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LETTER FROM THE EDITOR

On behalf on my fellow editors, as well as our faculty liaison Professor Jill Shapiro, it is my honor to bring you the first issue of *Sapient*, the Undergraduate Journal of Biological Anthropology.

This journal was created as an opportunity for students in all academic fields to submit works related to four topics: Human Variation and Genetics; Evolutionary Theory and History; Primate Behavior and Ecology; and Paleoarchaeology and Morphology. We are fortunate to have received submissions from across the country, representing a wide range of fascinating topics.

We hope *Sapient* will continue to act as a forum for undergraduate research, and we look forward to presenting you with future issues.

— *Gideon Wolf*

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Transgenerational Epigenetic Inheritance in Human Populations

Margarete Diaz Cuadros, Columbia University

Introduction

The pattern of human growth and development has been widely recorded to vary in response to environmental conditions. Developmental plasticity allows stunted children to experience significant catch-up growth once their nutritional status is improved (Steckel, 1987). Similarly, the timing of life history events, such as age of first menstruation or first reproduction, is remarkably sensitive to variation in the environment (Herman-Giddens, 2007). Perhaps the most extreme form of plasticity takes place prenatally, as exposure to hazardous chemicals during this time has the most serious phenotypic impact (Gilbert, 2010). In the past few decades, biologists have elucidated a number of epigenetic mechanisms that seem to account for this heightened prenatal plasticity. As the embryo develops in utero, chemical marks are laid down on top of the genome to direct gene expression and cellular differentiation. This process of fetal programming is sensitive to elements in the uterine environment, such as methyl donors and stress hormones. The resulting epigenome directs multiple aspects of postnatal growth and development, including risk for adult-onset degenerative diseases (Kuzawa, 2012).

The epigenome can be understood as a form of environmental adaptation because it is laid down anew with every generation (Gilbert, 2010). Thus, fetal programming allows the individual to fine-tune its development in response to particular cues in the embryonic environment. Nevertheless, observations that adverse environmental conditions can have transgenerational effects in human populations, as well as recent data collected from mouse models, suggest that some aspects of the epigenome can be passed down from one generation to the next (Pembrey, 2002). This phenomenon has been termed transgenerational epigenetic inheritance (TEI) and may be caused by the failure of some epigenetic marks to be erased during gametogenesis. Although TEI remains to be fully demonstrated, the possibility that environmental conditions experienced by one generation can have a direct impact on the phenotype of generations to come is groundbreaking.

Transgenerational epigenetic inheritance represents a form of Lamarckism –the evolutionary theory asserting that evolution can occur through the inheritance of acquired traits – because an environmentally acquired trait is made heritable through stable epigenetic marks (Jablonka and Lamb, 1995). Furthermore, TEI has serious implications for public health. If adverse environmental factors, such as pollutants, can affect the wellbeing of multiple generations, then much stricter environmental policies are called for. In the present article, both the biological basis of fetal programming and studies conducted on laboratory animals to better characterize TEI are reviewed. Additionally, the evidence suggesting that TEI may be at play in human populations is analyzed in detail. Overall, it seems that environmentally induced epigenetic traits do cross the generational barrier, yet whether this occurs through epigenetic inheritance or alternative mechanisms remains unclear.

Background

Widespread interest in fetal programming was first sparked by epidemiological observations that adverse prenatal conditions are highly predictive of adult chronic disease (Kuzawa, 2012). For instance, infants of low birth weight have been shown to have increased risk of developing cardiovascular disease (Leon et al., 1998) and diabetes (Eriksson et al., 2002). The molecular mechanisms through which fetal programming occurs have not been fully characterized, but they have been documented to include epigenetic modifications (Hochberg et al., 2011). Broadly speaking, the epigenome refers to the set of chemical markings imposed on top of the genome that are capable of modulating gene expression without altering the genetic material itself (Kuzawa, 2012). The best-studied forms of epigenetic modification are DNA methylation and histone remodeling. Attaching methyl groups to the promoter regions of genes is known to result in silenced gene expression. In addition, methylation and acetylation of certain histone residues have the potential to inhibit or enhance transcription by tightening or loosening chromatin, respectively (Gilbert, 2010).

Epigenetic markings are closely associated with fetal programming because they are progressively laid down as the cell fate is determined, and the embryo develops from a single cell to a complex organism. In fact, epigenetic markings such as DNA methylation are completely erased first during gamete formation and again in the early zygote to make sure that the epigenome is reset as development begins (Gilbert, 2010). The ability of embryonic stem cells to give rise to all cell types in an organism largely rests on their relatively blank epigenome (Youngson and Whitelaw, 2008). Crucially, variations in the fetal environment can modify the way in which epigenetic marks are laid down. For example, gestational protein restriction results in hypomethylation of the angiotensinogen receptor gene in the adrenal gland of mouse pups, thus increasing receptor levels and resulting in high blood pressure (Bogdarina et al., 2007).

Transgenerational epigenetic inheritance (TEI) is based on the observation that some epigenetic marks seem to escape reprogramming during gametogenesis and fertilization, thus passing unmodified to the next generation. Because the epigenome is sensitive to the environment and now seems to be partially heritable, TEI has been compared to Lamarckism (Daxinger and Whitelaw, 2010). The best evidence for TEI comes from animal models, namely mice that have been inbred to the point that they are genetically identical. Precisely because these mice are isogenic, variations in their phenotype can be safely attributed to epigenetic factors (Morgan and Whitelaw 2008). This model has allowed for the identification of a small number of genes whose expression depends on a randomly determined DNA methylation pattern. Termed metastable epialleles, these genes have been of great aid in assessing whether epigenetic states can be passed down the germline (Daxinger and Whitelaw, 2010).

The best-studied metastable epiallele in mice is the agouti *viable yellow* gene. This is a mobile genetic element containing a promoter region that controls the expression of the agouti gene. When the promoter is methylated, the agouti gene is silenced and the mouse shows a normal phenotype, i.e. brown coat color and controlled body weight. However, when the promoter is unmethylated, the agouti gene is constitutively expressed and the mouse has a yellow coat usually accompanied by obesity (Lane et al*.,* 2003). Significantly, the epigenetic state at this promoter is transmitted across generations. Female mice with yellow phenotype are more likely to give birth to yellow pups, and vice versa (Morgan et al., 1999). This correlation is maintained even after embryo transfer experiments, thus ruling out uterine environment as the causative factor (Morgan et al., 1999). Moreover, the epigenetic state of the *viable yellow* epiallele can be modified through environmental manipulations. For instance, supplementing the mother's diet with methyl donors such as folic acid causes an increase in the percentage of pups with brown coats (Waterland and Jirtle, 2003).

Since the discovery of the *viable yellow* gene, similar epialleles have been documented in mice. These include the *axin fused* epiallele as well as numerous transgenes (Youngson and Whitelaw, 2008). These epigenetic modifications are sensitive to environmental factors and are capable of being transmitted down the germline, thus making a strong case for transgenerational epigenetic inheritance. Nonetheless, it remains to be determined whether these particular epigenetic marks are truly escaping erasure during gametogenesis and zygote formation. The observed transgenerational effects could alternatively be explained by direct fetal reprogramming. A pregnant female has within her not only the F1 generation represented by the fetus, but also the F2 in the form of the fetuses' own primordial germ cells (Daxinger and Whitelaw, 2010). As a result, environmental stressors experienced during pregnancy may directly affect three generations at once. Murine studies thus demonstrate that epigenetic states can be altered by the environment and inherited, yet the exact mechanisms of inheritance remain unclear.

TEI in Humans

While transgenerational epigenetic inheritance has been extensively investigated in mouse models, human studies are still in the early stages. The case for transgenerational epigenetic inheritance in humans is especially difficult to make, mainly because metastable epialleles are almost impossible to identify in outbred populations. Phenotypic variation can never be safely attributed to epigenetic factors, as underlying genetic differences cannot be ruled out as causative. Even in monozygotic twins, variation in the number of gene copies makes the study of epigenetic inheritance problematic (Bruder et al., 2008). As a result, the best method to assess non-genetic transgenerational effects is through the analysis of epidemiological data. Periods of famine or over-nutrition provide us with naturally occurring experimental scenarios. By looking at the growth and development of a cohort's descendants, we can at least determine whether environmental stressors experienced by one generation can have lasting effects in the following generations.

A classic case often cited as illustrative of transgenerational epigenetic inheritance in humans is the Dutch famine of 1944–1945. Infants that were conceived during the famine had significantly lower birth weights than controls (Stein and Susser, 1975). Furthermore, it has been found that these infants exhibited hypomethylation at the promoter region of the *insulin-growth factor 2* gene (*Igf2*), a critical hormone controlling pre-natal growth, even when analyzed six decades after the initial exposure to famine (Heijmans et al., 2008). Nevertheless, the case of the Dutch famine birth cohort must be taken simply as an example of fetal programming. The individuals in question were directly exposed to famine while in utero and thus experienced altered epigenetic programming. Since there is no suggestion that the phenotype-causing epimutation was inherited through the germline, a call for transgenerational epigenetic inheritance is not warranted.

More recently, an attempt was made to analyze true transgenerational effects in the descendants of the Dutch famine birth cohort. In this case, data were collected on the offspring of females who had been prenatally exposed to the famine. An initial report indicated that prenatally starved females gave birth to lower birth weight babies than controls (Lumey, 1992). Nevertheless, these results could not be reproduced by the same author once the sample size was expanded (Stein and Lumey, 2000). Thus, it remains unclear whether gestational famine can have lasting effects in the growth and development of following generations. Moreover, there is no molecular evidence suggesting that such transgenerational effects would even occur through epigenetic inheritance mechanisms. Since this study follows the female line, it is important to consider that the P0, F1 and F2 generations were present at the time of the famine.

Given that the female line causes significant ambiguity regarding the mechanisms of transgenerational effects, perhaps it is better to follow phenotypic variation down the male line. This experimental setup eliminates the possibility that fetal programming could be responsible for the observed phenotype, because the fetus does not share a uterine environment with its father. In addition, it is convenient that sperm cells carry almost exclusively genetic material. Molecules such as proteins and mRNA laid down in the egg prior to fertilization are capable of mediating transgenerational effects, yet this confounder is bypassed in the male line (Gilbert, 2010). Perhaps the only disadvantage to male line studies is that histone proteins are replaced by protoamines during spermatogenesis (Gilbert, 2010). As a result, it is impossible for epigenetic marks in the form of histone modifications to be passed down in sperm cells. Nevertheless, the epigenetic inheritance of DNA methylation patterns can still be assessed in this setting. Taken together, these elements suggest that the male line provides a better system for the study of transgenerational epigenetic inheritance in humans.

Researchers were once reluctant to entertain the idea that adverse environmental conditions experienced by the father could have significant effects in the growth and development of his offspring. This would require environmental information to somehow be encoded in the sperm's chromosomes (Pembrey et al., 2006). A clever experiment that proves beyond reasonable doubt that male exposure to environmental factors can influence the phenotype of the next generation was recently conducted. Data from the *Avon Longitudinal Study of Parents and Children* (ALSPAC) in Bristol, England, revealed differences in the growth patterns of children whose fathers had begun smoking in pre-adolescence. Men who reported smoking before the age of 11 years had juvenile sons with increased body mass index (BMI) (Pembrey et al., 2006). Interestingly, this tendency for increased BMI exhibits a transgenerational effect down the male line in a sex specific manner. Evidence regarding the specific mechanism of inheritance at work is currently unavailable, and so this case cannot be attributed to TEI yet.

A more in-depth study of transgenerational effects across the male line was conducted using data from the Överkalix cohort. Överkalix is small community in northern Sweden for which yearly harvest records are available. A sample of 94 children born in 1905 in Överkalix was followed and age of death was recorded for as many individuals as possible. Data on longevity were cross-referenced to food availability during the juvenile years of the children's paternal grandfathers. The researchers found that paternal grandfathers who had experienced a food surfeit during their slow growth period had grandchildren with decreased lifespans (Bygren, Kaati and Edvinsson, 1999). The inverse was also found to be true. More recently, the Överkalix sample was expanded to address the grandchildren's risk of chronic adult disease. After conducting a similar analysis, it was found that a surfeit of food during the paternal grandfather's slow growth period was associated with increased risk of cardiovascular disease and diabetes in the grandchildren (Kaati et al., 2002). Taken together, these studies indicate that juvenile grandparental over-nutrition has a deleterious effect on the health and survival of grandchildren through a non-genetic transgenerational mechanism.

The results from the Överkalix studies suggest that risk of adult-onset chronic diseases is not exclusively influenced by fetal programming, but also by transgenerational effects across the male line. In addition, the fact that an environmental event experienced by one generation has a detectable effect in the phenotype of following generations is evocative of transgenerational epigenetic inheritance. Unfortunately, no data regarding possible mechanisms have been collected for the Överkalix cohorts. The investigators suggest that altered imprinting patterns may be at work. Imprinted genes are expressed in a parent-of-origin specific manner and undergo differential DNA methylation during gametogenesis (Youngson and Whitelaw, 2008). Incorrect imprinting can result in serious developmental abnormalities and has been previously associated with diabetes (Pembrey, 2002). Given that male imprints are laid down postnatally, it is possible that juvenile over-nutrition may result in hypo or hypermethylation at certain imprinted loci. This altered epigenetic state could then escape reprograming during sperm formation in the son's testes and be passed down to the grandson through TEI. Nevertheless, this mechanism is purely speculative.

The epidemiological and statistical studies conducted on human populations so far indicate that some sort of non-genetic transgenerational effect might be at work. Nevertheless, it would be unfounded to assert that transgenerational epigenetic inheritance is responsible for the observed results. First, the studies fail to address societal factors as an alternative explanation for the apparent inheritance of acquired traits. A shared postnatal environment could account for the transgenerational phenotypic similarities. Moreover, molecular evidence is still unavailable. No data on the epigenetic states or imprinting patterns has been collected for F2 subjects. While the hypomethylation of *Igf2* has been associated with decreased birth weight in the Dutch famine birth cohort, this evidence comes from F1 individuals and is likely to represent an instance of fetal programming. Thus, there is currently not sufficient evidence to claim that TEI has been demonstrated in humans.

Surprisingly, the most likely case of transgenerational epigenetic inheritance in humans comes not from epidemiological studies, but rather from the clinic. An individual has been found with an epimutation at the promoter region of the tumor suppressor gene *MLH1*, which codes for a DNA mismatch repair protein. Epigenetic silencing of this gene has resulted in nonpolyposis colorectal cancer in the patient. Given that this epimutation is present in the three germ layers, it is assumed that it was inherited (Hitchkins et al., 2005). The epimutation most likely arose in the parental germline and failed to undergo reprograming in the early embryo. What this means is that it might be possible for epigenetic marks to bypass reprogramming germ cell differentiation and human development. Nevertheless, it would still be incorrect to say that this is a confirmed case of human TEI. While the MLH1 gene itself is free from mutations (Hitchkins et al., 2005), it is impossible to rule out mutations at distant genetic regions as phenotype-causing.

Summary and Conclusion

Fetal programming has been well-documented to have profound effects on the pattern of human growth and development, as well as human health and longevity. The adaptive value of fetal programming rests on the fact that the epigenome is reset at every generation, thus allowing for environmental plasticity and preventing the perpetuation of altered epigenetic states. However, murine studies suggest that epigenetic modifications can sometimes escape erasure during gametogenesis and zygote formation. Because epigenetic marks are sensitive to environmental factors and have a wide range of phenotypical outcomes, the plausibility of transgenerational epigenetic inheritance is paradigm-shifting. As once postulated by Lamarck, it may be that environmentally induced traits can be passed down to the following generations (Jablonka and Lamb, 1995).

While the study of metastable epialleles in mice, such as the *viable yellow* retrotransposon, has made it clear that epigenetic states can be transmitted transgenerationally, the precise molecular mechanisms through which this occurs remain obscure. The simplest explanation seems to be that DNA methylation patterns at certain loci fail to be erased during development, but this has not been fully demonstrated. In humans, the study of transgenerational epigenetic inheritance is greatly complicated by the lack of isogenicity in human populations. Phenotypic differences due to *trans*-acting genetic factors cannot be completely ruled out. Nonetheless, cross-generational records of growth and development as well as environmental conditions allow us to probe human populations for signs of non-genetic transgenerational effects. Most notably, studies conducted on the Dutch famine birth cohort and the Överkalix cohort point to the long lasting effects of environmental factors across multiple generations. Interestingly, these transgenerational effects are not limited to the female line and have the potential to modulate health and longevity.

Despite the various historical examples pointing to transgenerational epigenetic inheritance in humans, no conclusions can be reached until molecular mechanisms are elucidated and societal factors properly accounted for. Perhaps it would be wise to select study subjects for whom epigenetic data could be collected, thus clarifying the involvement of epigenetic mechanisms in transgenerational effects. Furthermore, the study of monozygotic twins offers an isogenic background that may allow for the identification of metastable epialleles in humans that should be explored. Even as transgenerational epigenetic inheritance in humans remains to be fully demonstrated, these preliminary data should attract the attention of biologists, public health officials and concerned parents. The observed transgenerational effects indicate that environmental conditions have a much more long-lasting and profound role in human development, health, and longevity than previously thought.

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The Adaptiveness of Antisocial Personality Disorder: A Review and a New Hypothesis

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Antisocial personality disorder (ASPD) is a personality disorder whose definition, manifestation and ultimate causes have been subject to much disagreement among researchers and clinicians of different backgrounds. Individuals whose symptoms are detected by society generally become ostracized or feared whereas those whose symptoms are not recognized as harmful are able to manipulate their way into positions of high status and reproductive success (Mealey, 1997; Miric et al., 2005). These two extreme possibilities for individuals with ASPD make them a particularly interesting group to study in terms of evolutionary fitness. The objectives of this article are (1) to review the literature that presents evidence for the gene-environment interactional causes of ASPD in individuals; (2) to analyze the ultimate explanations for ASPD's continued prevalence in society; (3) to synthesize the two aspects of ASPD listed above into one hypothesis that addresses why it can be adaptive for humans to develop ASPD after exposure to long-term abuse or neglect; and (4) to suggest a study design that would test this new hypothesis.

Before delving into the specifics, the delineations (or lack thereof) between ASPD, dissocial personality disorder (DPD), sociopathy and psychopathy ought to be addressed. The terms used to describe individuals who suffer from what is currently defined as ASPD by the American Psychiatric Association (APA) have fluctuated over the last several decades, and there is still some disagreement over how distinct each of the four terms is from the others (Ogloff, 2006). Currently, the APA and the World Health Organization (WHO) use nearly the same criteria to diagnose what the APA defines as ASPD and what the WHO defines as DPD. The distinguishing symptoms are

> "Callous unconcern for the feelings of others; gross and persistent attitude of irresponsibility and disregard for social norms, rules and obligations; incapacity to maintain enduring relationships, though having no difficulty in establishing them; very low tolerance to frustration and a low threshold for discharge of aggression, including violence; incapacity to experience guilt or to profit from experience, particularly punishment; marked proneness to blame others, or to offer plausible rationalizations, for the behaviour that has brought the patient into conflict with society" (World Health Organization, 1992 p.159).

The WHO asserts that DPD includes antisocial, psychopathic and sociopathic personality disorders (World Health Organization, 1992). Similarly, the APA's definition of ASPD indicates that psychopaths are individuals who exhibit particularly severe symptoms of ASPD (American Psychiatric Association, 2000). Many researchers claim that these all-encompassing definitions are too simplistic (Ogloff, 2006). Hare (1996) argues that psychopaths should have a separate diagnosis from ASPD, claiming that the ASPD diagnosis limits the predictions of a psychopath's institutional treatment and behavior following release from prison. However, because this article is concerned primarily with the symptoms and behaviors themselves and not the intricate political ramifications behind each distinct term, the terms ASPD, DPD, psychopathy and sociopathy will be referred to collectively as ASPD. This reflects an American bias, as the majority of the research papers presented here use the APA's terminology, but a few of the studies to be analyzed do use other terms to describe individuals who display symptoms of ASPD.

The majority of researchers and clinicians classify psychopathy as an exaggerated form of ASPD rather than a separate illness because of evidence indicating that human populations have a normal distribution of genes that predispose individuals to ASPD (Mealey, 1997). Therefore, people who display the most severe forms of ASPD are further from the mean in terms of genetic predisposition than those whose symptoms are considered less severe (Mealey). Studies of many diverse populations have concluded that the percentage of people diagnosed with ASPD in non-prison populations ranges from 1-4%, and two to three times more men than women have ASPD (Mealey, 1997; Miric et al., 2005). Mealey argues that the 1-4% prevalence rate is evidence of a normal distribution of the trait on the basis of game-theoretic models. If the genes that code for ASPD are normally distributed throughout a population, then within a certain range of the distribution, the ASPD genes may be latent, meaning that the individual has a genetic predisposition for ASPD but is not guaranteed to exhibit symptoms of the disorder later in life (Mealey, 1997). These individuals are of particular interest here, for the circumstances under which genetically predisposed individuals do and do not develop ASPD may hold implications for the adaptiveness of ASPD under specific conditions.

Genetic predisposition is a condition in which, due to genetic mutations, an individual has a higher risk of displaying a particular phenotype than does the average person, who lacks those genetic mutations. This does not guarantee that a person with a particular set of genetic mutations, or with a family history of a particular phenotype, will display that phenotype (Roberts and Jackson, 2008). Predisposition is generally described in terms of gene-environment interaction, a pathway in which an individual's outside environment affects his/her internal cellular environment, causing a reaction in the DNA that alters gene expression. In this way, an organism's surroundings can have a profound impact on its gene expression (Roberts and Jackson, 2008). Gene expression can be turned on or off based on outside influences, but an individual's actual genetic makeup is fixed. Thus, the same outside stimuli may effect two organisms differently because their genetic material is different and may respond in different ways. Roberts and Jackson (2008) use the blue-headed wrasse, a species of fish that travels in harems of one male and many females, as an example of gene-environment interaction. They explain that if the sole male of the harem dies, then one of the females becomes male overnight. This is because all females in this species have the genetic potential to be males, but their genes do not express the male traits unless they are responding to the absence of a male in the harem (Roberts and Jackson, 2008). Other species of fish cannot do this because their females do not have the genetic predisposition to become male as a reaction to their environment.

Researchers have found that several of the defining symptoms of ASPD can be attributed to gene-environment interaction between a mutated genotype and a neglectful or abusive childhood environment (Button et al., 2005; Cadoret et al., 1983; Caspi et al., 2002; Davis and Weere, 2007; Mealey, 1997). Button et al. (2005) sought to demonstrate the effect of gene-environment interaction in adolescents with antisocial symptoms. After studying hundreds of monozygotic and dizygotic twin pairs, the researchers found a significant interaction between dysfunction in adolescents' families and a predisposed genotype that increased adolescents' susceptibility for developing antisocial conduct. In other words, adolescents who were both genetically predisposed and faced dysfunctional family lives were more likely to develop ASPD than those who were affected by only one of the two factors. The researchers did not, however, target any specific genes that could be responsible for this interaction. Instead, they relied solely on statistical models, which may not be accurate representations of real-life scenarios, to provide evidence of gene-environment interaction.

Caspi et al. (2002) took a different approach to studying gene-environment interaction with regards to ASPD by investigating why some children who experience long-term abuse or neglect develop ASPD later in life, while others do not. They found that individuals who experienced the same level of maltreatment but whose genotype expressed higher levels of monoamine oxidase A (MAOA) were less likely to develop ASPD. In a prior study, Brunner et al. (1993) found an association between aggression and high levels of criminality (both symptoms of ASPD) and a genetic mutation that inhibited production of MAOA. These findings correspond well with Mealey's (1997) theoretical claims that the genetic mutations coding for ASPD are normally distributed throughout the population. The cohort from Brunner et al. (1993) would be considered the farthest extreme on a normal distribution curve, for their MAOA expression was blocked entirely. The individuals studied by Caspi et al. (2002) show a greater range on the distribution curve. Following Mealey's (1997) model, the individuals in Caspi et al.'s study who had low, but not necessarily null, levels of MAOA expression would be close to the farthest extreme of ASPD genetic coding. Those with higher levels of MAOA would be closer to the population mean, which helps to explain why they did not tend to develop ASPD.

Davis and Weere (2007) also studied individuals' childhood environments in relation to their antisocial behaviors later in life. These researchers were specifically concerned with individuals' reproductive efforts as a consequence of agonistic stressors, including harassment from peers, that the study participants faced in middle school. They found associations between adolescent agonistic stress and early fertility, high fertility, and a lower likelihood of forming long-term pair bonds over a ten-year period. Additionally, they found that antisociality was the mediating factor for both early fertility and the tendency not to form pair bonds in these individuals. Davis and Weere argue that when an organism feels jeopardized or its life expectancy appears to be decreased, the organism's immediate reproductive effort increases in an effort to ensure some level of reproductive success before death. This study represents one of the few original research papers examining the associations between ASPD and reproductive effort, but it still only viewed ASPD as a mediator and not the driving factor behind mating choices. Still, Davis and Weere's study provides insight, as well as a good segue, into the discussion of evolutionary explanations and implications of the gene-environment interactional causes of ASPD.

The body of theoretical literature posits different explanations for why ASPD has not been selected against to the point of becoming nonexistent in human populations. One example often used to describe an ASPD individual's role in society is the Prisoner's Dilemma, a game which, when played over several rounds with the same group of people, favors cooperation between the players to maximize the good of both the group and of each individual (Barclay, 2004; Mealey, 1997). Cheaters, or people who signal that they will be cooperative but then deceive the other members of the group and act in a selfish manner, are swiftly penalized, and this exemplifies the importance of reputation and castigation within societies (Mealey). Mealey argues that ASPD individuals are perpetual cheaters. The existence of cheaters in societies leads to coevolution in those societies, in which cooperators adapt better methods of detecting cheaters and cheaters adapt better methods of avoiding detection (Mealey). This coevolutional theory is one explanation for why ASPD has not been eliminated, despite human societies' tendencies to punish cheaters; the cheaters have evolved to become better and better at cheating without getting caught, and thus they are able to obtain the resources and mating opportunities necessary to pass their ASPD genes to the next generation (Mealey).

Miric et al. (2005) put forth a paper advocating that ASPD has evolved as a mechanism that is beneficial to the ultimate reproduction and survival of societies as a whole. They claim that societies with ASPD individuals have adapted to catch exploitative individuals, while societies (if any ever existed) lacking ASPD individuals have become extinct because they never developed the traits necessary to detect cheaters and ended up cheated out of existence (Miric et al.). Miric et al.'s group selectionist hypotheses may bother some members of the scientific community, but the assertion that ASPD may be an adaptive trait for some individuals, and that cooperation and cheater detection among non-ASPD individuals may have evolved, in part, as a response to ASPD cheaters, is still an important and compelling one, regardless of whether the selection occurred at the group level, as Miric et al. assert or the individual level, as Mealey (1997) asserts.

An evolutionary explanation for the adaptiveness of ASPD in men has to do with sexual coercion. Antisociality is associated with increased sexual coerciveness in men and is also associated with higher reproductive effort (Lalumière and Quinsey, 1996). This correlation indicates that symptoms of ASPD can increase a man's reproductive success because these traits can lead him to manipulate multiple women into having sexual encounters with him (Davis and Weere, 2007; Lalumière and Quinsey, 1996). This evolutionary benefit may help explain why ASPD is two to three times more prevalent in men than women. According to Bateman's principle, male reproductive strategies tend to favor more mates and less parental investment than female reproductive strategies (Brown et al., 2009). Thus, the behaviors of ASPD, especially the tendency not to form pair bonds and not to feel empathy (an important emotion for a mother raising a child), seem more suited to maximize male reproductive strategies than those of females.

Extensive research has been performed on the gene-environment interaction of ASPD. There is also a significant, though not quite as robust, amount of theoretical literature and original research that present possible evolutionary explanations for the persistence of ASPD in gene pools cross-culturally. However, none of these evolutionary models of ASPD account for why the disorder is expressed as a reaction to the environment rather than as a trait that is apparent early in a person's life (American Psychiatric Association, 2000). Thus, I propose a new hypothesis, one that accounts for the gene-environment interaction mechanism present in ASPD. It has been demonstrated that the genes coding for ASPD traits are most often expressed when individuals are in conditions of high stress, abuse, neglect or family dysfunction (Button et al. 2005; Cadoret et al. 1983; Caspi et al. 2002). I argue that it is to the stressed individual's advantage to display tendencies such as lack of emotion and manipulation of others when he/she is exposed to adverse environmental factors because this may be the only way to obtain resources and mates in such an unfriendly and uncooperative environment. Had the same individual grown up in a safe, secure and cooperative environment, it could be very costly for him/her to cheat members of his/her community because they had already trusted and provided for that individual. If an individual displays ASPD traits in a favorable environment, then that individual risks losing the society's trust and acceptance. This consequence negatively affects the individual's fitness because those who would have been willing to share resources or mate may no longer do so because the ASPD individual now has a reputation of being a cheater.

This hypothesis very closely parallels one proposed by Roth (2011) concerning the facultative adaptations of homicide. He argues that patterns of murder across societies can be explained by facultative adaptations, or gene-environment interactions, that render murder to be an adaptive strategy under specific (usually stressed or adverse) conditions. Roth explains, "Facultative adaptation facilitates cooperation and sacrifice in one social situation, and aggression and self-aggrandizement in another" (2011, p.537). This explanation concurs with the demonstrated ASPD disparity between individuals in non-stressed and stressed circumstances and proposed hypothesis.

This newly formed hypothesis could be tested by carrying out a study similar to that conducted by Davis and Weere (2007), who studied adolescents' reproductive effort over a period of many years. In this proposed study, however, researchers would measure the reproductive effort (in terms of early fertility, high fertility and tendency to form long-term pair bonds) of adolescents who experienced agonistic stress and developed ASPD in comparison to adolescents who experienced agonistic stress and did not develop ASPD. In either a simultaneous or a separate study, researchers could compare the three same measures of reproductive effort in adolescents who did not experience agonistic stress and developed ASPD with those who did not experience agonistic stress and did not develop ASPD. If those who developed ASPD had higher reproductive success among the stressed group and those who developed ASPD had lower reproductive success among the unstressed group, then the study would provide evidence supporting this new hypothesis.

It is important to note that this hypothesis does not exclude other explanations of the ultimate causes of ASPD. It is still entirely possible that the presence of ASPD individuals in society allows for the society's cooperative members to coevolve cheater detection strategies as a response to the ASPD cheaters in their midst, and it is highly probable that ASPD behaviors can increase reproductive success under certain circumstances, particularly for males. This new hypothesis simply attempts to build on previous ones by explaining the adaptiveness of ASPD manifestation as a response to the environment rather than manifesting in every person whose genetic mutations are shifted a certain amount past the mean.

It is clear that further study is needed to ascertain the precise mechanisms of the gene-environment interaction present in ASPD and to provide additional evidence to either support or refute the theoretical claims concerning the ultimate causes of ASPD. To test the hypothesis derived from the analysis of other realms of ASPD research in this analysis, research examining the association between ASPD and reproductive success in stressed and non-stressed environments will be crucial.

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An Adaptive Perspective on the Origins of Psychopathy

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Abstract

Analyzing mental disorders from an evolutionary perspective provides much needed insight into the origins of human behavior. One disorder, psychopathy, has been argued to have an evolutionary basis to its origin. Psychopaths are manipulative and superficially charming, do not participate in reciprocal altruism, and reproduce excessively as an alternate reproductive strategy to passing on their genes. Most individuals have few children and take very good care of them until they can reproduce. Psychopaths, however, have as many children as possible without providing needed care to any single one in hopes that at least one will reach sexual maturity and reproduce. One theory attributes early neglect and abuse to exacerbating psychopathic tendencies in individuals, while another theory suggest the disorder is genetically inherited. Present findings suggest that psychopathic traits have a high genetic heritability. Thus, the high reproductive viability these traits confer to the individual, support psychopathy as being an alternate reproductive strategy of engaging in excessive sex and displaying non-reciprocation to pass on their genes through the generations. This paper argues for an integrated approach to intervention and treatment of the disorder as well as further development of laws and public policies for psychopathic criminals.

Psychopathy is a mental state in which an individual is remorseless, manipulative, superficially charming, and inadequately motivated (Fersch, 2006). Psychiatrists now believe that as many as one in a hundred people are psychopaths, not all of who are sadistic mass murderers. Most psychopaths are rational and well aware that their illegal actions are wrong in the eyes of society but have the ability to dismiss these concerns with a startling casualness (Lilieneld and Arkowitz, 2007). Psychopaths can be found in the upper echelons of power: the CEOs of major corporations, or generals, or politicians (Babiak and Hare, 2007). They are in many ways blind to the aspect of human existence, sometimes driving them to commit deranged, violent acts like murder and rape.

In an attempt to further understand the mechanisms that cause psychopathy, it has been postulated that the environment in which an individual was reared could play a significant role in exacerbating psychopathic tendencies (Ridley, 2003). In direct opposition to this claim, researchers have also investigated psychopathy from an evolutionary perspective and postulated that the traits that define a psychopath are in fact an evolutionary adaptation that has allowed a subset of humans to use deception and cheating to get resources from others without reciprocating. Humans tend to reciprocate altruistic behaviors towards one another as a means of maintaining close bonds with those individuals that will help engender more offspring and extend our genetic line (Workman and Reader, 2008). Psychopaths show no signs of reciprocation and cheat, deceive and manipulate. Furthermore, their sexual promiscuity and early sexual maturation permits them to develop an alternate reproductive strategy to passing on their genes (Harris et al., 2007). From an evolutionary standpoint, these traits could confer some increased chance of survival compared to other non-psychopath individuals, as their selfishness and lack of conscience aid their chances of survival and their tendency to reproduce unconcernedly continue their presence in the gene pool. However, before we can designate psychopathy as an evolutionary adaptation certain criteria must be met that would qualify a psychopath's behavior as such: psychopathy must be functional in improving the survival of the individuals by conferring a reproductive advantage to the individuals and must also be genetically heritable (Workman and Reader, 2008). Understanding the origins of the development of psychopathy will undoubtedly allow for better management and fair treatment of the condition.

Differences between psychopathic and non-psychopathic individuals

Psychopaths tend to suffer from deep emotional vacancies that leave them incapable of experiencing many genuine, human emotions like love and compassion. Their inability to comprehend such emotions is rooted in the neurological differences that exist between them and non-psychopathic individuals (Oakley, 2007). An fMRI study conducted by Yale psychologist and neuroscientist Kent Kiehl was able to map areas in the brain related to the limbic and paralimbic levels (very old parts of the brain in evolutionary terms that can also be found in fishes and reptiles) (Oakley, 2007). Kiehl and his group discovered that criminal psychopaths showed much less activity in these areas when repeating emotionally charged words such as *blood, sewer, hell, and rape,* than non-psychopathic individuals. Another distinct attribute of psychopaths is their impairment in recognizing fearful facial expressions, highlighting their fearless temperament (Decety, 2012). In laboratory studies measuring physiological fear responses, non-psychopathic individuals displayed signs of sympathetic arousal associated with fear (sweat on palms, increased heart rate, increased blood pressure, etc.) when provoked by threats such as an impending electrical shock. However, psychopathic participants subjected to the same circumstances actually displayed reduced sympathetic arousal, with some showing attenuated subjective experiences of fear in response to frightening real-life events (Decetey, 2012). Generally, most normal individuals are good at fear conditioning. Since childhood we have been reprimanded for misbehaving and have learned to associate antisocial behavior with punishment. Therefore, we have been conditioned to fear the consequences that can ensue from misbehavior (Oakley, 2007). However, the distinct neurological system of psychopaths inhibits them from developing such fear response. For example, damage or dysfunction in the dorsolateral, ventromedial and orbitofrontal areas in the pre-frontal cortex appears to be strongly associated with antisocial behavior.

In addition to having an attenuate response to fear, psychopaths have a reduced capacity of making inferences about the mental states of other people, otherwise known as theory of mind (Oakley, 2007). Psychopaths are also notorious for being manipulators and deceivers, which would require skills to infer the knowledge and intentions of others. Therefore, in her research study, Shamay-Tsoory (2008) argued that theory of mind could be split into two distinct aspects: the ability to infer knowledge and belief in others and another that allows for the understanding of emotions. To test her hypothesis that patients with damage to the frontal lobes of the brain lacked the ability to understand emotions in theory of mind, Shamay-Tsoory examined criminals who displayed psychopathic tendencies as well as patients with damage to the frontal lobes of the brain. The results demonstrated that psychopathic patients showed remarkable similarities in behavior to those patients with frontal lobe damage corroborating the hypothesis that psychopathy may be a direct result of a dysfunction in the frontal lobe (Shamay-Tsoory et al., 2008), specifically to the ability to understand emotions.

Furthermore, there are other areas of the brain that display differences between psychopaths and non-psychopathic individuals. Data have demonstrated that psychopaths have difficulty processing abstract concepts. Normal individuals showed more activity than psychopaths in the right anterior superior temporal when processing abstract concepts, such as *justice*. In contrast, normal, declarative words like *plate* would elicit the same response in the area on both normal and psychopathic individuals (Oakley, 2007). Again, these results further support that psychopathic individuals cannot process complex and abstract social emotions like love, empathy, guilt, and remorse and have difficulty understanding and controlling behavior in these areas (Decetey, 2012).

Is psychopathy due to a genetic predisposition or largely a result of environmental influences?

Common postulations for the occurrence of psychopathy tend to vary from a range of genetic and environmental influences. There has been much discussion concerning whether psychopathy is a function of neurological factors or of specific environmental influences. It is a common belief that psychopathic traits may be exacerbated by early childhood abuse or neglect. Although there is almost no scientific knowledge on the efficacy of interventions to reduce psychopathic features in young children, researchers of psychopathy have singled out parenting as a potentially strong influence in the development of psychopathy (McDonald et al., 2011). Parenting exerts an environmental influence on child behavior, and can be a predictor of child antisocial behavior. In particular, harsh parenting and parent-child aggression are associated with the development of child conduct problems as well as with the development of psychopathic features (McDonald et al., 2011).

In his study on the levels of psychopathy in incarcerated youths, Dembo et al., (2007) and his research team reported correlations between psychopathy and abusive childhoods among 203 incarcerated youths in residential commitments programs in Pennsylvania, Ohio, and Delaware. In their results, Dembo et al. reported significant linear trends between psychopathy and experiencing stressful events, as well as between psychopathy and family conflict. Generally, the more stressful events the youths had experienced and the more reported conflict with family members they had, the more psychopathic traits they displayed (Dembo et al. 2007).

Support for this theory is further corroborated by the research done by McDonald and her research team on whether Project Support, a parenting intervention shown to reduce child conduct problems, would also exert positive effects on features of psychopathy in children (McDonald et al., 2011), The participants of the study were a set of 66 mothers and children recruited from domestic violence shelters who participated in a randomized controlled trial evaluating the benefits of Project Support. Each of the participating families had at least one child between the ages of four and nine who displayed clinical levels of misconduct. These families were randomly assigned into either the Project Support intervention condition or an existing services condition. Families in the Project Support condition received parent-training and emotional support to mothers, which included child management skill sessions and regular therapy visits, respectively (McDonald et al., 2011). The existing services condition consisted of monthly phone calls to the families providing similar help to Project Support but lacking in clinical and therapy visits to address parenting and child behavior. Overall, children in families enrolled in Project Support exhibited greater reductions in features of psychopathy than the children of families enrolled in the existing service. According to the data, Project Support's effect on the features of psychopathy in children was mediated by improving mothers' harsh parenting. Therefore, improvements in parenting could be attributed to reductions in features of psychopathy, supporting the theory that the effects of parenting in early childhood can have an effect on the behavioral pattern in children.

However, while children who grew up in abusive, stressful conditions may grow up to have violent criminal tendencies, there seems to be a weak correlation between early childhood abuse and the development of psychopathy (Ridley, 2003). Studies performed on monozygotic and dizygotic twins show a significantly higher concordance rate for antisocial personality disorders (APD) (a characteristic trait of individuals with psychopathy) for monozygotic twins than for dizygotic twins substantiating the high genetic heritability of psychopathy (Workman and Reader, 2008). Similarly, adopted children of biological parents who suffered from an APD also showed statistically significant levels of APD, even when raised by nurturing and caring adoptive parents (Workman and Reader, 2008). Furthermore, children who suffer from neglect and hostility early on tend to participate in some of the cruel, law-breaking activities that psychopaths are often notorious for. However, these individuals are distinguished for their proclivity to express varying levels of physiological distress, such as anxiety and low self-esteem. On the other hand, psychopaths tend to display palpably opposite characteristics: unnaturally high self-esteem and attenuate distress (Ridley, 2003).

In arguing a child's deviant behavior and psychopathic tendencies purely as a result of the abusive behavior of the parents, the notion of why the parents treated their offspring so badly should be challenged. Perhaps the parents also had a genetic component to their pathological behavior, which they passed on to their children (Harris, 1998). The predisposition to develop psychopathy seems to be more highly attributable to the genetic variance of the trait rather than by the environment in which the individual was nurtured. Additionally, behavioral genetic research utilizing samples of children, adolescents, and adults show there is a significant genetic contribution to the development of the low levels of emotional arousal the underlie psychopathy (Barry et al., 2011). Therefore, since there is good evidence to suggest that the traits that predispose individuals to psychopathic tendencies are genetically heritable it can be argued that these traits were evolutionary selected for.

The alternate life reproductive strategy of psychopaths

Some evolutionary psychologists hold the idea that much of our social behavior is based around acts of reciprocal altruism, which is defined as beneficial acts that are later repaid by the beneficiary (Workman and Reader, 2008). Reciprocal altruism is likely to have played a pivotal role in hominoid evolution and must have served as crucial mechanisms that gave rise to our basic patterns of social organization (Zahn-Waxler et al., 1986). The capacity to cooperate and share, to nurture, nourish and protect one another can be viewed as a critical feature of evolutionary fitness and survival (Zahn-Waxler et al., 1986). Evolutionarily, the food-sharing systems of many hunter-gatherer communities allowed them to invest their excess food into the group, benefiting all participants in the group (Barber, 2004). Among humans there are examples of sacrificial behaviors from military heroism to health-damaging overwork (Barber, 2004). However, when reciprocal altruism began to evolve as a strategy for survival and future reproductive success so did the possibility of cheating this system; non-reciprocating individuals did not participate in the sharing, nurturing and nourishing characteristics that define the reciprocal altruism strategy. Concurrently, there was a selective pressure on favoring the ability to recognize these non-reciprocating individuals. Human behavior did not develop this strategy—if psychopaths were identifiable no one would reproduce with them (Workman and Reader, 2008).

From an evolutionary perspective psychopathy may confer some survival advantages. Two strategies exist for getting genetic material into the next generation: 1) have few children and take very good care of them until they can reproduce or 2) have as many children as possible without providing needed care to any single one in hopes that at least one will reach sexual maturity and reproduce. Psychopaths are very irresponsible when it comes to birth control, and most tend to become sexually promiscuous (Harris et al., 2007). Many are notorious for regularly abandoning lovers and families. Although they have many offspring, most will be neglected or abused in some way. Psychopathic mothers, for example, tend to be abusive and negligent towards their children, often appearing detached or uninterested in them. They might abandon their children but only under the circumstances in which they could enhance her reproductive potential, such as by guaranteeing that the child could be cared for by others (Harris et al., 2007). Roughly three percent are males while one percent is female. This indicates that in a society made up primarily of reciprocating individuals, genes for non-reciprocators may enter the population and remain in the gene pool provided that these individuals reproduce. This evolved "cheater" strategy hypothesis suits men by allowing them to move from group to group more frequently without being noticed; they will find access to a female (either forcefully or through beguilement) to reproduce and successfully pass down his genes (Workman and Reader, 2008). These individuals will put a lot of energy into acquiring sexual partners, often exploiting their deception and coercive sexual strategies to do so.

In their paper titled *Coercive and Precocious Sexuality as a Fundamental Aspect of Psychopathy* Harris et al. (2007), argue that sexual behavior is closely associated with delinquency and crime and that psychopaths engage in sexual activities at a young age, have many partners, and are uncommitted in sexual relationships as part of their reproductively viable, alternate reproductive strategy. To test their hypothesis that "early onset, high frequency and coercive sexuality would be a key, unique and diagnostic feature of psychopathy" Grant et al. studied the case histories of 512 male sex offenders and established the Hare Psychopathy Checklist (PCL-R) score for each individual, which gives a numerical assessment of the level of psychopathy of an individual

(Harris et al., 2007, p. 17). A prototypical psychopath would receive a maximum score of 40, while someone with absolutely no psychopathic traits or tendencies would receive a score of zero. Any PCL-R score over 30 would qualify the individual for a diagnosis of psychopathy. The study also analyzed the sexual histories of the offenders prior to age of 15, which revealed a stark correlation between early and frequent sexual behavior and sexual coercion (Harris et al., 2007). Grant et al., posited that at the precocious and coercive sexuality of the individuals were indictors of psychopathy and that ultimately psychopathic individuals were not physically defective or medically ill but were simply employing the alternate reproductive strategy of engaging in excessive sex and displaying non-reciprocation via their lack of empathy and emotional understanding to pass on their genes through the millennia (Harris et al., 2007). Furthermore, they proposed "interpersonal sexual and nonsexual aggression are not best conceived of as the consequence of psychopathic personality traits, but as fundamental aspects of the condition itself" (Harris et al., 2007, p 18).

Applying an evolutionary understanding of psychopathy to improve the treatment and management of the disorder in court

Too often media portrayal of psychopathy distorts the underlying basis and cause of the condition (Lilienfield and Arkowitz, 2007). While certain neurological characteristics of psychopathy are understood and some of the current research hints at a genetic predisposition of the disorder, some may argue that it matters little whether psychopathy has been a reproductively viable life history strategy during human evolution. However, assumptions about the ultimate basis of psychopathy have profound implications on how to best manage the disorder. Currently, psychopathy is untreatable (Lilienfield and Arkowitz, 2007). Pharmaceuticals have not shown to fully alleviate individuals from their psychopathic tendencies and those who have received therapy tend to have a higher, not lower, rate of recidivism (Abbott, 2007). While some pharmaceuticals can be an option for bringing aggressive, impulsive behaviors under control, no pharmaceutical agents have been developed to restore a psychopath's core defect in emotional experience (Felthous and Sass, 2007). Without employing this evolutionary perspective on the origins of psychopathy, psychopaths will continue having their behavioral tendencies held against them without appropriate understanding of the context in which their condition has developed.

William Borema, one of the inmate subjects in Christian Keysers' study at the University of Groningen investigating the neuroimaging differences between "normally" empathetic people and those who lack empathy, described his problem with the term "psychopath." According to Borema, whose PCL-R rating lies at a staggering 35, he viewed the term as a fashionable label abused by the judicial system to keep people like himself from being released (Abbott, 2007).

"The courts looks at your PCL-R rating and add two years to your sentence, then another two years, and then another" (Abbot, 2007, p. 943). Borema states that as a current inmate he feels the psychopathy label is extremely damaging as it prompts everyone to see him as a potential killer, which he affirms he could never be. Nevertheless, he does believe that his alarmingly high PCL-R score is more of a talent than a disorder; it allows him to make good firms decisions and gives him proper distance when interacting with people (Abbot, 2007).

Borema's perception of his own psychopathic tendencies is not too far removed from the evolutionary foundation that has been hypothesized to describe the origins of psychopathy. Although the behavior of psychopaths can be summarized by an array of variable characteristics, psychopaths do not have a predisposition for criminal behavior or murder (Workman and Reader, 2008). In many ways, some psychopathic features have been argued to not necessarily be a bad thing for society. In a few professions, certain psychopathic tendencies may be of benefit. For example, too much empathy on the part of a police officer or a politician would inevitably interfere with their duties (Abbot, 2007). In their book, *Snakes in Suits: When Psychopaths Go to Work*, Babiak and Hare (2006) argue that some psychopathic personality traits could be considered as talents as they could seem attractive in job applicants and contribute to their success at being hired. Their superficial charm and ability to manipulate individuals can beguile even the most wary of interviewers, making the job interview process a perfect place for psychopaths to put forth their skills (Babiak and Hare, 2006). Babiak and Hare propose that the scientific literature on the development of psychopathy has been geared towards clinical research and as such has left a gap in understanding the functions that psychopaths serve in the work setting. Additionally, research has assessed that around 50 percent of psychopaths remain undiagnosed, contributing to the idea that functionality of psychopathic traits might suggest a successful strategy for many, unbeknownst to society (Workman and Reader, 2008).

Dr. Hare's argument elucidating some of the potential benefits of having certain psychopathic tendencies implies that psychopathy confers a selective advantage to some individuals. This inevitably hints at the naturalistic fallacy that because the mechanisms that lead to the development of psychopathy (whether it be environmental influences or a genetic predisposition) are natural, then psychopathic traits are good. While psychopathic tendencies may be useful in the work-setting examples he described, psychopathic traits are generally detrimental, driving people to actions that may endanger surrounding individuals. Nevertheless, it is imperative to understand the ultimate cause of psychopaths: how their strategy of excessive sex and non-reciprocation has allowed them reproductive success, and how such an understanding can lead to an integrated approach to the intervention and treatment of the disorder as well as the development of laws and public policies regarding how the disorder is handled in the criminal justice system.

The current social stigma for psychopathy is that unlike the mentally ill, who should be treated within the mental health system, the psychopathically disordered should be dealt within the criminal justice system (Felthous and Sass, 2007). Not surprisingly, a substantial proportion of imprisoned offenders has psychopathy and is highly disposed to recidivism. As is demonstrated in their research on recidivism and its relation to psychopathy in a group of men convicted of homicide, Laurell and Daderman (2005) conclude that psychopathy is a risk factor for recidivism. In their research, the team did a follow-up study of 35 men convicted of homicide and assessed retrospectively for psychopathy. Fourteen of the 35 men were classified as psychopaths and this group relapsed more frequently into their criminal behaviors than the non-psychopaths did (Laurell and Daderman, 2005). Since recidivism traits are extremely high in psychopaths, they are often given longer prison sentences than nonpsychopathic offenders and are more readily sentenced to death (Fersch, 2006).

Currently, treatment programs for psychopathy are virtually nonexistent in prisons, hospitals or the community. Mental health systems aim at treatment for mental illness, not psychopathic disorders. On the other hand, correctional systems are designed to secure and maintain order, not intervene in the psychological growth of the inmates. The limitations of both mental health and correctional programs beg for the development of programs that are specially designed to treat and rehabilitate individuals with psychopathic disorders. For such a program to be functional it must have a built-in research component to determine which measures are effective in attenuating psychopathic tendencies such as targeting the features of impulsivity, irresponsibility and need for stimulation (Fersch, 2006). The development of effective treatment alternatives would also greatly reduce annual prison expenses as psychopaths tend to be sentenced to a high number of years in high-security prisons. The proposed treatment that could be offered to psychopathic prisoners, known as cognitive behavioral therapy, costs less than half the cost of keeping an inmate in prison for the same length of time. Innovative treatments would then not only allow for the application of new ideas for the improvement of psychopathy but would also minimize prison expenses (Fersch, 2006).

When psychopathy and the legal system collide, certain issues arise regarding how best to prosecute such individuals. Psychopaths understand the implications and ramifications of their law-breaking behavior. Therefore, it is nearly impossible for them to employ the insanity defense during criminal trial because its definition of irrational and disturbed thinking paired with hallucinations and delusions is not characteristic of psychopaths (Fersch, 2006). Psychopaths may believe that the laws should not apply to them but they generally prove capable of understanding the demands and definitions of laws. In a legal sense, a psychopath is sane and herein lies the problem. The standards used to prosecute psychopathic criminals disregard the unique characteristics of the disorder and instead subvert psychopathic individuals to long incarceration periods and limited targeted treatments. Understanding the origins of psychopathy from an evolutionary perspective provides a unique application for improving treatment and general awareness of the disease. From an evolutionary lens the neurological differences between psychopaths and non-psychopathic individuals stem from their alternate reproductive strategy of unconcerned reproduction and non-reciprocation to pass down their genes. When analyzing how exactly a psychopath behaves it is difficult to deny that their alternate life strategy is ensuring their reproductive success; they are cheaters and exploiters, taking advantage of a strategy that normal individuals would not.

The implications that can ensue by regarding psychopathy as an alternative reproductive strategy are sure to stir debate that will undoubtedly challenge the social stigma that surround psychopathic individuals as well as the judicial system; how do you prosecute a psychopathic criminal individual that is simply employing the reproductive strategy it evolved with? While the moral transgressions committed by psychopathic individuals cannot be justified, analyzing the disorder from an evolutionary perspective gives much needed insight into the origins of behavior. This mode of assessing the disorder will allow for the modification of current law practices so that both prosecutors and the general public are more aware of the ultimate cause of psychopathy and thus able to make informed, sound decisions about the future of targeted treatments and how these can reduce the high rates of recidivism displayed by psychopathic individuals.

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Phallacies of Race: Othering the Non-White Penis in Contemporary Culture

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In contemporary Western culture, penis size matters. Although men are often reassured by their female significant others that "size doesn't matter," the understood truth of that statement is that size is in fact important and that the possession of a larger penis will result in the ability to provide women with greater sexual satisfaction (McKee, 2004). Penis size is not only important in heterosexual relationships: gay men also report seeking a large penis in their ideal mate (Drummond and Filiault, 2007). Both homosexual and heterosexual men experience dissatisfaction regarding their penis size, often wishing for a larger genital organ (Martins *et al.*, 2008). According to McKee, the possession of a large penis is required to be seen as powerful. Lying outside these phallic norms, however, is the black penis (McKee). Since the first explorers caught sight of it, the black penis has been the subject of inquiry and the object of derision for white observers (Friedman, 2001). The assumption that all black men have large penises permeates the white male imaginary and Western popular culture (Mercer, 1994). Along with the East Asian penis, which is seen as smaller than average (Goto, 1994), the black penis is seen as existing outside of mainstream Western sexuality (Mercer). The mythical sizes of these non-white penises are connected to a view of these groups as different from and less than the white majority.[i]

In Western civilization, the penis has always been more than the male organ of sexual reproduction (Friedman, 2001). It is both a physical object and an idea; as Friedman writes, the penis is "a conceptual but flesh-and-blood gauge of a man's place in the world" (Friedman, p. 6). In Sumerian mythology, composed in the world's first written language, the god Enki gives life to the cradle of civilization by filling the Euphrates and the Tigris with his ejaculate (Friedman). The power of the penis was flaunted by both Egyptian god Osiris, who was said to greet visitors to his Underworld dominion by introducing himself with the epithet "stiff of penis", and American president Lyndon B. Johnson, who showed his penis to reporters as a means of explaining why his country was still fighting in Vietnam (Friedman). Johnson's display recalls the Egyptian view of virility as victory and impotence as defeat; Egyptians kept track of the number of penises they had cut off of those they had defeated (Friedman). Osiris flaunted his erect penis as an emblem of power; a Jungian analysis by Monick (1987) defines this erection as phallos and connects it to a psychic force and an existential god-image. For Monick, the phallos is the source of male authority and power; moreover, the erect penis is like a god: a sacred, divine, wondrous, and sometimes odd taskmaster. In short, the importance of the penis, and, especially, the erect penis, in Western civilization cannot be overstated.

Since the erect penis holds such an important place in Western culture, discussion of its size, and the variation of its size, is widespread (McKay, 2004). Recent studies have investigated whether penile length could be correlated with digit ratio (McQuade, 2011), shoe size (Shah and Christopher, 2002), and sexual orientation (Bogaert and Hershberger, 1999). However, although a number of popular websites feature maps of average penis length by country or charts of average penis length by race (Penis Size Chart (By Race) ... [updated 2009]; Penis Size Average Results by Country ... [updated 2011]), no reputable scientific study from the last two decades reporting penis length varying by race or country of origin could be found. Rushton and Bogaert (1987) report a difference between the measured length of the erect penis of different groups: 4 to 5.5 inches for Orientals, 5.5 to 6 inches for Caucasians, and 6.25 to 8 inches for blacks. Even if these data are accurate, the differences in size are only significant when comparing the low extreme of the East Asian penis to the high extreme of the black penis. Nevertheless, all of the aforementioned penis size maps and charts place black men, or African countries, at the top and East Asian men, or East Asian countries, at the bottom (Penis Size Chart (By Race); Penis Size Average Results by Country). This ternary penis size myth, in which the Asian penis is smaller than the white penis and the black penis is larger than the white penis, although unsubstantiated in the scientific literature besides Rushton and Bogaert, permeates the Internet in pseudoscientific form.

The black penis has been on object of fascination and fear in Western civilization for millennia (Friedman, 2001). The ancient Greeks and Romans saw the black African penis as oversized and grotesque and portrayed it in exaggerated form in art, where it existed in stark, often erect contrast to the small, flaccid penis of the Greco-Roman male (Friedman). When Europeans rediscovered black Africans in the fifteenth century, they once again wrote of the Africans' supposedly enormous genital organs (Friedman). In Richard Jobson's 1623 memoir *The Golden Trade*, an account of the author's adventures in West Africa, Jobson describes the tribesmen he encounters as "furnisht with members" so large as to be "burdensome to them" (Cited in Friedman, p. 103). In the nineteenth century, Reverend Josiah Priest claimed that "between the sexual

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[i] For the purposes of this paper, and to reflect the popular terminology of contemporary culture, "white" is used to refer to people of European descent, "black" is used to refer to people of African descent, and "Asian" is used to refer to people of East Asian descent.

members of the negro and the brute called an ass, there is but little difference as to elongation and magnitude" (Cited in Friedman, p. 112). Throughout the institutionalized scientific racism of the nineteenth century, measurements of black and white body parts were used to confirm two contrasting ideas: that the larger white brain confirmed the white man's superiority and civility, and that the larger black penis confirmed the black man's inferiority and savagery (Friedman). According to Poulson-Bryant (2005), the superiority embraced by white men in the antebellum American South resulted in the creation of the black penis myth, a myth that both degrades black men and makes them more fascinating.

A prominent example of the fetishization of the black penis is Robert Mapplethorpe's 1980 photograph "Man in a Polyester Suit" (Mercer, 1994). Mercer states that the photograph confirms the most fixed of racial myths, that every black man has an exceptionally large penis. The foregrounding of the black penis in the photograph presents it as a sexual threat, signifying "the fear that the Other is more sexually potent than his white master" (Mercer, p. 185). The photograph also turns the black man entirely into a penis by neglecting to show his head; it is the photographic pinnacle of nineteenth-century science: a black man with a brain so small it is not even pictured and a penis so large it is the focus of the entire photograph (Friedman, 2001). In private, Mapplethorpe had said he was searching for the perfect black penis, for "Super Nigger," a man with a gorilla's primitive masculinity, base mentality, and genital superiority (Cited in Friedman, p. 144). Mapplethorpe thought he found this man in the subject of the photograph, Milton Moore, who felt that Mapplethorpe saw him like a monkey in a zoo (Friedman). This view of black man as ape or monkey or animal, prevalent through the Western racist canon, can be reinforced with the myth of the large black penis; racist thought states that animals such as apes and donkeys seem to have large penises, and so do black men, so there must be some close connection between them (Friedman).

This photographic decapitation stands in contrast to the routine castration of black men during lynchings in the United States (Mercer, 1994). In 1932, for instance, a black man, Claude Neal, was accused of raping and killing a white teenaged girl. Before he could be tried, Neal was killed by the girl's father, who kidnapped him with the help of a thousand-person mob. Prior to his death, however, the mob cut off Neal's penis and testicles and forced him to eat them. Neal's accusers needed to punish him not just by killing him, but by killing his true self, the self shown in Mapplethorpe's work: his big black penis (Friedman, 2001). This murder and castration of a likely innocent man is an example of both the fear of the black man as a sexual threat to white women and the vision of the black man as his black penis (Friedman).

Rushton and Bogaert (1987) study race difference in sexual behavior from an evolutionary standpoint, focusing on Negroids, Caucasoids, and Mongoloids/Orientals (those of African, European, and East or Southeast Asian descent, respectively). Rushton and Bogaert hypothesize that Orientals will have more sexual restraint than whites, who in turn will have more sexual restraint than blacks. The authors test this hypothesis by analyzing a large amount of data, including the age at which the hymen broke, the length of the penis, and the incidence of fellation with prostitutes. Rushton and Bogaert confirm their hypothesis through an analysis of this data, and connect certain physical features of the different groups, including the smaller testes of Asians and larger penises of Africans, to the evolution of sexual difference among these groups. Those of African descent, for instance, have larger penises, shorter menstrual cycles, and longer periods of intromission because they have evolved to, in essence, be more sexual (Rushton and Bogaert).

Lynn (1989) critiques Rushton and Bogaert's work, and argues that many physical differences, including penis size, can be explained in environmental terms and cannot contribute to an evolutionary argument about racial sexual differences. Lynn is especially critical of Rushton and Bogaert's use of an *r/K* continuum of reproductive strategies, in which they argue that blacks are most *r*, meaning that they have a large number of offspring but provide little parental care, and that Orientals are most *K*, meaning that they have a small number of offspring but provide much parental care. Although Rushton and Bogaert's work does not feature the overwhelmingly racist language of nineteenth-century science (Friedman, 2001), it takes a similar approach: it ignores certain facts in order to connect the black penis to rampant sexuality and reduced civility, seen here in the form of less parental contribution. Therefore, just as in Enlightenment science, lack of sexual control is inscribed upon black bodies as exaggerated sexual features, namely the black penis (Spongberg, 1997). And whites, falling in the middle of the sexuality spectrum, remain free of scrutiny (Fung, 2005).

Whereas black men are seen as hypersexualized in the contemporary construction of race and sex as exemplified by Rushton and Bogaert, East and Southeast Asian men are seen as undersexed (Fung, 2005). Fung states that, in contrast to the black man being defined solely as a penis, "the Asian man is defined by a striking absence down there" (Fung, p. 237). The Asian man can take on many stereotypical roles in the popular culture, usually either egghead or kung fu master, but he is always characterized by a desexualized asceticism, a lack of sexuality (Fung). Fung analyzes the eroticized Asian in gay video porn to bolster his argument. In one video, *Below the Belt,* a white character, Robbie, fantasizes about sex with his white Karate instructor. In the fantasy, however, Robbie is played by an Asian actor, who takes a passive sexual role by performing oral sex and receiving anal sex without any obvious signs of pleasure; the Asian Robbie's penetration is merely an act of submission. As white Robbie, however, he takes an active sexual role, receiving oral sex and performing anal sex (Fung). In another video *Asian Knights*, two Asian men have sex in the presence of a white psychiatrist, while the psychiatrist watches from the center of the frame; the audience is therefore watching from his white perspective (Fung). Both of these videos demonstrate the desexualized Asian male: in the former, he is submissive and take no pleasure from sex, and in the latter, Asian desire is deflected and replaced by white desire (Fung). In both, the Asian penis is all but absent.

Like the small or absent Asian penis myth, the big black penis myth is also seen in pornography (Davis and Cross, 1979; Poulson-Bryant, 2005). Davis and Cross report that white males and females, no matter their level of education, perceive black males as more sexually potent than their white counterparts in pornographic stories. Poulson-Bryant analyzes the use of black men in pornography as objects of white male fantasy and control. He argues that the black penis, a cultural object constructed by white men into the big black penis myth, is used as a tool by white men to degrade white women in pornography. In other words, the black penis, once seen as freakishly large and a danger to white women, is now being used for its large size to do sexual damage to white women for the pleasure of white men (Poulson-Bryant). Black male porn actors, according to Poulson-Bryant, must act white enough, i.e., without the stereotypical trappings of black culture, as to remain palatable to white male viewers watching the pornography for their own sexual arousal. The black penis is being used as a tool for white sexual arousal within the constraints of white definition while the man to whom it belongs is being asked to define himself by white norms; the black penis is made blacker while the black man is made whiter (Poulson-Bryant). In pornography, therefore, the black penis is no longer an object of fearful sexuality to white men, but an object of controlled male domination belonging to a controlled black man (Poulson-Bryant).

Contemporary popular Western cinema can serve to elucidate the black penis myth (Rehling, 2009). Rehling states that DiCillo's 1997 film *The Real Blonde*, demonstrates white male fears and anxieties regarding the black Other and his penis. In the film, the protagonist, Jo, a struggling young boxer-wearing actor, is relegated to the back of a Madonna video in favor of tight-brief-wearing, well-endowed black men. Citing Kaja Silverman, Rehling argues that this is an instance of the white man fearing the black man's larger penis as it places the white man on the side of smaller rather than larger and therefore closer to the white woman.

In contemporary popular Western cinema, the black penis is often neutered or even feminized to allow for the reconstruction of white heterosexual masculinity (Rehling, 2009). In Cattaneo's 1997 film *The Full Monty*, Horse, the one black male character left over from the original idea of an all-black cast, buys a penis pump because he fears living up neither to the prevalent stereotype of black penis size nor to his nickname, which the other characters speculate is related to his presumably horse-sized member (Rehling). Horse's actions and the other characters' assumptions show that both black and white men have internalized the black penis myth, regardless of its verity. Horse's lack of a horse-sized penis both emasculates him and allays the audience's paranoia about black penis size (Rehling). In Jordan's 1992 film *The Crying Game*, Fergus has a sexual encounter with Dil, who he thinks is a woman but who is in fact a man. Fergus' white penis is never shown, but Dil's black penis is shown, flaccid. Fergus' presumably erect penis, the recent recipient of oral stimulation, is allowed to remain the object of power (the phallus), even though Dil's penis is being shown (Rehling). Since Dil's penis is flaccid, it does not carry the same ritual or racial power as Fergus' veiled, but erect, penis (Rehling). The reversal of phallic norms here confirms Fergus' masculinity, especially in light of Dil's previously presumed femininity (Rehling). The black penis is expected to be large and erect, and presenting it differently plays on the audience's knowledge of the black penis myth.

The different sizes of white and black penises are used in different ways in Western TV and film (Poulson-Bryant, 2005). In Dickerson's 2003 telefilm *Good Fences*, a black character named Tommy-Two is seduced by the Japanese mother of his best friend during a sleepover. After asking him to model for her, she praises the size of his penis and mentions how large it is compared to those of white men and Japanese men (Poulson-Bryant). Poulson-Bryant argues that the scene is an abrupt and exploitative moment in a film about black people adjusting to upward mobility in northeastern American suburbia, a moment in which Tommy-Two is suddenly revealed as not just an adolescent black man but a hung stud. The moment dehumanizes him, transforming him into the trope of the big black penis (Poulson-Bryant). In Coppola's *The Godfather*, on the other, the large size of Sonny Corleone's penis is revealed early in the film and is used as one element of his character, a metaphor for his boldness and bullishness. Sonny's penis is part of his character development, as opposed to as a facile representation of racial difference (Poulson-Bryant). The big black penis takes over the character, whereas a large white penis enhances the character.

This phallic binary seen in TV and film is also found in Hollywood at large. As Poulson-Bryant (2005) reports, when *Details*, a celebrity-driven men's magazine, featured a list of the Hollywood actors with the largest physical endowments in the May 2003 issue, not a single black man was included on the list. Although Hollywood's films and television frequently use the big black penis myth, that myth is not perpetuated on the list. Poulson-Bryant states that this may be because it is more interesting for readers to read about well-hung white men, who are not expected to have as large penises. Alternatively, Poulson-Bryant argues, the lack of black men on the big penis list could relate to the lack of black men in romantic leads in Hollywood films: black actors are in a different category, as are their penises.

The stereotypes about Asian and black penises seen in pornography and mainstream film are upheld outside of popular entertainment. Wilson *et al.* (2009) reveal that, in a study of men looking for male bareback sex partners on the Internet, participants in all racial groups upheld the stereotype that black men are expected to have large penises. Furthermore, all racial groups upheld the stereotype that Asian men are expected to have small penises. The participants in the Wilson *et al.* study also reinforce sexual norms associated with these penis myths; many described sex with black men as aggressive, rough, and raw, whereas sex with Asian men is boring and reserved. Schwartz (1985) reports that a doctor who has performed thousands of vasectomies believes that black men have larger penises than white men, who in turn have larger penises than Asian men. Stereotypes of non-white penis size are part of the shared cultural consciousness (Friedman, 2001; Poulson-Bryant, 2005).

Penis size myths are problematic because of their reinforcement and/or creation of negative stereotypes about groups as a whole. As Friedman (2001) reports, the myth of the large black penis has helped white men characterize black men as hypersexualized, animalistic, and radically different from the rest of civilization. A large penis came to mean a more sexual person, and a large black penis came to define a black man altogether (Friedman). On the other end of the spectrum, the myth of the small Asian penis has fed into a conception of Asian men as desexualized and feminized (Fung, 2005; Goto, 1994). Other racialized penis myths have existed and do exist: the Jewish penis, for example, was once seen as marked by its circumcision and therefore cursed by God, and helped Christians connect Jews to perversions and disease (Friedman). More recently, the Latino penis is seen as stereotypically uncut, meaning uncircumcised, and this is associated with a view of Latino men as being foreign and preternaturally passionate (Wilson *et al.*, 2009). The black and Asian penis myths, however, seem to be the most persistent and the most well-known.

Penis size matters in Western culture (McKee, 2004). The erect penis has been an important symbol of male power and prowess throughout Western civilization (Friedman, 2004). Although mostly unsubstantiated by science, a widely held myth states that black men's penises are larger than those of white men (Friedman). Throughout the history of Western civilization, the large size of black penises has been connected to hypersexualized and animalistic behavior in the men to whom the penises belong (Friedman). The black penis alone has come to represent the black man entirely; the black man has been conceptualized as his large penis (Friedman; Mercer, 1994). Researchers have attempted to draw scientific conclusions connecting the size of the black penis to increased sexuality in black men (Rushton and Bogaert, 1987), although this work has been criticized (Lynn, 1989). East and Southeast Asian men are seen as undersexed in Western culture, as exemplified by their submissive and disinterested behavior in pornography (Fung, 2005). The black penis is used as a white male tool to degrade women in pornography, in which black men are shown as hypersexual (Davis and Cross, 1979; Poulson-Bryant, 2005). In mainstream photography, film, and celebrity culture, the black penis is also fetishized and stereotyped (Mercer; Poulson-Bryant; Rehling, 2009). The myths surrounding the black penis and the Asian penis exist within the cultural consciousness (Wilson *et al.*, 2009). The view of the black penis and the Asian penis as Other, a different size from the mainstream, normative white penis, reinforces racist thought about the sexual behavior of these minority groups.

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The History of Sexual Selection: Darwin's Other Great Theory of Evolution

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The Birth of Sexual Selection

In November of 1859 Charles Darwin published The Origin of the Species, a revolutionary work on evolution via natural selection which described how a *natural* law could explain speciation. The underlying tenet behind evolutionary view up to the Origin was that a creator was responsible for the existence of life on earth, but Darwin reasoned that if the cosmos could be explained by the governance of certain physical laws, then why could the existence of life *not* be explained by the same.

Darwin introduced the idea of natural selection as the accumulation of variation through time that if they aid in the individual's struggle for survival, then those variations will be produced time and time again and spread throughout the population. He proceeds by making us think just how complex and well-fitted animals are to their habitats (and to other animals) and asks us to think of the large number of possible structural variations (Darwin 1859) that each individual could have in the struggle to survive (Darwin 1859). If we imagine that these possible variations could give certain individuals a higher chance of survival and reproduction over others, then we can also imagine that injurious variations would have the opposite effect and thus be eliminated from the population (Darwin 1859) Natural selection, therefore, would tend to preserve favorable variations, no matter how odd they may be. "Nature," he wrote, "cares nothing for appearances in so far as they are useful to any being." (Darwin 1859, p.21) "Appearances" blanketed any character that would provide an advantage, that extra edge, over others. Although it sounds that the extra edge was reserved for the struggle for survival, the "advantage" also included those characteristics involved in the struggle for access mates, i.e. display behavior, differences in coloration, and exaggerated markings among others. And thus, out of the theory of natural selection, sexual selection was born and defined it as depending,

> *" not on a struggle for existence in relation to other organic beings or external condition , but on a struggle between the individuals of one sex, generally the males, for possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring..."*(Darwin 1859, p.21)

since the opposite sex will choose the successful competitor (Darwin). Males, Darwin argued, compete against each other by displaying seemingly injurious traits to females who then choose males based on the "attractiveness" of those traits (Darwin). In other words, the more attractive the trait is, the higher the advantage that male has over others when competing for access to females and since those traits give males an extra edge, sexual selection can offer an explanation as to why traits that natural selection would not favor because they may be injurious to the individual, actually appear and remain in a population (Darwin). By doing this, Darwin gave non-human females a sense of beauty and in so doing, opened Pandora's Box: can non-humans *choose*? Do they possess a sense of aesthetics? And if so, does that mean that evolution is *directed?* If so, then this counteracts the effects of natural selection and may even render it obsolete in the process...and for the next 100 years, naturalists would continue to concentrate their efforts on the unbiased and undirected effects of natural selection and on the way, prove that sexual selection is nothing more than another form of natural selection (Cronin 1992) and sexual selection, as Darwin defined it, disappears from the scientific literature, only to resurface, *as* sexual selection, in the 1970s.

I wrote this paper in the hopes to understand why Darwin's other major theory of evolution was silenced soon after its introduction. Not surprisingly, I found that it was the ultra-Darwinians of the 19th and 20th centuries who dissected and dismantled sexual selection theory so that it ceased to exist as Darwin intended it to and instead it was forced to fit the more rigorous and utilitarian doctrine of natural selection. Considering the difficulties and ridicule Darwin and his followers felt with the introduction of evolution via natural selection in 1859, with its long struggle and subsequent acceptance, fighting for its existence as the one law that explained evolution was, simply, the natural progression of things, so that fighting against the actions, or existence, of sexual selection as having any evolutionary effect was only practical...and thus began the dissolution of the Theory of Sexual Selection.

Sexual Selection by Darwin

In 1874, Darwin finally explained sexual selection in detail. In the introduction of Descent of Man and Selection in Relation to Sex he wrote that he had spent many years collecting data on the origins of man without ever wanting to publish any of it (Darwin 1874) fearing that his theories on origins would further add to the criticism already thrust upon natural selection. However, his peers saw hat his work was applicable to man and thus pressured him to publish, and so he did. Descent aims to explain how man descends from another species, how we develop through time, and to account for the different races found throughout. Darwin's 619-page tome ends by stating that man not only descends from a lower ancestral form, but also that sexual selection indeed may have played an important role in the evolution and in the mental powers of man and the propagation of racial diversity. Race itself, Darwin argued, was not an elaborate trait, like the peacock's tail, but race was a trait that was under female choice because of the manner in which females seem to choose mates. Darwin hypothesized that the attraction of a trait, even a detrimental one, was key in sexual selection, but to explain it, he first divorced it from natural selection.

As mentioned earlier, natural selection in Origins is defined a process that shapes organs and traits with respect to the species' habitats and lifestyles, with each sex having adaptive traits conditioned by the organism's environment (Darwin 1874), and any trait that serve other purposes besides reproduction are subject to natural selection, and those that serve reproduction are subject to sexual selection. We can see the different selective forces acting, especially in species that have a high degree of sexual dimorphism (differences in body size/colouration between the sexes) where one sex tends to be more elaborate; the opposite sex tends to be more drab-looking. Furthermore, in sexually dimorphic species it is the elaborate sex who uses its ornamental traits to find and keep mates, and the drab looking sex seems to choose. Therefore, Darwin concluded, those overdeveloped characters must give that sex displaying them an advantage over others (Darwin 1874; Mayr 1972) not in the struggle to survive, but in the struggle to seek and retain mates (Darwin).

Interestingly enough, although Darwin argues for sexual selection as another mechanism of evolution, he did not quite know how it worked (Darwin 1874); yet, he knew that it must play an evolutionary role in the development of secondary sexual characteristics[1] (SSCs from now on),

> *"female birds in a state of nature, have by a long selection of the more attractive males, added to their beauty or other attractive qualities...this implies powers of discrimination and taste on the part of the female..."* (Darwin 1874, p.18)

For Darwin, the matter of male-male competition for access to females was unquestionable, so it was only sensible for females to have the opportunity to select a male amongst many. In migratory birds, for example, male birds arrive at the breeding ground before females, preparing males to fight other males for access to females. Similarly, the male birds who arrive at the breeding ground before other males are the best nourished, the more vigorous, the winners in the battle of survival (Darwin 1874) so that by the time they arrive at the breeding ground, the females will have the opportunity to select the best of the best. Unfortunately, a pool of the best nourished males and selecting females does nothing to illuminate the mechanism behind sexual selection, but we can get an idea of the mechanism by looking at the 'pool'. Males and females are subject to natural selection, so it is not just a portion of males that arrive early at the breeding ground, it also the case for females. Now, if the number of males equals the number of females, then all males and females would pair equally and their offspring would carry their parents' traits that made them fitted to their environment; however, if the number of males is greater than the number of females, then the males will compete with each other for access to females. Therefore, sexual selection exists in situations where males outnumber females (Darwin 1874). Moreover, for traits to be passed on through generations, it must be that the best males breed with the best females (Darwin) so the early arriving males would compete with each other for access to the first arriving females who will choose amongst the males. It is also the case, Darwin argued, that in situations where males outnumber females, males carry very elaborate traits (Darwin) and females are dull looking. The early arriving breeders (males and females) would have an advantage over the late arrivals in terms of producing, and caring for, a greater number of offspring (more resources available at the beginning of the breeding season than in the middle or towards the end), so there will be more male offspring with very elaborate traits and more female offspring carrying the preference for males with elaborate traits. Thus, Darwin argued, females would continuously choose males with slightly more elaborated traits, and is so doing, drive the evolution of secondary sexual characteristics.

The paragraphs above are a quick rendition Darwin's theory of sexual selection which can be summarized as follows: males have elaborate traits that should be detrimental to their survival, but because males are still able to survive with such a cost, then those traits must provide males an advantage over other males. The evidence came from females seemingly choosing the most attractive males or the males with the most elaborate trait. In a nut shell, Darwin argued that non-human females have a sense of beauty, but a sense of beauty comparable to the "lowest savages, who admire and deck themselves with any brilliant, glittering, or curious object" (Darwin, p.18) and not to a "cultivated man, with his multiform and complex associated ideas" (Darwin, p.18) ...either way, Darwin found himself in trouble: he attributed the sense of aesthetics to non-human animals without scientific evidence to support it and should, therefore, not be part any evolutionary theory.

Sexual Selection Theory and Its Discontents: 1871-1900

Dismantling Sexual Selection: Mr. Darwin's Critics

The publication of Descent turned out to be a fiasco. Victorian England was not ready to read that animals have a sense of beauty comparable to man and, this is purely conjectural, that females have a choice in their reproduction. Immediately after the publication, two key players would begin to dismantle the theory of sexual selection: enter Alfred R. Wallace and St. George Mivart. Shortly after Mivart, Edward B. Poulton would finish off what Alfred and Mivart could not do.

Not surprisingly, sexual selection's prime demolition was natural selection's co-discoverer Alfred R. Wallace. As an ultra-Darwinian, Wallace believed that all traits are subject to natural selection because ornamentation had been selected for other purposes, and not because females choose them. For Darwinists of the 1880s, natural selection served a utilitarian purpose, and was unbiased and undirected; sexual selection, on the other hand, was the opposite: biased and directed.

Like Darwin, Wallace touched on color, ornaments, and scents. What Darwin considered SSC, Darwinists saw as non-adaptive, their value being in that they provided something beautiful for the human eye (Cronin 1992; Wallace 1889), yet this anthropocentric view of beauty did not, and could not, explain the reason for their existence. Wallace focused on the inconspicuous coloration and believed that female coloration was adaptive and selected through natural selection for the purpose of protection of the female and eggs during incubation. Just like inconspicuous coloration, bright colors served to camouflage the individual in its environment and to recognize members of the same species and help identify potential mates (Wallace). Thusly, viewing ornamentation with this frame of mind allowed the Darwinian natural selection model to be followed.

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[1] Primary sexual characteristics are traits that are directly involved in sex. Traits involved in sexual reproduction but not in sex itself are secondary sexual characteristics.

One of Wallace's great achievements was his provision of examples of animal coloration to the theory of natural selection. Wallace's focus on drab coloration of female birds turned the question of female choice for elaborate traits upside down. Wallace argued that female coloration is selected because egg production is very costly, so she needs richer resources than the males to produce costly eggs; therefore, the best camouflaged, or the more drab the female, the more eggs she will get to produce throughout her lifetime because she will have access to more resources than those females whose camouflage or dull coloration are not as good. Thus, drab coloration is necessary to protect her not only for egg production, but also while incubating her eggs (Wallace 1889). Even if males and females are brightly colored, Wallace noticed that the nests, themselves, are hidden and when the female has conspicuous coloration, the male incubates and is usually drab. Even in cases when the female is brightly colored and the nest is open, the female is protected in some other way, perhaps by blending into the surrounding (Wallace). In any case, he connected *coloration* of males and females to *nest protection* which would result in larger number of offspring. He finds the same sort of evidence in insects where both sexes mimic leaves or with females looking like a completely different inedible insect species because of its bright coloration (Wallace).

Personal letters between Darwin and Wallace indicate that Wallace initially supported sexual selection (van Wyhe 2002-2008) but by the publication of Descent in 1871, and finally, in his 1889 Darwinism, we see Wallace trying to prove that other selective forces and not female choice were behind secondary sexual characteristics. Wallace argued that males display, not for the sake of females, but to release or ease their sexual burdens, and mating, as a result of display, occurred indirectly since "display was probably correlated to the desire to move or to do something and not to attract" (Wallace 1889, p.15). He based this supposition by noting that even unornamented birds display and they still mate, so female choice was dispensable (Wallace). For Wallace, the fact that physiology and ornamentation happen together indicates that they develop together and so co-evolved in a dependent fashion. The many examples he gives

> *"help explain the general dependence of marking on structure... For, as the nerves everywhere follow the muscles, and these are attached to the various bones, we see how it happens, that the tracts in which distinct developments of color appear, should so often be marked out by the chief divisions of the bony structure [and] brilliant color usually appear just in proportion to the development of tegumentary appendages."* (Wallace 1889, p.15)

Therefore, by dismissing display as a behavioral phenotype and instead forcing it into a purely functional perspective bound by the animals' physiology, Wallace views male coloration as being non-adaptive and, as such, did not need to be explained in terms of selection.

Wallace's explanation for the evolution of male ornamentation is that it arose not through sexual selection but through some unknown causes, and sexual dimorphism exists "perhaps due to his smaller size and greater vigour" (Wallace 1871) and "partly of more or less protective tints acquired by female alone on account of her slower flight and greater need for protection while depositing her eggs" (Wallace, p.17). So while females drab coloration is adaptive, male coloration is not, and even if sexual selection does happen in nature, Wallace argues, it is subservient to natural selection (Wallace 1889). Sexual selection could exist if there were supportive evidence of female preference of coloration (Wallace 1889) and to Darwin's argument that if females do not choose then pairing would be left to chance, Wallace replied that it must be "the most vigorous or most persevering male that is chosen, not necessarily one more brightly or differently colored, and this will be true 'natural selection'" (Wallace, p.15) because the female chooses the strongest or better fitted individual. And this is where Wallace contradicts himself, almost trying to save instances of both theories while remaining loyal to natural selection. His argument so far is that male coloration is a side effect of the animal's physiology, it is circumstantial, so it is not adaptive; female coloration is adaptive because it helps her survive, and produce and care for offspring. He has also argued that there is no evidence of female choice for coloration since she chooses the strongest individual, but for this to work he has to first distinguish adaptive versus non-adaptive characters.

Wallace made a fact of distingushing the physical and biological aspects of color The physical aspect of color was its expression, its existence in the material world, its matter-of-fact. The expression of color is as much a physical reality as the sky is, but the biological side of color is slightly different (Wallace 1889). It is that which has been specialized by natural selection because of its location on specific structures of the body. Therefore, Wallace argued, this distinguishing feature of colour is not only biological but also adaptive! (Wallace). It is interesting to see how selection happens here: coloration becomes adaptive *indirectly* because the *structure* on which the color rests is subject to natural selection and IT is selected because it is adaptive. But he has already argued that male coloration is not adaptive and contradicts himself by saying that it is adaptive insofar as it meets physiological criteria, but does it work only on female coloration? Or does it only work on male coloration? Unfortunately, Wallace does not provide us with a clear answer, instead he provides us with a contradiction, with a means of remaining within the scope of natural selection because

> *"the extremely rigid action of natural selection must render any attempt to select mere ornaments utterly nugatory, unless the most ornamented always coincides with 'the fittest' in every other respect; while if they do so coincided, then any selection of ornament is superfluous...natural selection renders it [female choice] as ineffective."* (Wallace 1889, p.15)

And in one swoop, Wallace dismisses female preference on colors and links ornamentation to the animals' physiology (Mayr 1972; Wallace 1889).

Once a good friend of Darwin's, St. George Mivart had become increasingly more irritated by the 'scientifically unanswered' questions of skeletal homologies found throughout different orders. Seduced by Owen's work (Richards 1987) on comparative anatomy and belief that a Creator is responsible for the existence of mankind, Mivart transformed into, I think, 20th and 21st century Intelligent Design 'bull-dog', divorcing Darwinism in favor the more natural theology perspective. Unlike Darwin and his followers, he believed that species evolved in saltations and were guided by an inner force, so that when Darwin published Descent, he wrote a scathing review not just of the sexual selection theory, but of Darwin himself, accusing him of backing away from his canonical theory of natural selection by finding "grave defects and serious shortcomings" (Mivart 1871b, p.22) in his theories. Mivart would use Darwin's own words in Descent against him, almost pettishly, sarcastically, and at times, maliciously; thus

> *"a false theory which keenly solicits the imagination, put forward by a writer widely and deservedly esteemed, and which reposes on a multitude of facts difficult to verify, skillfully interwoven, and exceedingly hard to unravel, is likely to be very prejudicial to science"* (Mivart 1871b, p.22)

was a clear rebuttal to Darwin's plea in Descent that false facts and false views are injurious to the progress of science (Darwin 1874), so much so, that Mivart asked that sexual selection be carefully reviewed and criticized, especially when a celebrated name accompanies a theory.

Mivart's proposal is a counter-offer and a warning to the reader. He argued that sexual selection was not proven and ran the risk of being interpreted and accepted as a tested theory by the lay person. He used Descent to review Darwin's whole position on evolution by appealing to the revisions Darwin himself made to the theory of natural selection,

> *"if he has been over-hasty and seriously mistaken previously, we must be the more careful how we commit ourselves to his guidance now...Mr. Darwin's convictions have undergone grave modifications, and that the opinions adopted by him now are quite distinct from, and even subversive of, the views he originally put forth. The assignment of the law of 'natural selection' to a subordinate position is virtually an abandonment of the Darwinian theory; for the one distinguishing feature of that theory was the all-sufficiency of 'natural selection'." (Mivart 1871b, p.22)*

Then, again, just a few pages later, Mivart suggested to the reader to measure the amount of credibility we give to Darwin's theories because,

> *"the formidable objection to Mr. Darwin's theory [sexual selection], that the great break in the organic chain between man and his nearest allies, which cannot be bridged over by any extinct or living species, is answered simply by an appeal 'to a* belief *in the general principle of evolution (vol. i. p. 200) or by a confident statement that 'we have* every reason to believe *that breaks in the series are simply the result of many forms having become extinct' (vol. i. p. 187)."* (Mivart 1871b, p.22)

Mivart's attacks on Darwin stem from Mivart's view that neither selection theory, sexual or natural, provide a natural explanation for animal origination, rather, Darwin's data is speculative and that his theories should be received as an "article[s] of faith" (Mivart 1871b, p.22).

Mivart then, divided sexual selection into its components: male/male competition and female-choice. He agreed with the first, but argued that it falls within natural selection; and female choice alone should be labeled as sexual selection, if sexual selection exists at all. For Mivart, male/male competition consisted of the action of strength and activity by which one male succeeded in obtaining and restraining a mate, and that is natural selection. However, female choice was incorrect because in horses, it is the males that choose: he never saw a horse reject mares, but he saw mares reject horses. Moreover, and to appeal to the incredibility of female choice, he cited Darwin's example of the female toad smothered by males while they embrace her and wrote, quite sarcastically, that "sexual selection...must be admitted to have been singularly infelicitous to the female toad" (Mivart 1871b, p.22). Attacks such as these are rampant throughout the review, with rare instances when the objections are more civilized: to Darwin's argument that display is for the purpose of attraction, Mivart countered that display is a method to excite the nervous systems of both sexes to elicit copulation, a similar argument of other naturalists of the time and, more specifically, Wallace (Mivart). Then, just as suddenly, Mivart reverts to sarcasm and takes us to the heart of Darwin's argument: sexual selection and the mental powers of man.

Mivart argued that Darwin's comparison of man with other species is simply to show that man is an animal, and although it was not a novel idea, Mivart implied that Darwin appropriated it (Mivart 1871b). Now it gets interesting as it drives Mivart's theologian view of the origin of man. Mivart's interpretation of Darwin's idea of descent by modification is that as an animal, man must have followed the same mode of origin as other animals which would be sensible if one accepted Darwin's views on man's mental powers. But because fossil data is saltatory, Mivart argued, man's evolution becomes an argument of probabilities...and these 'probabilities' might be secured or remedied with "another mode of origin",

> *"Mr. Darwin says:-- 'It is only our natural prejudice and that arrogance which made our forefathers declare that they were descended from demi-gods, which leads us to demur to this conclusion' (vol. i. p.32). But this is not the case; for many demur to his conclusion because they believe that to accept his view would be to contradict other truths which to them are far more evident."* (Mivart 1871b, p.22)

Mivart's review of Descent is not so much a review of the theories inside it as it is an attack on Darwinism itself and what Mivart believed to be amoral and atheistic views. To Mivart, Darwin erred in his treatment of man, for man more than just an animal with different mental powers. Mivart's view of man was of a free moral agent immensely incomparable to other beings (Mivart 1871b) and concluded the review of Descent by saying that Darwin failed

> *"in the only part of his work which is really important. [His] errors are mainly due to a radically false metaphysical system in which he seems (like so many other physicists) to have become entangled. Without a sound philosophical basis, however, no satisfactory scientific superstructure can ever be reared; and if [his] failure should lead to an increase of philosophic culture on the part of physicists, we may therein find some consolation for the injurious effects which his work is likely to produce on too many of our half-educated classes."* (Mivart 1871a, p.18)

I was hesitant at first of including Mivart in this paper, especially because he was not as influential in discrediting sexual selection as Wallace was; however, after careful consideration, I think Mivart was influential in a different manner. By invoking a philosophical origin of man, Mivart may have actually pushed Darwinians to prove that natural selection, and not the supernatural, was the responsible force in the evolution of man. If, however, Mivart's influence on the theories of sexual and natural selection were not as strong as I think it may have been, Descent of Man brought out other critics.

Edward Poulton, an English entomologist and staunch supporter of Darwin and foremost exponent of his theories, would be a key player in turning sexual selection on its head. Although he believed in sexual selection and supported the idea of female choice, for a reason I do not yet understand, Poulton classified the colors of animals according to their use and, in so doing, changed the way sexual selection would be studied for next 80 years.

Poulton accepted Darwin's theory of sexual selection right away and disagreed with Wallace's assumption that there was no evidence of female choice. Poulton (1890) rebutted Wallace by writing a whole book, Colors of Animals, in which he gave examples after examples of cases of female choice and cases where choice and display can be reversed so that males choose attractive females as well (Poulton 1890). But then, in the summary of the book, he classified colors into an intricate system showing the purpose of each category of color. The classification erases female choice from the system while animal coloration is redistributed to the following: I) Apatetic Colors: colors that make animals resemble other animals. This category has two sub-categories, each containing two subdivisions. Category A is Cryptic colors which are protective and aggressive resemblances; and Category B is Pseudosematic Colors which are false warning and signaling colors of animals. Category A, Subcategory 1 hold the Procryptic Colors which resemble protective coloration; Subcategory 2 hold the Anticryptic Colors which resemble aggressive coloration. Category B, Subcategory 1 hold the Pseudaposematic Colors which are the protective and mimicry colors; Subcategory 2 hold the Pseudepisematic Colors which are the aggressive, mimicry, and alluring colors (not involved in sexual reproduction but alluring to prey); II) Sematic Colors divided into subcategories: Aposematic Colors which are only warning colors and Episematic Colors which are colors for recognition; and finally, what is left over of sexual selection, III) Epigamic Colors which are displayed in courtship. Then, in 1896, Poulton revisited sexual selection but saw it as playing a minor role and concluded that naturalists "further accept Darwin's opinion that its action has always been entirely subordinate to natural selection" (Poulton 1896, p.27), and by doing so, he reduced sexual selection to fall well within the scope of natural selection. Poulton was so influential in eclipsing sexual selection that by the 1930s, sexual selection would be studied in terms of intra-sexual competition and epigamic colors. But the 19th century was not finished dismantling sexual selection: the same year that Poulton dismissed sexual selection, psychologist Karl Groos accepted sexual selection (with the exception of female choice). He believed that females succumbed to males as they overcame their reluctance at being seduced (Groos 1898). The reason it is still sexual selection, argued Groos, is because the competition is **between** males and females, where these finally accept males for pairing and maintenance of the species (Groos 1898).

Wallace's Legacy

Wallace's push for the disintegration of sexual selection reached its zenith by the 1900. By the time naturalists of the 19th century were finished with Darwin's second incendiary theory, sexual selection would be viewed as subservient to natural selection and secondary sexual characteristics were the result of natural selection and female choice is not choice at all but females being sexually excited who succumb to males (Groos 1898). Finally, Poulton's classification of animal coloration (1890) and divorce from sexual selection (1896) would devour Darwin's definition of sexual selection. Darwin's second theory would be regurgitated as epigamic characters and intra-sexual selection since epigamic characters avoided the confusing aspect of choice and of sexual selection altogether (Cronin 1992) and intra-sexual selection because it fit within the scope of natural selection

1900-1940 The Reign of Natural Selection

The key player in supporting natural selection as the evolutionary force behind secondary sexual characteristics was Julian Huxley. Although considered to be an expert on the theory of sexual selection, Huxley's writings on the subject had a utilitarian perspective (Cronin 1992). The two premises that guided his work were: 1) there is intra-sexual competition for access to females; and 2) traits that help in the male/male competition and makes males successful in the struggle for a mate are adaptive, and those advantageous traits would remain irrespective of their selective value. He argues that female choice does not exist, rather, display of conspicuous traits initiates a readiness to mate irrespective of female choice (Huxley 1938), thus, Poulton's 'epigamic characters' function to stimulate emotion and "when visual characters are present, they are always combined with special actions" (Huxley, p.28). The reason that display is widespread in each species is a result of its contagious effect where "'the presence of other birds going through the same display seemed to provide mutual encouragement, ' the display then lasting longer and being more vehement" (Huxley, p.28). Huxley's statement begs to ask, how long is "longer"? Is it the male that outlasts all other males the one that mates? If so, which female mates with the winning male? I have yet to find Huxley's answers.

In 60 years of history we quickly skimmed, female choice has all but disappeared. Wallace argued that it was not adaptive because females choose the most vigorous males; Poulton discarded it altogether when he categorized animal coloration by its functionality; Mivart did not even consider it; and Huxley just condemned it by arguing that females do not choose because their "choice" is the result of a contagious effect...yet, why are there extreme male traits? Are male traits a result of Huxley's contagious effect? Darwin himself argued in Descent that females can drive a trait to an extreme but that natural selection would constrain it. This being the case, then it would mean that female choice was adaptive as well, but how? The question would remain unanswered until 1930 when R. A. Fisher provided a theory called runaway selection. It would be the first time since Darwin's argument that female choice would be explained in terms of the health of the individual being selected.

Fisher argued that females choose males based on their attractiveness because she will have sons who will also be attractive (Fisher 1930). Granted, he argues, there is very little direct evidence of female choice (Fisher), but if we look at 'choice' as a product of evolutionary change measured by the advantage that 'choice' could have, then it would not be surprising to find instances in which a particular kind of choice may have a selective advantage and thus appear and remain in a population (Fisher). Furthermore, whenever appreciable differences appear in one sex , and these differences are correlated with a selective advantage, then there would be selection on the opposite sex to be able to discern those differences and select the individual with the greatest degree of the advantageous variation, so much so, that 'choice' or 'discrimination' may be more widespread than the opposite sex's phenotypic (physical or behavioural) variation (Fisher). Moreover, this scenario may be prevalent in situations where one sex influences the number of offspring the opposite sex will have (Fisher), which usually happens when one sex outnumbers the other...not far from Darwin's asymmetrical variation of sex-limited phenotypes mentioned earlier. In these cases, Fisher continued, the secondary sexual characteristics evolve due to the intensity of the preference by the opposite sex (Fisher). The intensity of preference will be under intense selection as long as the offspring carrying the secondary sexual characteristic has an advantage over other offspring (Fisher) and this type of sexual selection will further the development of the secondary sexual characteristic beyond the point when, left to natural selection, the advantage of having the trait has passed (Fisher).

> *"The two characteristics [plumage in males and preference in females for plumage] affected by such a process...must advance together, and so long as the process in unchecked by severe counterselection, will advance with ever-increasing speed. In the absence of such checks, it is easy to see that the speed of development will be proportional to the development already attained... sexual selection is capable of conferring a great reproductive advantage, the potentiality of runaway process, which,...unless checked, produce great effects, and in the later stages with great rapidity."* (Fisher 1930, p.29)

But if carried too far, counter-selection will favor the less ornamented male to balance the effects of female choice and both traits will become stabilized and last longer than the amount of time it took for the traits to evolve in the first place (Fisher 1930). Unfortunately, Fisher's theory of the evolution of secondary sexual characteristics as a product of sexual selection sat in the bookshelves for years. Even Huxley, who in the early 1900s (Bartley 1995) supported Darwin's original sexual selection would, by 1930s, reduce it to belonging within natural selection. Fisher's explanation for the evolution of female choice would be swept under the carpet, only to be unearthed 30 years later by population geneticists wanting to use the Fisherian Model to support Darwin's theory of sexual selection and, at last, Darwin would be vindicated.

1940 – 1980 The Modern Synthesis: The Genetics of Sexual Selection

The 1940s brought about a change in the way evolution would be studied: there would be a marriage of the sciences. The Modern Synthesis brought together genetics and biology as a way to explain how evolution really worked...yet, it would not change things in any way. If anything, The Modern Synthesis stressed that natural selection superseded any other selective process; therefore, it was the driving force behind evolution and evolution could be understood in terms of genetic mutations and recombination of particular genes. So for the next 30 years, Dobzhansky and other population geneticists would concentrate the genetic aspect of evolutionary biology. These genetic aspects resulted in models after models of evolutionary change, and thus the history of evolutionary biology would run its course of events until the 1970s when a 1948 paper resurfaces.

In the 1972 Robert Trivers was a graduate student taking a population genetics reading class with world reknowned evolutionary biologist, Ernst Mayr. Interested in sex ratios and parental investment, Mayr instructed Trivers to read Bateman's 1948 paper, which, as Trivers would find out, contained the key to understanding sexual selection: the differential reproductive success of males and females linked to asymmetrical parental investment. Darwin argued, and Fisher later theoretically proved, that the sex that invests more on parental care would influence the reproductive success of the opposite sex (Darwin 1874; Fisher 1930). This 'influence', as we saw earlier, happens in situations where males outnumber females, and *this* is correlated with elaborate male ornamentation (see above). Theoretically, it is a sound argument, but was this the case in practice? Enter Bateman's 1948 paper on *Drosophila melanogaster*.

Drosophila are promiscuous fruit flies and pairing and copulation occur right away. Bateman was interested in determining whether the type of courtship behaviour influenced the number of mating events, and to test intra-sexual selection, he introduced five males to five females. Darwin had argued that if the number of males equals that of females, then intra-sexual selection would not occur because, given enough time, all individuals would pair equally and the offspring would carry both parents' traits (Darwin 1874). Bateman's results, however, were different. His tests showed that intra-sexual competition occurs between males; that there is differential reproductive success in the sexes; that competition happens mainly among males, but there's no clear hypothesis as to the reason for this; and quite importantly, the intensity of intra-masculine competition depends on the fertility of males and frequency of inseminations. In other words, males compete against each other for females and in a single breeding season, the number of offspring produced is different between males and females, and, surely enough, the degree of male/male competition depends on the amount of gametes males and females produce. Therefore, female reproduction is limited not only due to her ability to produce eggs and not by her ability to have her eggs fertilized, but also by the number of male inseminations. Bateman concluded that in promiscuous species, the number of males to females is proportional to the number of offspring for which each sex is genetically responsible. Finally, Bateman generalizes the findings so that in any animal, the fertility of any female is more limited than the fertility of any male (Bateman 1948).

Imagine Trivers' excitement when he found the link. In 1972 he wrote a review paper on sexual selection in which he investigated Darwin's basic premise of intra-sexual competition and female choice and all components associated to each component. Bateman's paper furnished him with the genetics of parental investment and differential reproductive success. Through Fisher, he learned that in monogamous systems, females have a higher mortality rate than males; the opposite being true in polygamous systems (Fisher 1930). The adaptive consequences of polygamous systems is important: in breeding systems where males invest very little in offspring care, there would be selection for male adaptations that would lead to high reproductive success, even at the cost of the sex's increased mortality. So Fisher, Bateman, and Trivers offered a way to tackle intra-sexual competition between males, but an explanation of the adaptive value of female choice, the cause of the great debate, remained elusive.

The 19th and early 20th centuries offered two ways to tackle this matter; the new field of genetics would offer a third way. The 19th century offered a simple solution: females choose for the sake of beauty. Seen this way, 'choice' is, in terms of natural selection, maladaptive because if reproductive success is important for the female, who prefers to mate with the most 'handsome' male, then female choice increases the effects of male/male competition (Trivers 1972) so that 'choice' augments the intensity of the secondary sexual characteristics past the point when natural selection would not select against those traits. The other solution is Wallace's counter offer and is purely an ultra-Darwinian one that would remain through the early 20th century: females must be choosing something else that must be masked by 'beauty'. Females must be choosing "the most vigorous or most persevering male that is chosen, not necessarily one more brightly or differently colored, and this will be true 'natural selection'" (Wallace 1889, p.15) rendering female choice adaptive because females choose the functional and utilitarian aspect of the individual. The reason I brought back Wallace into the conversation is that by appealing to the 'something else' hypothesis, Wallace inadvertently set the stage for a brand new set of research that the advent of genetics would lead. In 20th century terminology, Wallace pushed to find the genetic component for female choice.

There are three theories that the 1970s are responsible for in trying to comply with Wallace's request: markers, conflicts of interest, and evolutionary arms race (Cronin 1992). 'Markers' signal the quality of the individual, that is, they signal his robustness. Wallace had argued that ornamentation and physiology co-evolve (Wallace 1889), so females choose males not because of the ornament, but because the ornament is a marker of something else: the individual's useful quality (Cronin 1992). Cronin's 'conflicts of interest' theory is a cheater detector theory in that because males exaggerate the trait (overcompensate, let's say) to cover flaws in their condition, females have evolved an adaptation that helps them detect the liars. The cheater detector keeps females from mating with the deceiving males. Unlike the male/female 'conflicts' arms race, the 'evolutionary arms race' is between competitors who spend their time becoming better at doing one thing instead of getting better at doing different things (Cronin). Male widow birds, for example, compete to have the longest tail possible so that selection will favor the tail that is slightly longer than the average (Cronin).

What a bomb for Darwinians! Remember that Darwinians are acute selectionists and, as such, believe that evolution is undirected, random; therefore, selection can only work at the species level, yet here we have three theories that go against the good-for-the-species selectionist view. Suddenly, it seems, evolution is directed... by genes! The 1970s put natural selection and her proponents are at a crossroads. We have gone from the non-biased utilitarian forces of natural selection to a selection process at the individual level: what one sees will affect one's choice which will affect what future generations see which will affect their choices which will affect their descendants, so on and so forth. We have, here, a quasi non-biased selection process.

I say non-biased because in this selection process, an individual's choice determines the appearance and increase of sex-limited traits. Female choice, Trivers argues, is directly associated with relative parental investment since it affects the choices that females make (Trivers 1972): the more a female invests in offspring, the choosier she will be so that she will pick the male that would contribute most to her offspring's survival and reproduction (Cronin 1992). The only thing that he can contribute, then, are his genes, but since females have no way to detect 'good genes', she will use the markers which will indicate how healthy or strong the male is which he will pass on to their offspring. So females pick physical attributes (biased selection) that are markers for other benefits (unbiased selection). At last, Wallace's 'vigorous' argument has paid off...for now.

Then, in 1975, there appears a new theory on the market called the handicap principle and it will defy Wallace's assumption that female choice is not costly to the male or to her reproductive success. Zahavi's 1975 paper states that even if male advertisement is costly yet makes it to reproductive age, then the liability (or handicap) of carrying the display indicates that the male can handle the cost. The fact that even with such a handicap the male survives to reproductive age signals his good genes so the female will choose the male with the most indicative handicap (Zahavi 1975) because of what he will pass on to their offspring. Hence, it is not surprising to find variation associated to any secondary sexual characteristics precisely because females constantly pressure males to develop the most extreme traits possible. Similarly, it is not surprising to find females responsible for eliminating that same variation which made them choose those males in the first place (Cronin 1992); therefore, it seems that females push the envelope at all times, doing and undoing variations and choices. Females do so because the definition of what is best is never ending: what are good genes at one time, may not be so at another time, so if females choose the average trait, genetic variation decreases and creates a possible problem for further generations as they cope with ever changing environments.

Wallace's legacy had a huge impact on how sexual selection was studied in the first three quarters of the 20th century. He required explanations for the evolution of female choice and how such a trait could be adaptive. Fisher's runaway selection, based on Darwin's 'beauty' argument, provided an explanation. Bateman's experiment showed us how differential parental investment linked to the unequal number of males and females influences choice. And finally, Zahavi's handicap principle showed us that even costly traits *can* be beneficial if they tell us something about the quality of the individual carrying them. Thusly, I suggest that Fisher, Bateman, and Zahavi be linked together in the good genes theory since the sex that invests more on offspring care is choosy and it will choose a mate, not for its beauty, but for what it can contribute to the offspring (***her*** offspring which carry 50% of her genome), and any deviation from the average can be an indicator of the individual's genetic makeup that can be passed on to the next generation and affect its survival and reproduction (and the continuation of part of her genome)...this is not your Darwin's sexual selection.

1980-Present Testing Genetics and Revisiting Darwin's Sexual Selection

The theories developed in the 70s would push the 80s and 90s to yield a wealth of field data on mechanisms that test, not only intra-sexual competition, but also female choice. The plethora of articles and books on sexual selection is a testament to the important role that sexual selection plays in evolution. No one disputes that now, Darwin was correct although he was short on explanations for the evolution of sexual selection, which Wallace pointed out, and which the 20th century aimed to discover.

History is still being written, but the tables are turning back to Darwin's original definition of sexual selection. The literature from these last ten years shows that the 20th century was successful in explaining sexual selection via different methodologies, but this time around, evolutionary biologists are concentrating their efforts on testing the Fisherian and Zahavian hypotheses by asking if female choice is based on direct or indirect benefits. For Kirkpatrick (1996) direct benefits are two-fold: one is immediate and happens when the female receives resources as a result of preference on a trait which leads to mating, and the other is more subtle and occurs when genes that affect female preference have pleiotropic effects (Kirkpatrick 1996). In other words, "The female "preference" thus seems to be a side effect of another behavior that was established by direct selection on the same genes in a different context" (Kirkpatrick 1996, p.33). Indirect benefits, however, is the good genes theory, and although the jury is still out on this one, data indicates that direct benefits may play a slightly larger role than indirect benefits (Kirkpatrick 1996; Kirkpatrick 1997; Moller 2001). Until a verdict is reached, however, Kokko, et. al. (2003) ask that the study of female choice should be all inclusive where direct *and* indirect benefits play a role because

> *"In practice, even mating biases that evolve because preferred males provide greater direct benefits, or because a naturally selected sensory bias has a pleiotropic effect on mate choice, end up producing indirect benefits because males almost always vary in their ability to produce attractive signals. Indirect benefits arise because choosy females acquire genes for their offspring that increase net fitness through any possible mixture of increased mating success, fecundity and survival in sons and/or daughters."* (Kokko 2003, p.36)

and sum up the argument so far by writing that,

> *"The key goals for the future are therefore to document the magnitude of key parameters (e.g. genetic correlations, intensity of selection on mating biases, additive genetic variation in mating biases, preferred male traits and net fitness) and to find general patterns to see whether there are repeatable differences in these across taxa or ecological context."* (Kokko 2003, p.36)

Personally, I think the research done to date is limited. Descent of Man was an exploration into what makes man unique as he descended from a lower life form. The thousands of examples Darwin studied were supporting evidence that sexual selection exists not just in humans but also in other taxa; however, I feel that research on the evolution of man with respect to sexual selection is lacking. Perhaps a problem lies in our own biases, so that studying ourselves as biological systems within our constantly changing constructed environment becomes problematic. Yet, it needs to be done and should be done considering our deep evolutionary time frame instead of concentrating on a few hundred thousand years so that we can better understand the biological and ecological bases of human behavior. In so doing, I think, anthropologists, other social sciences, and anyone interested in human evolution will be the better for it.

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Varieties of Primate Self-Medication and its Social Transmission

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Introduction

In the past twenty years there has been increased recognition and study of the self-medication, or zoopharmacognosy, across primate taxa. Zoopharmacognosy is generally defined as utilization by animals of plant secondary compounds or other non-nutritive compounds to combat or control disease, especially parasitic infection (Huffman, 1997; Huffman, 2003). One of the first documented cases of self-medicative behavior in primates occurred in 1983, when Wrangham and Nishida observed Tanzanian chimpanzees folding and swallowing leaves of the *Aspilia* species without chewing them (Wrangham and Nishida, 1983). Subsequent research correlated leaf-swallowing with the appearance of undigested leaves and expelled parasitic worms in the feces (Huffman and Caton, 2000).

Unusual behaviors thought to be self-medicative in function—including leaf swallowing, clay and soil ingestion, and bitter pith chewing—have been observed across primate taxa (Huffman, 1997). These actions are thought to have medicative properties because, in a number of cases, they were observed in individuals suffering from visible signs of parasitic infection or other illness. Some New World monkeys were observed to anoint their fur with pungent plant substances, and a self-medicative explanation was put forth for self-anointing behaviors as well (Meunier et al., 2008).

Huffman (1997) compiled a review of the literature concerning self-medicative behavior in primates. In this review he discusses the evidence for classifying these behaviors as self-medicative, described a variety of these behaviors across primate taxa, and put forth hypotheses explaining the origin of self-medication in primates. He focused mainly on bitter pith chewing and leaf swallowing in African apes, as these were the best-documented examples of primate self-medication at the time. He also mentioned fur rubbing with pungent substances as a potential example of self-medication, though at the time the possible medicinal benefits of this behavior had not been studied extensively. Finally, he discussed future directions for research and ways that this research could be applied to the medical treatment of humans and livestock in Africa and around the world.

In the years since Huffman's review, much more has come to light concerning the pharmacological and mechanical means by which the substances used in self-medicative behaviors combat infection (Huffman and Caton, 2000; Huffman, 2001; Huffman, 2003). Experimental studies of leaf-swallowing behavior in naïve captive chimpanzees, or those which have never been exposed to the behavior, have contributed to our knowledge of the origin and social transmission of the action (Huffman and Hirata, 2004; Huffman et al., 2010). These studies suggest a mechanism for the transmission of self-medicative behaviors in general. New World monkeys' anointing behaviors, in particular, have been documented extensively, and the list of substances used has expanded beyond plant-materials to include insects, millipedes, and even anthropogenic materials such as hand-sanitizing wipes (Zito et al., 2002; Verderane et al., 2007; Perry and Manson, 2008; Meunier et al., 2008; Lynch Alfaro, 2011). More recently, de Roode et al. (2013) have called into question the "self" in "self-medication," as research shows that animals often treat kin and offspring as well. In this paper, I will review the recent literature on zoopharmacognosy, summarize what is known, and evaluate the current evidence for various hypotheses concerning social transmission of self-medicative behavior.

VARIETY OF SELF-MEDICATIVE BEHAVIORS ACROSS PRIMATE TAXA

A. Ingestion of Anthelmintic Plants in Lemurs

Among the strepsirhine primates, brown lemurs (*Eulemur fulvus*) are known to ingest a number of plants with demonstrated *in vitro* anthelmintic (antiparasitic) properties (Nègre et al., 2006). As measured by analysis of stool contents, brown lemurs provisioned by humans have a higher level of parasite infestation compared to those that utilize only natural feeding sources, suggesting that antiparasitic plants are important in minimizing the lemurs' parasite loads (Nègre et al., 2006). The anthelmintic may represent an indirect benefit of ingesting secondary compound-rich plants for their nutritional value, but at least one of these antiparasitic plants was ingested very infrequently, suggesting that it may be selected by lemurs specifically for its medicinal properties (Nègre et al., 2006). This research is still inconclusive because the behavior has not been observed in visibly sick lemurs, and because it has not been demonstrated that antiparasitic properties affect lemurs' choice of foods.

B. Anointing in New World Monkeys

Since the late 1990s, there has been an explosion of research concerning anointing behaviors among New World monkeys. Anointing has been observed extensively in capuchin monkeys, spider monkeys, and owl monkeys (Zito et al., 2002; Verderane et al., 2007; Perry and Manson, 2008; Meunier et al., 2008; Lynch Alfaro et al., 2011). Researchers now distinguish between fur rubbing, when plant materials are used, peat-bathing, when peat is used, self-anointing using millipedes, and anting, in which formic-acid producing ants are used (Meunier et al., 2008). Wild capuchins with access to human settlements have been observed to self-anoint with such man-made materials as laundry soap, DEET insect repellent, cigarettes, bleach, and cologne (Lynch Alfaro et al., 2011).

Perry (2008) provides a detailed and vivid account of fur rubbing with *Jacquinia pungens* fruits within a group of white-faced capuchin monkeys (*Cebus capucinus)* in her study population at Lomas Barbudal, Costa Rica. Fur rubbing was a highly social activity among her study group, with individuals tolerating nips and slaps from other group members in their efforts to join what Perry describes as "one big ball of writhing monkeys in a state of frenzied motion" (2008, p. 67). She noticed that several individual monkeys made an effort to rub the fruit into the fur of infants too young to anoint themselves. In several instances, she observed that when a saliva-covered fruit being used for fur rubbing was accidentally dropped, monkeys would retrieve the already-used fruit from the ground instead of picking another one, even though fresh, unused *Jacquinia pungens* fruits were readily available. Although Lynch Alfaro (2011) describes this behavior of retrieving dropped anointing materials as typical, purpose remains unclear.

Several explanations exist as to the possible benefits provided by self-anointing behavior and the mechanisms of this behavior. Many of the substances used in self-anointing by New World monkeys are known to repel insects or have antimicrobial properties, and plants used by *C. capucinus* in Costa Rica are used for medicinal purposes by humans (Meunier et al., 2008; Lynch Alfaro et al., 2011). In many cases, seasonal increases in primate self-anointing behaviors correlate with periods when parasite infections are most likely (Lynch Alfaro et al., 2011). The highly social nature of fur rubbing behavior in many species is hypothesized to supply the group with protection against ectoparasites that might be transmitted between individuals (Meunier et al., 2008). At a proximate level, it is likely that anointing with pungent items is a behavioral response to chemical stimuli, probably manifesting itself as a pleasurable physical sensation (Perry, 2008; Lynch Alfaro et al., 2011).

The correlation between the chemical properties of a material used to self-anoint, its parasite-repelling effects, and seasonal variation in the incidence of both parasites and self-anointing behavior has been particularly well documented in the case of anting with carpenter ants by tufted capuchins (*Cebus apella*) (Verderane et al., 2007). Carpenter ants (*Camponotus rufipes)* secrete formic acid in concentrations that can reach up to 54% (Verderane et al., 2007). Verderane et al. demonstrated in laboratory experiments that 50% formic acid solution possesses a high repellent effect against nymphs of the tick *Amblyomma cajennense,* a parasite of wild tufted capuchins. Several species of capuchins self-anoint with carpenter ants but none do so with leaf cutter ants, which do not produce formic acid (Lynch Alfaro et al., 2011). Tufted capuchins ant with carpenter ants at significantly higher rates during the months at which nymphs of *A. cajennense* occur than in months with no incidence of tick nymphs (Verderane et al., 2007). Taken together, the evidence points compellingly toward anting as a form of self-medication that acts to reduce capuchins' ectoparasite load. If a similarly detailed body of evidence can be developed for other forms of self-anointing behavior, much more will be known about the causes, mechanisms and possible evolutionary pressures controlling anointing as self-medication.

C. Geophagy in New and Old World Monkeys

Geophagy, the ingestion of clays and soil, has been hypothesized to provide nutritional benefits, alleviate gastrointestinal ailments, detoxify harmful plant secondary compounds, and protect against parasites and pathogens (Ferrari et al., 2008; Link et al., 2009; Pebsworth et al., 2012). It has been observed in some New World monkeys, including species of howler monkeys, spider monkeys, and pitheciids, and in baboons (Ferrari et al., 2008; Link et al., 2009; Pebsworth et al., 2012). Though geophagy has been reported much more extensively since Huffman's 1997 review, these reports are still mostly observational in nature, and experimental studies in captive populations will be necessary to clarify the medical benefits primates receive from ingesting soil.

D. Bitter Pith Chewing in African Great Apes

According to Huffman (1997), chimpanzees and other great apes often self-medicate with species of *Vernonia*, removing the outer bark and leaves to chew on the exposed pith with its bitter juice. Pith chewing behavior is extremely rare, being primarily exhibited in the rainy season by individuals showing symptoms of illness or parasitic infection (Huffman, 1997). *Vernonia* species are used in ethnomedicine across Africa to treat intestinal upsets, parasitic infection, diabetes, fever, gonorrhea, and a number of other ailments (Huffman, 2003). A number of *Vernonia* species contain a class of compounds known as sesquiterpene lactones, which are well known for their anthelmintic, anti-amoebic, antitumor, and antibiotic properties (Huffman, 1997; Huffman, 2001). The highest levels of these cytotoxic compounds occur in the leaves and bark of the plant, which are the parts of these plants that chimpanzees are known to avoid (Huffman, 2001). This suggests that chimpanzees are aware not only that certain plants have beneficial properties but also that particular parts of the plants have these properties while other parts are harmful.

Adult conspecifics in proximity to an individual exhibiting bitter pith chewing show no interest in imitating the behavior (Huffman, 1997). However, infants of ill mothers will occasionally taste the pith discarded by their mothers, and Huffman (1997) reports one instance in which a healthy mother prevented her infant from picking up a piece of pith discarded by a sick adult. It is unclear whether these brief and infrequent exposures to pith chewing behavior would be enough to ensure the transmission of the behavior to infants through social learning. It is even more difficult to say how such self-medicative behavior could have originated. Huffman (2001), noting the high degree of conservatism in chimpanzee feeding habits, points out that random sampling of novel food items does not occur frequently. He proposes that behaviors such as bitter pith chewing might have originated during a period of "extreme food scarcity, when ill and hungry apes who were forced to try new foods recovered their health and associated their recovery with the new food item" (Huffman, 2001, p. 659). More evidence is required to determine whether Huffman's hypothesis is valid.

E. Leaf Swallowing in African Great Apes

Like bitter pith chewing, leaf swallowing is primarily observed in African great apes, including lowland gorillas, four subspecies of chimpanzees, and bonobos (Huffman, 1997; Huffman and Caton, 2000; Fowler et al., 2007). When leaf swallowing, animals select leaves one by one from a plant with rough, hairy leaves, fold them with the tongue and palate, and then swallow them whole. This method of ingestion allows leaves to pass through the gastrointestinal tract visibly unchanged, often accompanied by parasitic intestinal nematodes (Huffman and Caton, 2000). In two experiments, captive chimpanzees that had never been exposed to the plant species used for leaf swallowing in Africa were presented with plants of a similar texture that were native to Europe and Japan (Huffman and Hirata, 2004; Huffman et al., 2010). In both cases, some of the naïve chimpanzees developed leaf swallowing behavior over time, demonstrating that it is the rough, hispid qualities of these plants that stimulate leaf swallowing (Huffman and Hirata, 2004; Huffman et al., 2010).

At the time of Huffman's 1997 review, two major hypotheses, which were not mutually exclusive, sought to explain the mechanism by which leaf swallowing behavior expelled intestinal worms. The first of these proposed that the rough, hairy surfaces of the plants used in leaf swallowing swept parasites out of the gut mechanically, like a "rasping plug or 'Brillo' pad" (Huffman, 1997, p. 188). The second argued that secondary compounds in the plants used for leaf swallowing had nematocidal activity, which might decrease a worm's ability to attach to the intestinal wall and make it more likely to be swept out of the gut by the mechanical action of the rough leaves.

Huffman and Caton (2000) subsequently showed that neither of these suggested mechanisms was correct. Instead, leaf swallowing in chimpanzees functions to irritate the gastrointestinal tract, causing increased gut motility and diarrhea (Huffman and Caton, 2000). These factors act to detach adult parasitic nematodes (*Oesophogostomum stephanostomum*) from the intestinal wall and expel them, and to flush out some of the incoming infective larvae before they are able to penetrate the intestinal wall and reach the adult stage (Huffman and Caton, 2000). Chimpanzees exhibit almost all of their leaf swallowing behavior early in the morning, on an empty stomach, which increases the irritating effect of the leaves on the gastrointestinal tract (Huffman and Caton, 2000).

Further research on the correlation between leaf swallowing behavior and the expulsion of specific parasites has been somewhat inconclusive. McLennan and Huffman (2012) found that chimpanzees in Bulindi, Uganda, an area that has experienced significant anthropogenic habitat change, showed a higher frequency of leaf swallowing than chimpanzees at other sites. Leaf swallowing was shown to correlate with adult nematode expulsion, but not with the expulsion of tapeworm proglottids. To explain this result, McLennan and Huffman (2012) hypothesized that leaf swallowing is a general behavioral reaction to intestinal discomfort, even though the adaptation may not be effective at expelling all parasitic infections.

Social Facilitation and Transmission of Self-Medicative Behaviors

In the years since Huffman's review, perhaps the most extensive progress in the study of self-medication has been made in clarifying the social mechanisms by which self-medicative behaviors are transmitted within groups and across generations of primates. Specifically, researchers have expanded the understanding of the social facilitation of fur rubbing in capuchins, and of the transmission of leaf swallowing behavior within groups of naïve captive chimpanzees. I will treat each of these behaviors in turn, exploring recent studies of the significant social factors in each case.

Social Facilitation of Fur Rubbing Behavior

Both the *Cebus* and *Sapajus* genera of capuchins exhibit social fur rubbing, with up to 14 *Sapajus* individuals observed to anoint simultaneously on one occasion (Lynch Alfaro et al., 2011). Meunier et al. (2008) studied the synchronization of fur rubbing in a group of captive white-faced capuchins, who self-anoint in subgroups varying in size from six to fifteen. The researchers' observations demonstrate that fur rubbing in these capuchins involves a mimetic process, in which individuals begin to anoint their fur with a pungent substance when they observe conspecifics doing so with the same substance (Meunier et al., 2008). The researchers suggest that, given the proposed antiparasitic benefits of self-anointing, synchronized fur rubbing acts as a collective barrier against ectoparasite transmission within the social group (Meunier et al., 2008).

In light of the observations by Perry (2000) of adult white-faced capuchins actively anointing infants too young to anoint themselves, such group fur rubbing behavior may also represent an opportunity for infants and juveniles to learn how to engage in fur rubbing. Lynch Alfaro et al. (2011) note that adult capuchins are highly tolerant of juveniles taking away food from them, a phenomenon known as passive sharing, and suggest that passive sharing in the context of anointing behavior contributes to the transmission of preferences for particular anointing substances. Further research is necessary to clarify the role of social anointing in transmission of the behavior.

Leaf Swallowing and Social Learning

In experiments with captive-born chimpanzees that had never been exposed to the plants used for leaf swallowing in the wild, some individuals spontaneously exhibited typical leaf swallowing behavior using plants with rough, hispid leaves (Huffman and Hirata, 2004; Huffman et al., 2010). Most of the other chimpanzees in the study subsequently acquired the behavior after closely observing the original adopter, though some individuals never overcame an initial phobia of the new stimulus (Huffman and Hirata, 2004). This initial spontaneous acquisition of leaf swallowing behavior suggests that the behavior is based in part on an innate propensity to fold and swallow rough, hairy leaves, but that the spread of the behavior within a group occurs through social learning (Huffman and Hirata, 2004). The chimpanzees in this captive study were not infected with parasites, indicating that leaf swallowing can develop independently of the stimulus of pain from intestinal parasites (Huffman and Hirata, 2004).

More recent research has demonstrated that this social transmission of leaf swallowing behavior extends to the specific variant of the behavior that a group exhibits (Huffman et al., 2010). Huffman et al. presented rough, hairy leaves to two naïve groups of captive chimpanzees that could not come into contact with one another. Individuals in each group initially responded in a variety of ways, but over time one group adopted a method of leaf swallowing that the researchers designated "partial leaf swallowing," while the other group adopted a variant method dubbed "complete leaf swallowing" (Huffman et al., 2010). These results suggest the possibility of a spontaneous emergence of cultural variation in this behavior as a product of its social transmission, a possibility that could have fascinating implications extending beyond primate self-medication to the future study of many socially transmitted behaviors.

Conclusion

Vast strides have been made in the study of self-medication since the late 1990s. Specifically, we now know much more about the actual mechanisms by which self-medicative behaviors such as leaf swallowing and self-anointing improve primate health, and about the social transmission of these behaviors within a population. The data on self-anointing, in particular, have grown in nearly exponential fashion. There is still much to learn, however, about less-studied behaviors such as geophagy. Another fascinating subject for future research is the question of the ultimate evolutionary origin of self-medication in primates. Future research should also delve into the question of the possible applications of self-medication in non-human primates to human medicine. Our primate relatives have much to teach us about the possible pharmacological uses of naturally occurring compounds, such as plant toxins and the chemicals that many insects use in their defense responses.

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