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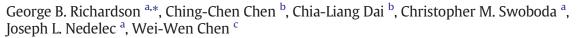
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Original Article

Substance use and mating success



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ABSTRACT

Psychoactive substance use has been typical of most traditional and modern societies and is maintained in the population despite the potential for abuse and related harms, raising the possibility that it (or its underlying causes) confers fitness benefits that offset its costs. Although it seems plausible that psychoactive substances have facilitated survival among ancestral and modern humans, it is not clear that this enhancement has translated into Darwinian fitness through mating and ultimately reproductive success. In the current study, we discuss potential mechanisms by which substance use might make unique contributions to mating success, attend to the possibility that the effects between substance use and mating success are instead confounded, and use structural equations and nationally representative data to determine whether these effects are more likely causal or spurious. Our findings indicate that once we know participants' scores on "third" variables at each round in early young adulthood, their substance use gives us little additional information about their current prospects for acquiring sexual partners and no additional information about of their future prospects. Thus, if adaptations for substance use evolved, their adaptive value does not seem to be found in mating success.

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Psychoactive substance use has been typical of most traditional and modern societies (Durrant & Thakker, 2003; Merlin, 2003; Russo, 2007) and maintained in the population despite the potential for abuse and related harms, raising the possibility that it (or its underlying causes) has conferred fitness benefits that offset its costs (Gerald & Higley, 2002; Hagen, Roulette, & Sullivan, 2013). Smith (1999) described a number of ways in which substance use may have contributed to fitness among ancestral humans (see also Durrant & Thakker, 2003). For instance, stimulants like coffee and coca suppress appetite and reduce fatigue, sedative-hypnotic substances such as alcohol relieve anxiety, and analgesics like opium alleviate pain, generate euphoria, and relieve diarrhea. In addition, Dudley (2002) discussed the natural biology of alcohol consumption and reviewed potentially adaptive primate uses of ethanol, including use to locate fruit crops, stimulate appetite and thereby consumption of transient nutritional resources, and derive caloric benefits. Finally, Hagen et al. (2013) described design features in humans that appear to regulate consumption of plant neurotoxins to prevent or treat macro-parasite infection; Roulette et al. (2014) found evidence that tobacco use wards off helminths; and Roulette, Kazanji, Breurec, and Hagen (2015) extended this finding to marijuana use. Thus, it is

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plausible that the use of at least some psychoactive substances reflects specialized adaptive functions.

Researchers have also theorized that substance use could enhance Darwinian fitness by facilitating mating success (Hagen et al., 2013; Richardson & Hardesty, 2012). Consistent with this, substance use has been linked to greater sexual activity, including larger numbers of sexual partners (e.g., Bailey, Pollock, Martin, & Lynch, 1999; Cavazos-Rehg et al., 2011). However, it is not yet clear that the effects between substance use and indicators of mating success are non-spurious. Thus, in the current study, we discuss potential mechanisms by which substance use might make unique contributions to mating success, attend to the possibility that the effects between substance use and this outcome are instead confounded (e.g., by impulsivity, mating effort, and/or life history strategy), and use structural equations and nationally representative data to determine whether these effects are more likely causal or spurious.

1. Substance use and differential mating success

Given that much of the variance in substance use stems from genetic factors (e.g., Hicks, Iacono, & McGue, 2012; see also Polderman et al., 2015), it is puzzling that the phenotype has been maintained in the population despite the related harms. Recently, Borkowska and Pawlowski (2014) provided a potential explanation for this by applying Zahavi's Handicap Principle to substance use, hypothesizing that substance use is generally an honest indicator of biological quality. The idea is that humans engage in substance use despite the health costs to display

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evidence that they are of such biological quality that they can afford to do so. If this were the case, substance use could increase attractiveness to potential mates, facilitating mating success. Bringing data to bear on this possibility, Borkowska and Pawlowski studied the relationships between various substance use indicators and fluctuating asymmetry (FA), a well-accepted indicator of biological quality, and found no effects between FA and substance use. As additional possibilities, substance use may not serve as a cue to biological quality, but instead as an advertisement of sexual maturity (Hagen et al., 2013) or availability. To our knowledge, these possibilities are untested.

Another possible explanation for the prevalence of substance use is that it contributes to mating success by modulating brain function. In the U.S., three of the most commonly used psychoactive substances are alcohol, tobacco, and marijuana (SAMHSA, 2014). Alcohol myopia theory suggests that alcohol amplifies pre-drinking intention to have sex (Steele & Josephs, 1990). Consonantly, research indicates that alcohol increases disinhibition (Fillmore & Vogel-Sprott, 1999) and delay discounting (Bickel et al., 2007), which can lead individuals to ignore cues to long-term costs associated with risky sex or weigh the shortterm benefits of sexual intercourse (e.g., hedonic effects) more heavily than future outcomes. Similar findings have been reported for marijuana (Vangsness, Bry, & LaBouvie, 2005). Research has shown that these effects are common to many substances and can be partly attributed to inhibited neural activity in the prefrontal cortex, the area of the brain responsible for simulating the future and integrating behavioral alternatives with context and long-term goals (George & Koob, 2010). Research in affective neuroscience has also shown that alcohol and other psychoactive substances sensitize incentive salience (i.e., experienced utility) through their effects on mesolimbic dopamine transmission (Berridge, 2012; Berridge & Robinson, 2011). In this way, up to moderate levels of consumption, psychoactive substances can enhance the salience of natural rewards in the local environment (e.g., food and potential mates) and boost associative learning (Anselme, 2009). Thus, at levels of use that are not chronic or excessive, psychoactive substances may promote allocation of attention, memory, and motivation toward pursuit of natural rewards that are immediately available, including potential mates.

Consistent with the above, people do seem to expect substance use to enhance their social behavior in ways that could be conducive to mating success. For instance, Fromme, Stroot, and Kaplan (1993) reported that substance users reported positive expectancies including increased sociability (e.g., more outgoing and energetic), liquid courage (e.g., more daring, powerful, and creative), and sexuality (e.g., better lover, enjoy sex more, be sexier). Individuals may learn these expectancies through their experiences of the effects of substances on disinhibition and the salience of natural rewards in the local environment, or via cultural information.

All considered, it seems plausible that substance use may facilitate achievement of short-term local reproductive optima by (1) signaling sexual maturity and/or availability, (2) increasing sexual motivation (i.e., through disinhibition and by increasing the salience of potential mates), and (3) enhancing associative learning of behaviors that achieve mating success. Consistent with these notions, Bailey et al. (1999) found that adolescents with alcohol use disorders were more sexually active, had greater numbers of partners, and initiated sexual activity at slightly younger ages, while Cavazos-Rehg et al. (2011) linked

teen alcohol, marijuana, and tobacco use to greater probability of sexual intercourse and pregnancy. Cooper (2002) also reviewed a mass of evidence indicating that drinking has been strongly associated with decisions to have sex and indiscriminate forms of "risky" sex.

1.1. Potential confounders

Above we discussed potential causal effects of substance use on mating success. However, it is also important to attend to the possibility that the associations between substance use and this outcome are spurious, or attributable to omitted causes of each (i.e., confounders). For instance, Cooper (2002) noted that a larger lifestyle variable might account for the relationships between alcohol use and sexual behavior, while Justus, Finn, and Steinmetz (2000) and Kalichman, Heckman, and Kelly (1996) found that controlling for potential confounders, sensation seeking fully explained the covariation between drinking and risky sex.

Gerald and Higley (2002) pointed out that nature may have selected for excessive alcohol use indirectly by favoring impulsivity and aggression, which could have enhanced fitness among ancestral humans by enabling them to better exploit novel environments through migration as well as compete for resources in times of scarcity. Consistent with this argument, the authors reviewed evidence that Rhesus Macaques with low central nervous system (CNS) serotonin turnover (i.e., levels) are more impulsive, leave their social groups at younger ages, suffer greater premature mortality, but experience greater reproductive success at younger ages. Importantly, these Old World monkeys and their human counterparts (also characterized by low CNS turnover) engage in more excessive alcohol use. In a similar vein, Vanyukov et al. (2012) reviewed evidence that antisocial (i.e., behaviorally disinhibited and deviant) youth tend to manifest a variety of risky behaviors including substance abuse, along with evidence that in adolescence, antisociality and liability to substance use disorder (i.e., trait risk for heightened use, abuse, and dependence with respect to a variety of substances) converge in a common liability to risky and antisocial behavior.

Gerald and Higley (2002) also pointed out that their findings imply that alcohol use may reflect a faster life history strategy (LHS), or tendency toward mating effort and early reproduction at the expense of somatic and parental effort (for a review, see Ellis, Figueredo, Brumbach, & Schlomer, 2009). Consonantly, Jones and Figueredo (2007) found that mating effort predicted smoking in college students, Richardson, Chen, Dai, Hardesty, and Swoboda (2014) reported evidence that heightened substance use reflected faster LHS in a nationally representative sample of young adults in the U.S., and Richardson et al. (2016) found that fast LHS fully explained the developmental stability of substance use from adolescence to young adulthood. Perhaps the potential fitness costs of substance use are byproducts of an LHS that continues to confer fitness gains, either before substance-related harms accrue (i.e., antagonistic pleiotropy) or in individuals who are liable to but, for one reason or another, do not become substance abusers.² Taken together, the findings discussed above suggest that variables such as impulsivity, sensation seeking, antisociality, mating effort, and/or an overarching LHS variable, may confound the effects between substance use and mating success.

¹ However, future research could test for heterogeneity in the effect between FA and substance use. For instance, there is some evidence that psychopathic and non-psychopathic offenders have greater FA than non-offenders, but among offenders, psychopathy is associated with lower FA (Lalumière, Harris, & Rice, 2001). Perhaps something analogous is the case for substance use, such that higher levels of use are associated with lower FA to a greater extent within more antisocial groups. Consistent with this, Vanyukov, Neale, Moss, and Tarter (1996) suggested that anti-sociality and disinhibition might impact inclusive fitness via peer selection and assortative mating. Perhaps substance use is a key manifest indicator on which antisocial individuals select peers and mates.

² We also note that substance use may enhance reproductive success among slow life history strategists or those employing a long-term mating orientation. For instance, alcohol could do this by enhancing sexual experience (e.g., reducing anticipated sexual problems, increasing arousal, and increased erection at low blood alcohol content (BAC) levels; for discussion, see Prause, Staley, & Finn, 2011) and thereby pair bonding and fertility. However, the costs of excessive use are likely greatest for slow strategists (Richardson & Hardesty, 2012). Alcohol and other psychoactive substances sensitize the salience of substance-related stimuli, making them important Pavlovian cues (Berridge, 2012; Berridge & Robinson, 2011). As use becomes excessive and/or chronic, attention narrows to such cues, manifesting as sign-tracking at the expense of goal-tracking (Anselme, 2009; Robinson, Robinson, & Berridge, 2013). This implies a shift away from long-term goal pursuit, which should be more costly in predictable/safe environments where slow life history strategy is more viable.

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