H., & Hucker, S. (1983). The courtship disorders. *Archives of Sexual Behavior*, 12, 369–379.
- Goetz, A. T., & Shackelford, T. K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature*, 17(3), 265–282.
- Goetz, A. T., & Shackelford, T. K. (2009). Sexual coercion in intimate relationships: A comparative analysis of the effects of women's infidelity and men's dominance and control. *Archives of Sexual Behavior*, 38, 226–234.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Gottschall, J. A., & Gottschall, T. A. (2003). Are per-incident rape-pregnancy rates higher than per-incident consensual pregnancy rates? *Human Nature*, 14(1), 1–20.
- Gross, M. R. (1985). Disruptive selection for alternative life histories in salmon. *Nature*, 313, 47–48.
- Gross, M. R., & Charnov, E. L. (1980). Alternative male life histories in bluegill sunfish. *Proceeding of the National Academy of Sciences of the United States of America*, 77, 6937–6948.
- Guay, J., Ruscio, J., Knight, R. A., & Hare, R. D. (2007). A taxometric analysis of the latent structure of psychopathy: Evidence for dimensionality. *Journal of Abnormal Psychology*, 116(4), 701.
- Gunter, T. D., Vaughn, M. G., & Philibert, R. A. (2010). Behavioral genetics in antisocial spectrum disorders and psychopathy: A review of the recent literature. *Behavioral Sciences and the Law*, 28, 148–173.
- Harris, G. T., Lalumière, M. L., Seto, M. C., Rice, M. E., & Chaplin, T. C. (2012). Explaining the erectile responses of rapists to rape stories: The contributions

- of sexual activity, non-consent, and violence with injury. *Archives of Sexual Behavior*, 41(1), 221–229.
- Harris, G. T., Rice, M. E., Hilton, N. Z., Lalumière, M. L., & Quinsey, V. L. (2007). Coercive and precocious sexuality as a fundamental aspect of psychopathy. *Journal of Personality Disorders*, 21(1), 1–27.
- 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(4), 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(2), 387–397.
- Henson, S. A., & Warner, R. R. (1997). Male and female alternative reproductive behaviors in fishes: A new approach using intersexual dynamics. *Annual Review of Ecology and Systematics*, 28, 571–592.
- Hoelzel, A. R., LeBoeuf, B. J., Reiter, J., & Campagna, C. (1999). Alpha-male paternity in elephant seals. *Behavioural Ecology and Sociobiology*, 46, 298–306.
- Hoffmann, H. (2012). Considering the role of conditioning in sexual orientation. *Archives of Sexual Behavior*, 41, 63–72.
- Hsieh, C. C., & Pugh, M. D. (1993). Poverty, income inequality, and violent crime: A meta-analysis of recent aggregate data studies. *Criminal Justice Review*, 18(2), 182–202.
- Ingoldsby, E. M., & Shaw, D. S. (2002). Neighborhood contextual factors and early-starting antisocial pathways. *Clinical Child and Family Psychology Review*, 5(1), 21–55.
- Ingoldsby, E. M., Shaw, D. S., Winslow, E., Schonberg, M., Gilliom, M., & Criss, M. M. (2006). Neighborhood disadvantage, parent-child conflict, neighborhood peer relationships, and early antisocial behavior problem trajectories. *Journal of Abnormal Child Psychology*, 34(3), 303–319.
- Irvin, D. E., & Price, T. (1999). Sexual imprinting, learning and speciation. *Heredity*, 82, 347–354.
- Jarjoura, G. R., Triplett, R. A., & Brinker, G. P. (2002). Growing up poor: Examining the link between persistent childhood poverty and delinquency. *Journal of Quantitative Criminology*, 18(2), 159–187.
- Jespersen, A. F., Lalumière, M. L., & Seto, M. C. (2009). Sexual abuse history among adult sex offenders and non-sex offenders: A meta-analysis. *Child Abuse & Neglect*, 33, 179–192.
- Kinner, S. (2003). Psychopathy as an adaptation: Implications for society and social policy. In R. W. Bloom & N. Dess (Eds.), *Evolutionary psychology and violence: A primer for policymakers and public policy advocates* (pp. 57–81). Westport, CT: Praeger.
- Kitchen, D. M., Beehner, J. C., Bergman, J. T., Cheney, D. L., Crockford, C., Engh, A. L., et al. (2009). The causes and consequences of male aggression directed at female chacma baboons. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 128–156). Cambridge, MA: Harvard University Press.
- Knight, R. A. (1999). Validation of a typology for rapists. *Journal of Interpersonal Violence*, 14(3), 303–330.
- Knott, C. D. (2009). Orangutans: Sexual coercion without sexual violence. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 81–111). Cambridge, MA: Harvard University Press.
- Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919–948.
- 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(5), 299–318.
- 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: A Journal of Research and Treatment*, 10(1), 5–15.
- Lalumière, M. L., Harris, G. T., & Rice, M. E. (2001). Psychopathy and developmental instability. *Evolution and Human Behavior*, 22(2), 75–92.
- Lalumière, M., & Quinsey, V. (1996). Sexual deviance, antisociality, mating effort, and the use of sexually coercive behaviors. *Personality and Individual Differences*, 21, 33–48.
- Lalumière, M. L., Harris, G. T., Quinsey, V. L., & Rice, M. E. (2005). *The causes of rape: Understanding individual differences in male propensity for sexual aggression*. Washington, DC: American Psychological Association.
- Långström, N., Sjöstedt, G., & Grann, M. (2004). Psychiatric disorders and recidivism in sexual offenders. *Sexual Abuse: A Journal of Research and Treatment*, 16(2), 139–150.
- Larsson, H., Tuvblad, C., Rijdsdijk, F. V., Andershed, H., Grann, M., & Lichtenstein, P. (2007). A common genetic factor explains the association between psychopathic personality and antisocial behavior. *Psychological Medicine*, 37, 15–26.
- Laub, J. H., & Sampson, R. J. (2001). Understanding desistance from crime. *Crime and Justice*, 28, 1–69.
- Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14, 163–176.
- Le Boeuf, B. J., & Mesnick, S. L. (1990). Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour*, 116(1–2), 143–162.
- Lieberman, D., & Smith, A. (2012). It's all relative: Sexual aversions and moral judgments regarding sex among siblings. *Current Directions in Psychological Science*, 21, 243–247.
- Lynam, D. R., Caspi, A., Moffitt, T. E., Loeber, R., & Stouthamer-Loeber, M. (2007). Longitudinal evidence that psychopathy scores in early adolescence predict adult psychopathy. *Journal of Abnormal Psychology*, 116, 155–165.

- Marcus, D. K., John, S. L., & Edens, J. F. (2004). A taxometric analysis of psychopathic personality. *Journal of Abnormal Psychology, 113*, 626–635.
- Marshall, L. A., & Cooke, D. J. (1999). The childhood experiences of psychopaths: A retrospective study of familial and societal factors. *Journal of Personality Disorders, 13*(3), 211–225.
- McGue, M., Bacon, S., & Lykken, D. T. (1993). Personality stability and change in early adulthood: A behavioral genetic analysis. *Developmental Psychology, 29*, 96–109.
- McKibbin, W. F., Starratt, V. G., Shackelford, T. K., & Goetz, A. T. (2011). Perceived risk of female infidelity moderates the relationship between objective risk of female infidelity and sexual coercion in humans (*Homo sapiens*). *Journal of Comparative Psychology, 125*(3), 370–373.
- McKinney, F., Derrickson, S. R., & Mineau, P. (1983). Forced copulation in waterfowl. *Behaviour, 86*, 250–294.
- Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *Behavioral and Brain Sciences, 18*, 523–599.
- Mesnick, S. L., & Le Boeuf, B. J. (1991). Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. *Behaviour, 117*(3–4), 262–280.
- Mitani, J. C. (1985). Mating behavior of male orangutans in the Kutai Game Reserve, Indonesia. *Animal Behaviour, 33*, 392–402.
- Moeliker, C. W. (2001). The first case of homosexual necrophilia in the mallard *Anas platyrhynchos* (Aves: Anatidae). *Deinsea, 8*, 243–247.
- Moffitt, T. E. (1993). Adolescence-limited and life-course-persistent antisocial behavior: A developmental taxonomy. *Psychological Review, 100*(4), 674.
- Moffitt, T. E., Caspi, A., Harrington, H., & Milne, B. J. (2002). Males on the life-course-persistent and adolescence-limited antisocial pathways: Follow-up at age 26 years. *Development and Psychopathology, 14*(1), 179–207.
- Mulder, M. B., & Rauch, K. L. (2009). Sexual conflict in humans: Variations and solutions. *Evolutionary Anthropology, 18*, 201–214.
- Muller, M. N. (2007). Chimpanzee violence: Femmes fatales. *Current Biology, 17*, 365–366.
- Muller, M. N., Emery Thompson, E., & Wrangham, R. W. (2006). Male chimpanzees prefer mating with old females. *Current Biology, 16*, 2234–2238.
- Muller, M. N., Kahlenberg, S., & Wrangham, R. W. (2009a). Male aggression and sexual coercion of females in primates. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 3–22). Cambridge, MA: Harvard University Press.
- Muller, M. N., Kahlenberg, S., & Wrangham, R. W. (2009b). Male aggression against females in chimpanzees. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 184–217). Cambridge, MA: Harvard University Press.
- Muller, M. N., & Wrangham, R. W. (Eds.). (2009). *Sexual coercion in primates: An evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press.
- Neff, B. D., & Svensson, E. I. (2013). Polyandry and alternative mating tactics. *Philosophical Transactions of the Royal Society B, 368*, 20120045. doi:10.1098/rstb.2012.0045.
- Newton-Fisher, N. E. (2006). Wild female chimpanzees form coalitions against male aggression. *International Journal of Primatology, 2*, 1589–1599.
- Noble, K. G., Houston, S. M., Kan, E., & Sowell, E. R. (2012). Neural correlates of socioeconomic status in the developing human brain. *Developmental Science, 15*(4), 516–527.
- Ogloff, J. R. P. (2006). Psychopathy/antisocial personality disorder conundrum. *The Australian and New Zealand Journal of Psychiatry, 40*, 519–528.
- Oliveira, R., Taborsky, M., & Brockmann, H. J. (2008). *Alternative reproductive tactics: An integrative approach*. Cambridge, MA: Cambridge University Press.
- Palmer, C. T. (1989). Rape in nonhuman animal species: Definitions, evidence, and implications. *Journal of Sex Research, 3*, 355–374.
- Palmer, C. (1991). Human rape: Adaptation or by-product? *Journal of Sex Research, 28*, 365–386.
- Palombit, R. (2009). “Friendship” with males: A female counterstrategy to infanticide in chacma baboons of the Okavango Delta. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 377–409). Cambridge, MA: Harvard University Press.
- Paoli, T. (2009). The absence of sexual coercion in bonobos. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 410–423). Cambridge, MA: Harvard University Press.
- Patrick, C. J. (Ed.). (2008). *Handbook of psychopathy*. New York: Guilford.
- Perkins, C., & Klaus, P. (1996). *Criminal victimization 1994* (Bureau of Justice Statistics Special Series No. NCJ-163069). Washington, DC: US Department of Justice.
- Porter, S., Fairweather, D., Drugge, J., Herve, H., Birt, A., & Boer, D. P. (2000). Profiles of psychopathy in incarcerated sexual offenders. *Criminal Justice and Behavior, 27*(2), 216–233.
- Quinsey, V. L. (2003). The etiology of anomalous sexual preferences in men. *Annals of the New York Academy of Sciences, 989*, 105–117.
- Quinsey, V. L., Harris, G. T., Rice, M. E., & Cormier, C. A. (2006). *Violent offenders: Appraising and managing risk* (2nd ed.). Washington, DC: American Psychological Association.

- Quinsey, V. L., & Lalumière, M. L. (1995). Evolutionary perspectives on sexual offending. *Sexual Abuse: A Journal of Research and Treatment*, 7(4), 301–315.
- Quinsey, V. L., Skilling, T. A., Lalumière, M. L., & Craig, W. M. (2004). *Juvenile delinquency: Understanding the origins of individual differences*. Washington, DC: American Psychological Association.
- Ralls, K., Ballou, J. D., & Templeton, A. (1988). Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology*, 2, 185–193.
- Rhee, S. H., & Waldman, I. D. (2002). Genetic and environmental influences on antisocial behavior: A meta-analysis of twin and adoption studies. *Psychological Bulletin*, 128(3), 490–529.
- Rice, M. E., Harris, G. T., Lang, C., & Chaplin, T. C. (2008). Sexual preferences and recidivism of sex offenders with mental retardation. *Sexual Abuse: A Journal of Research and Treatment*, 20(4), 409–425.
- Robbins, M. M. (2009). Male aggression against females in mountain gorillas: Courtship or coercion? In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 112–127). Cambridge, MA: Harvard University Press.
- Russell, D. G. D., Sladen, W. J. L., & Ainley, D. G. (2012). Dr. George Murray Levick (1876–1956): Unpublished notes on the sexual habits of the Adélie penguin. *Polar Record*, 48, 387–393.
- Rylands, A., Hinz, R., Jones, M., Holmes, S. E., Feldmann, M., Brown, G., et al. (2012). Pre- and postsynaptic serotonergic differences in males with extreme levels of impulsive aggression without callous unemotional traits: A positron emission tomography study using C-DASB and C-MDL100907. *Biological Psychiatry*, 72, 1004–1011.
- Schein, M. W., & Hale, E. B. (1959). The effect of early social experience on male sexual behaviour of androgen injected turkeys. *Animal Behaviour*, 7, 189–192.
- Schmitt, D. P., & 118 Members of the International Sexuality Description Project. (2003). Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology*, 85, 85–104.
- Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation. *Psychological Science*, 15(10), 643–649.
- Seto, M. C. (2008). Pedophilia: Psychopathology and theory. In D. R. Laws & W. T. O'Donohue (Eds.), *Sexual deviance: Theory, assessment, and treatment* (2nd ed., pp. 164–182). New York: Guilford.
- Seto, M. C., Lalumière, M. L., & Kuban, M. (1999). The sexual preferences of incest offenders. *Journal of Abnormal Psychology*, 108(2), 267–272.
- Sewall, L. A., Krupp, D. B., & Lalumière, M. L. (2013). A test of two typologies of sexual homicide. *Sexual Abuse: A Journal of Research and Treatment*, 25, 82–100.
- Shackelford, T. K. (2002). Are young women the special targets of rape-murder? *Aggressive Behavior*, 28(3), 224–232.
- Shields, W., & Shields, L. (1983). Forcible rape: An evolutionary perspective. *Ethology and Sociobiology*, 4, 115–136.
- Shine, R., Langkilde, T., & Mason, R. T. (2003). The opportunistic serpent: Male garter snakes adjust courtship tactics to mating opportunities. *Behaviour*, 140, 1509–1526.
- Sinovas, P. (2009). Bombina variegata (yellow firebellied toad). Mating behaviour. *Herpetology Review*, 40, 199.
- Skilling, T. A., Harris, G. T., Rice, M. E., & Quinsey, V. L. (2002). Identifying persistently antisocial offenders using the Hare Psychopathy Checklist and DSM antisocial personality disorder criteria. *Psychological Assessment*, 14, 27–38.
- Skilling, T. A., Quinsey, V. L., & Craig, W. M. (2001). Evidence of a taxon underlying serious antisocial behavior in boys. *Criminal Justice and Behavior*, 28, 450–470.
- Smuts, B. B. (1985/2007). *Sex and friendship in baboons*. New York: Aldine Publishing.
- Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior*, 22, 1–63.
- Starratt, V. G., Goetz, A. T., Shackelford, T. K., McKibbin, W. F., & Stewart-Williams, S. (2008). Men's partner-directed insults and sexual coercion in intimate relationships. *Journal of Family Violence*, 23, 315–323.
- Steinberg, L. (2007). Risk taking in adolescence new perspectives from brain and behavioral science. *Current Directions in Psychological Science*, 16(2), 55–59.
- Stearns, S. C. (1992). *The evolution of life histories*. London: Oxford University Press.
- Stretesky, P. B., Schuck, A. M., & Hogan, M. J. (2004). Space matters: An analysis of poverty, poverty clustering, and violent crime. *Justice Quarterly*, 21, 817–841.
- Swedell, L., & Schreier, A. (2009). Male aggression towards females in hamadryas baboons: Conditioning, coercion, and control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 244–270). Cambridge, MA: Harvard University Press.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Taborsky, M. (1994). Sneakers, satellites and helpers: Parasitic and cooperative behaviour in fish reproduction. *Advances in the Study of Behavior*, 23, 1–100.
- Taborsky, M. (1998). Sperm competition in fish: 'Bourgeois' males and parasitic spawning. *Trends in Ecology and Evolution*, 13, 222–227.

- Taborsky, M. (2001). The evolution of parasitic and cooperative reproductive behaviors in fishes. *Journal of Heredity*, 92, 100–110.
- Taborsky, M., Hudde, B., & Wirtz, P. (1987). Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European Wrasse with four types of male behaviour. *Behaviour*, 102, 82–118.
- Taborsky, M., Oliviera, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: Concepts and questions. In R. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics: An integrative approach* (pp. 1–21). Cambridge, MA: Cambridge University Press.
- Thornhill, R. (1980). Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Animal Behaviour*, 28, 52–59.
- Thornhill, R., & Palmer, C. T. (2000). *A natural history of rape*. London: MIT Press.
- Thornhill, R., & Palmer, C. T. (2004). Evolutionary life history perspective on rape. In C. Crawford & C. Salmon (Eds.), *Evolutionary psychology, public policy and personal decisions* (pp. 249–274). Mahwah, NJ: Lawrence Erlbaum.
- Thornhill, R., & Thornhill, N. W. (1983). Human rape: An evolutionary analysis. *Ethology and Sociobiology*, 4, 137–173.
- Tittle, C. R., & Meier, R. F. (1990). Specifying the SES/delinquency relationship. *Criminology*, 28(2), 271–300.
- Tutin, C. G. E. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 6, 29–38.
- Utami Atmoko, S. S. (2000). *Bimaturism in orangutan males: Reproductive and ecology strategies*. PhD dissertation, Utrecht University, Utrecht.
- van den Berghe, E., Wernerus, F., & Warner, R. R. (1989). Female choice and the mating cost of peripheral males. *Animal Behaviour*, 38, 875–884.
- Vasey, M. W., Kotov, R., Frick, P., & Loney, B. R. (2005). The latent structure of psychopathy in youth: A taxometric investigation. *Journal of Abnormal Child Psychology*, 33, 411–429.
- Viding, E., Blair, R. J. R., Moffitt, T. E., & Plomin, R. (2005). Evidence for substantial genetic risk for psychopathy in 7-year-olds. *Journal of Child Psychology and Psychiatry*, 46(6), 592–597.
- Walters, G. D., Marcus, D. K., Edens, J. F., Knight, R. A., & Sanford, G. M. (2011). In search of the psychopathic sexuality taxon: Indicator size does matter. *Behavioral Sciences and the Law*, 29, 23–39.
- Walters, G. D., Brinkley, C. A., Magaletta, P. R., & Diamond, P. M. (2008). Taxometric analysis of the Levenson self-report psychopathy scale. *Journal of Personality Assessment*, 90(5), 491–498.
- Warner, R. R., & Lejeune, P. (1985). Sex change limited by parental care: A test using four Mediterranean labrid fishes genus *Symphodus*. *Marine Biology*, 87, 89–99.
- Westermarck, E. (1891). *A short history of human marriage*. London: Macmillan.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.
- Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology*, 6, 59–73.
- Wilson, M., & Daly, M. (1992). The man who mistook his wife for a chattel. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 289–322). New York: Oxford University Press.
- Wilson, M., & Daly, M. (1998). Lethal and nonlethal violence against wives and the evolutionary psychology of male sexual proprietariness. In R. E. Dobash & R. P. Dobash (Eds.), *Rethinking violence against women* (pp. 199–230). Thousand Oaks, CA: Sage.
- Wilson, M., Daly, M., & Scheib, J. E. (1997). Femicide: An evolutionary psychological perspective. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology* (pp. 431–465). New York: Chapman & Hall.
- Zimmerer, E. J., & Kallman, K. D. (1989). Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution*, 43, 1298–1307.

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