CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

Dietary Ethanol Ingestion by Free Ranging Spider Monkeys (*Ateles geoffroyi*):

An Evaluation of the Drunken Monkey Hypothesis

A thesis submitted in partial fulfillment of the requirements

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By

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ABSTRACT

Dietary Ethanol Ingestion by Free-ranging Spider Monkeys (*Ateles geoffroyi*):

An Evaluation of the Drunken Monkey Hypothesis

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The Drunken Monkey Hypothesis posits that the proclivity of modern humans to

consume alcohol may stem from a deep-rooted affinity present in all frugivorous

nonhuman primates for naturally occurring ethanol within ripe fruit (Dudley 2000, 2002

2004; 2014; Stephens and Dudley 2004). Ethanol is a natural by-product of the metabolic

activity of fermentative yeasts within fruit pulp that consume sugars made available as

the fruit ripens (Spencer and Spencer 1997). Here I investigate key assumptions and

predictions of the Drunken Monkey Hypothesis by examining the role that ethanol

concentration in *Spondias mombin* fruits plays in the diet of free ranging spider monkeys

(*Ateles geoffroyi*) on Barro Colorado Island, Panamá. Specifically, I aimed to answer the

following questions: (1) Do ripe or over-ripe fruits consumed by spider monkeys have

measurable ethanol content? (2) Do spider monkeys preferentially select and consume

fruit with higher ethanol content? (3) Is higher ethanol content inversely correlated with sugar content?

I predicted that I would find that: 1) ripe or over-ripe fruits consumed by spider monkeys have measurable ethanol content; 2) spider monkeys preferentially select and consume fruit with higher ethanol content; and 3) the fruits with higher ethanol content also have higher sugar content and thus greater caloric reward. This study demonstrates that Barro Colorado Island spider monkeys consume fruits containing ethanol. Additionally, it showed a non-statistically significant trend towards spider monkeys preferentially selecting – and consuming more of – fruits that contain higher levels of ethanol. There was no observed relationship between ethanol content and sugar content. Though the data presented here are too sparse to demonstrate that nonhuman frugivorous primates exhibit a proclivity to consume ethanol, they nevertheless suggest that this is an important avenue for future research, both to further characterize the diet and foraging behavior of spider monkeys and to directly address the Drunken Monkey Hypothesis.

Introduction

In this thesis I investigate dietary ethanol ingestion in black-handed spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panamá to evaluate the Drunken Monkey Hypothesis (Dudley 2000, 2002, 2004, 2014; Stephens and Dudley 2004). The Drunken Monkey Hypothesis proposes that humans' attraction to, and predilection to consume, ethanol is derived from our early primate ancestors' proclivity to seek out ethanol-laden fruits due to the nutritional rewards associated with ethanol.

Animals Are Good to Think With: A Theoretical Examination

The deliberate production and consumption of alcohol is nearly ubiquitous in human societies (Katz and Voigt 1987). Research into the production and consumption of alcohol around the world suggests that "at the time of European colonial expansion, only parts of the Pacific and North America seem to have been without indigenous versions of alcoholic drinks, and European forms were quickly adopted in those regions as well" (Dietler 2006:232). Surely, alcohol plays an integral role in myriad cultural and religious practices – from its associations with festivity and ceremonial events to ritualized consumption for ecclesiastical, spiritual and political purposes – and in cases such as these, alcohol is considered a central part of our most precious human experiences.

Ten thousand years after the advent of civilization – which biological anthropologist Solomon Katz argues was a consequence of group production of alcohol (Katz and Voigt 1987) – few answers exist as to why humans abuse alcohol – or even why alcohol is so appealing in the first place. One hypothesis that attempts to explore the genetic underpinnings of alcohol consumption and alcoholism in humans is the Drunken Monkey Hypothesis, which posits that the proclivity of modern humans to consume

alcohol stems from a deep-rooted affinity present in all frugivorous nonhuman primates for naturally occurring ethanol within ripe fruit (Dudley 2000, 2002, 2004, 2014; Stephens and Dudley 2004). The originator of the Drunken Monkey suggests that ethanol serves as a foraging cue to primates, who may have evolved the ability to locate this ripe fruit by the scent of ethanol, or what he calls "ethanol plumes." He also suggests that our primate ancestors that preferentially selected ethanol-laden fruit were provided with greater caloric rewards in the form of ethanol, as ethanol has more calories per gram than does sugar. Thus, primates' consumption of ethanol would be advantageous, giving rise to an evolutionary affinity for alcohol (Dudley 2000, 2002; 2004; 2014; Stephens and Dudley 2004).

Importantly, the Drunken Monkey Hypothesis does not actually propose intoxication. Rather, it argues for chronic, low-level ethanol consumption in an evolutionary context. Dudley invokes hormesis, a phenomenon in which substances thought to be toxic in high levels may actually be beneficial in lower levels, to explain the evolution of alcoholism in humans. Using this idea, alcoholism is suggested to result when ethanol, potentially healthy at lower concentrations, is readily available in modern times at very high concentrations – so-called diseases of civilization or diseases of nutritional excess. Like other diseases – diabetes, heart disease and obesity, for example – alcoholism may be the result of an evolutionary predilection for a substance that can be maladaptive in modern society.

In this study I will review the history of alcohol use and overconsumption. I will also address the current state of research on alcoholism, the theoretical assumptions that underlie the Drunken Monkey hypothesis, current research into primate foraging

behavior and the role that ethanol plays in primate diet and food choice. In doing so, I will utilize a variety of theoretical frameworks both within and beyond anthropology. I suggest that it is possible to investigate nonhuman primates and their behavior in their natural habitat under the assumption that, through doing so, one can draw conclusions pertinent to modern humans. In particular, I argue that nonhuman primates can be used as a homologue for modern humans in investigations of feeding behavior. I utilize ethological and primatological frameworks that examine the mechanisms that give rise to animal behavior and the evolutionary origins of that behavior. In addressing the modern conception of alcoholism as having a genetic component, I utilize a Darwinian medicine framework. In this work I will discuss these theoretical and methodological frameworks, their origins and development, and how they can be profitably applied to the study of alcohol consumption in humans.

It is useful to begin an exploration of alcohol through the contexts of chemistry and culture to broaden our understanding of the complexities of alcohol studies and to highlight some of the issues inherent in this area of research. While the chemical properties of ethanol – the form of alcohol that is produced by the natural process of fermentation – were discovered very recently in the 20th century, the ingestion of fermented products extends far back in time. It has been posited that the origins of alcohol in the diets of primates date back tens of millions of years (Dudley 2000, 2002, 2004, 2014; Stephens and Dudley 2004), and that humans began ingesting alcohol intentionally by at least the Stone Age (McGovern 2003). Regardless, the properties of ethanol produce predictable dose-related changes in central nervous system functioning and affect basic physiological processes. After ingestion of moderate to high doses of

alcohol reaction times are generally slowed; short-term and intermediate memory is likely to be affected; and muscle control, dexterity and eye-hand coordination may be impaired (The Social Issues Research Centre 1998:10). It is unclear whether achieving these physiological and psychoactive effects was the goal of alcohol consumption in pre-civilization or prehistoric times, or if it was simply a much-appreciated side effect. But the complex relationship between *drink* and *drunk* means alcohol researchers must attempt to contend with this issue in some way, so as to not under- or over-attribute consumption to these factors. How these factors, and how cultural perceptions of alcohol and its close ties with drunkenness have also affected the development of alcohol studies and scholarly examinations, will be examined in greater detail in following sections.

While physiological responses result from the ingestion of alcohol, specific behaviors that are expressed while inebriated are culturally mediated. The act of "…drinking is a rule-governed activity, hedged about with self-imposed norms and regulations concerning who may drink how much of what, when, how, in what contexts, what effects, etc. – rules which are often the focus of strong emotion" (The Social Issues Research Center 1998:7). The interaction, then, between culture and alcohol is of extreme importance to understanding cultural beliefs, values, and social norms of the time. It should also be noted that what constitutes alcohol is not a universally shared folk category. Our association of beer, wine, and liquor as falling under the umbrella term "alcohol" was a discursive product of the Temperance movement in the 19th century (Dietler 2006), and research into alcohol consumption – especially ethnographic or medical research – can be complicated by a failure to account for these cultural differences.

***Ergo bibamus:* A Brief History of Alcohol/ism**

The centrality of alcohol in the human diet and culture is not limited to recent times. Archaeological evidence suggests alcohol production may extend back 9000 years or more (Katz and Voigt 1987; Dietler 2006) and it is not a leap to imagine that the intentional ingestion of fermented products likely extends back much, much further; it is possible that "the discovery of fermentation probably [occurred] when primitive people [observed] that grapes and fruits naturally ferment when exposed to air" (Austin 1985:3). Over thousands of years, people became more adept brewers and vintners, and as the consumption and acceptance of alcohol spread, attitudes pertaining to drunkenness developed. Egyptians and Mesopotamians in 3000 BCE are thought to have had "very little antagonism to drunkenness" (Austin 1985:3), and entire regions developed reputations for heavy drinking, including Babylonia, whose famous law code dedicated four paragraphs to the strict regulations of "wineshops," without any mention of overconsumption nor warnings against doing so (Austin 1985). However, by the classical era, philosophers such as Xenophon, Plato, Aristotle, and Zeno extolled the health benefits of wine drinking in their writings, yet sharply decried drunkenness (Hanson 1995).

Alcohol as a Problem, Alcohol as a Disease

During this period, drunkenness, viewed in a similar manner to other "indulgences" such as overeating and greed, was restricted to individuals in the upper classes of society. The drinking that occurred in this stratum of society – due to "leisure time and wealth" – influenced the rise of inebriation in antiquity (Austin 1985:vxii). However, prior to the development of distillation, concentrations of alcohol in beer and

wine were limited by the natural fermentative processes of yeast to approximately 5 and

15 percent (Levey 2004), and it is likely that these concentrations were much lower in

early forms of beer and wine. But the development of distillation in 700 CE (see Dudley

2002) enabled alcohol concentrations to reach levels that were impossible through the

natural fermentative process. Distillation meant that one could become more inebriated

with smaller amounts of alcohol, even to the extent that overconsumption could result in

death. The consequences of overconsumption would soon become more evident.

For much of modern history, alcohol abuse was deemed a matter of sin, a problem

under the jurisdiction of the clergy (Edwards 2009). The problematic aspects of alcohol

abuse primarily arose from the actual actions that resulted from drunkenness – typically

lewd behavior, property damage, and fighting. The overconsumption of alcohol was

viewed as a moral failing that had negative impacts on society, but there were no real

concerns for the impacts on the individual drinker. However, an alternative viewpoint

soon arose in which alcohol abuse was viewed as a disease with physical manifestations

and causes, rather than resulting from a lacking moral fortitude. In the final years of the

18th century and in the first decade of the 19th, Benjamin Rush and Thomas Trotter, two

prominent doctors, separately published research on the harm one endured as a matter of

being drunk, marking the first attempts to describe alcoholism as a "disease" (Edwards

2009). Alcohol's damaging effects on the drinkers themselves became as important as the

drinkers' negative impacts on society.

For the next 150 years, the disease model – now attributed to E. Morton Jellinek

who popularized the term (Jellinek 1960) – took various forms and various names, and

gave rise to the term "alcoholism" (Edwards 2009). The mid-20th century witnessed a rise

in the use of the word "addiction" to describe human reactions to opiates, and by the end

of the 20th century the addiction terminology was extended to alcohol (Edwards 2009).

These perspectives would come to shape early discourse in this area. With the creation of

the National Institute on Alcohol Abuse in 1970 came greater support for alcohol

research in the way of funding, postdoctoral programs, and conferences that explored

topics such as social contexts of drinking, use among minorities, and epidemiology of

alcohol drinking problems (see Heath 1987). These qualitative methods yielded large

amounts of data, but the repeated emphasis on alcohol*ism* did not easily lend itself to

engagement with the archaeological or anthropological communities.

Anthropological Frameworks and Archaeological Discourse

Anthropological investigations into the relationship between alcohol and humans

were rare before the 1960s, though ethnographic examinations of alcohol consumption

among various populations were increasing (Heath 1987). In the early years of alcohol

studies:

> "the dominant approach, grounded almost exclusively in the disciplines of
> biology/medicine, public health, and social psychology, had focused on alcohol
> consumption primarily as an individual pathology or a social problem. This view
> began essentially with the emergence of the temperance movement in the early
> nineteenth century, the corresponding creation of alcohol as a collective category
> and dangerous substance, and the discursive construction of drinking as a problem
> and then alcoholism as a disease" (Dietler 2006:230).

These early frameworks clearly felt the lingering impacts of cultural associations of

alcohol and behaviors and exposed the ethnocentric assumptions underlying some

examinations.

In 1953, prior to any major anthropological discourse on alcohol, Robert

Braidwood convened a symposium entitled "Did Man Once Live By Beer Alone?".

Braidwood – an archaeologist specializing in the origins of agriculture in the Zagros mountains of eastern Iraq – asked his colleagues if the impetus for domestication of grains was bread or beer (Braidwood et al. 1953). The respondents to this question "read like a Who's Who of anthropology and archaeology at the time" (Katz and Voigt 1987: 23), but few had any knowledge of the beer-making process, and the topic of "beer before bread" failed to engender any major discourse outside of the symposium. For the most part, the question did not receive much scholarly attention until three decades later when a hypothetical reconstruction of cultivation for the purpose of beer production was presented (Katz and Voigt 1987). Due to a lack of hard data and the inherent un-falsifiable nature of the hypothesis, scholarly attention to this topic has been limited.

The problem, then, is not that archaeologists were ignoring the presence of alcohol in antiquity, nor was the problem that they were not examining the material culture associated with alcohol consumption and production; artifacts associated with alcohol production and consumption indeed have been examined by archaeologists for decades. Rather, "archaeological discussions about alcohol are typically fortuitous by-products of fieldwork that had other emphases" (Smith 2003:52), such as 'mainstream' foci on trade, elite consumption, and analyses of vessel production and typology (Perego and Iaia 2010).

Only recently have archaeologists begun to consider the social and cultural aspects related to alcohol production and consumption, yet it is still the case that "few archaeologists have rigorously applied historical and anthropological theories to help them explain their alcohol-related discoveries" (Smith 2003:52). Even within the discipline of anthropology at large, the study of alcohol has "remained a minority

research field within anthropology and anthropologists have never achieved more than a minority voice in the broader field of alcohol studies, nor have they shared in much of the abundant research funding supporting this field" (Dietler 2006:230; see Hunt and Barker 2001). However, what distinguishes the recent work of the past two decades "is [a] more systematic, concerted effort both to develop the theoretical understandings of drinking as a social practice and to improve techniques for detecting alcohol production and consumption in the archaeological record" (Dietler 2006:232).

Today, it is commonly accepted that the examination into the origins of alcoholism and humans' attraction to alcohol fundamentally addresses a complex interaction of human biology (nature) *and* culture (nurture). While genetic factors, such as the heritability of alcoholism, are heavily emphasized in biomedical research, environmental factors – including age of first drink, drug use, and incidence of sexual, physical or emotional abuse and – are critical to the equation. Research into addiction and the cultural and social factors that impact the development of alcoholism is beyond the scope of this work. I aim to study the key questions that underlie these examinations of the present by peering further back in time: What is the origin of these genetic factors? Can we examine nonhuman primates to ascertain modern humans' relationship with alcohol? The process of answering these questions rests on key assumptions inherent in the disciplines of ethology, primatology, and Darwinian medicine.

Primate Behavioral Ecology and Darwinian Medicine: We Are What We Eat?

The theoretical notions that underpin ethology and primatology led to the formation of primate behavioral ecology, a field that applies "evolutionary principles to understand the adaptive advantages of behavior under different ecological conditions"

(Strier 2000:26). Those employing a primate behavioral ecology perspective examine

behaviors through an evolutionary lens in which it is assumed that, as occurs for all other

traits, the genotype and the environment interact to produce the behavioral phenotype

(the specific expression of the genotype in the given environment). Thus, primate

behavioral ecology accounts for the dual influences of genes and environment, rather

than ascribing behavior to genes and genes alone.

      Of the various behaviors that are examined from a behavioral ecology perspective

– life history, reproductive strategies, interspecific conflict and others – feeding behaviors

and dietary strategies are specific to the matters at hand. As previously stated, the

Drunken Monkey Hypothesis posits that the proclivity of modern humans to consume

alcohol may stem from a deep-rooted attraction to alcohol in frugivorous primate

ancestors. Therefore, what primates choose to consume, and the methods they utilize in

doing so, are observed as the product of complex biological and ecological interactions.

The relevance here is direct, as alcoholism itself is fundamentally the product of

biological and ecological interactions, albeit with "ecology" broadly defined so as to

include not just the physical environment but also social and cultural influences. So while

the human "ecological" experience vis-à-vis alcoholism consists of more than just the

physical environment, the physical environment is nonetheless an important factor; we

would be remiss to ignore the interactions between human ancestors' biology and ecology

on an evolutionary timescale. In essence, these are the goals of Darwinian medicine, and

through this lens, the biological and genetic origins of alcoholism, like other diseases, can

be examined.

Evolutionary explanations for disease and illness explore the processes that render humans to be more likely affected by certain afflictions as opposed to others (Williams and Nesse 1994). While much research pertains to disease manifestation (i.e. the spreading of pathogens, cycles of growth), the growing field of Darwinian medicine seeks to develop and explore evolutionary hypotheses of the origins of disease to determine human susceptibility. Darwinian medicine – "a vital yet underused tool in our quest to understand, prevent and treat disease" (Williams and Nesse 1994:6) – investigates the proximate and ultimate explanations of disease, drawing from the same theoretical foundations of ethology that Tinbergen first proposed in 1963 (Burkhardt 2006).

One common framework under the umbrella of Darwinian medicine is the concept of a lifestyle disease, or disease of civilization. In this framework, human susceptibility to various diseases and illnesses is a result of extant neurologic and metabolic pathways that have been co-opted in a modern environment. The evolutionary origin of these pathways is often dietary in nature, whereby human urges and tastes arose as crucial foraging devices in ancestral environments. These urges and tastes, once highly adaptive due to their ability to positively influence the nutritional composition of the human diet, become highly maladaptive in the modern context. For instance, the human taste for sugar and fat, which may once have ensured proper nutritional intake, now operate in an environment in which sugar and fat are bountiful, easily obtained, and largely divorced from the full nutritional profile typically associated with them (e.g. vitamins and protein, respectively). This maladaptivity may increase susceptibility to diabetes, obesity and heart disease – thus, these diseases are often considered to have

their origins in human evolution, and are prime candidates for examination through the lens of Darwinian medicine (Williams and Nesse 1994).

The potential to study alcoholism through the same lens may prove fruitful. The dietary adaptiveness of sugar and fat is direct, well understood, and well studied. In order for alcoholism to arise out of a similar pathway, the dietary adaptiveness of alcohol must similarly be established – this is the primary goal of the study of the Drunken Monkey Hypothesis and the fulcrum upon which it rests. If ethanol does, in fact, have dietary significance and is the subject of some form of dietary urge, then a similar causal chain as described above for sugar and fat may be expounded upon. In this case, alcoholism, like diabetes, obesity, and heart disease, may be viewed conceptually as a disease of nutritional excess and further examined through the Darwinian medicine framework (Williams and Nesse 1994).

The Drunken Monkey Hypothesis: A Closer Examination

Research on primate food choice aims to characterize the diets of primates, the methods by which primates choose the composition of their diets, and the evolutionary underpinnings for those choices. The Drunken Monkey Hypothesis posits that the proclivity of modern humans to consume alcohol may stem from a deep-rooted affinity present in all frugivorous nonhuman primates for naturally occurring ethanol within ripe fruit (Dudley 2000, 2002; 2004; 2014; Stephens and Dudley 2004). Ethanol is a natural by-product of the metabolic activity of fermentative yeasts within fruit pulp that consume sugars made available as the fruit ripens (Spencer and Spencer 1997).

According to the Drunken Monkey Hypothesis, for millennia the diets of primates have included vast amounts of fruits where yeasts, present of the skin of fruits, convert

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sugars into alcohols. As a molecule, ethanol, the most abundant of these alcohols, is easily dispersed through the forests as an odor and acts as a signal for ripe fruit. Due to immense competition in highly populated forests for food, the ability to locate ethanol's odor and follow it to reach ripe fruit would have been extremely advantageous, and the pairing of ethanol with nutritional rewards was thus selected for in ancestral primates. Over millions of years, this propensity towards seeking out and perhaps enjoying alcohol, coupled with the wide availability of much more highly concentrated forms of alcohol in modern times, has led to alcoholism as a "disease of nutritional excess" (Dudley 2000; 2014; Stephens and Dudley 2004). Thus, alcoholism is analogous to these other "genetically-based behaviors adaptive in the ancestral environment" that "become disadvantageous in a modern human environment" (Dudley 2000:7) in a context of abundant resources.

A core, underlying tenet of the Drunken Monkey Hypothesis concerns the fermentation process that produces ethanol in fruit. Fruit evolved as part of a symbiotic relationship between immobile plants and mobile animals. Plants that were more successful in convincing animals to carry their seeds to far flung locations derived an evolutionary advantage from having offspring living in varied locations – particularly when the animal's very method of "carrying" ended with the seed finding itself nestled in a fertilizing pile of feces. Plants whose fruits were more nutritious, beneficial, and desirable to their animal symbionts would have experienced more success in attracting this animal dispersion vector. This nutritional quality means that microbes and yeasts, in addition to the intended vertebrates, also consume fruits, and these yeasts play a central role in the Drunken Monkey Hypothesis. Fermentation of fruit sugars by yeasts, which

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may occur on or inside the fruit, produces numerous alcohols, although ethanol is most prevalent in fruits (Dudley 2000; Milton 2004).

The first facet of the Drunken Monkey Hypothesis is the notion that monkeys could locate ripe, nutritious fruit based on the odor of ethanol, and therefore would have developed an affinity for that smell and taste because of the nutritional qualities of ethanol-laden fruit. Because competition among frugivorous animals seeking sustenance was often extreme, any course of action that resulted in greater nutrition was likely to be taken. Ripe fruits are not as well distributed in tropical forests as other kinds of wild plants (Milton 2004), and frugivorous primates may be privy to ethanol's odors in detecting ripe fruits (Dudley 2000; 2014). These plumes, which contain volatized ethanol and other alcohols, may serve as an indicator of ripe fruits over long distances across the tropical forests in which ancestral primates resided, and may have allowed for quick consumption of ripe fruit facing decay. The pairing of ethanol with nutritional rewards – and selection of it as an appetitive behavior – of fruit is common among other mammals, frugivorous vertebrates such as birds, and insects such as fruit flies (*Drosophila* spp.), and fruit-eating butterflies, and may have eventually led to alcohol abuse in humans (Dudley 2000; 2014).

However, the utilization of scent cues for ethanol as a mechanism in primate food choice has not been well documented. The role of olfaction has been minimized as a mode of finding food in primates (Milton 2004), though for spider monkeys (*Ateles* spp.), "sniffing may be particularly important to verify the status of ripeness" (Pablo-Rodríguez et al. 2015:217). Squirrel monkeys (*Saimiri sciureus)* and pig-tailed macaques (*Macaca nemestrina*) have been shown to distinguish alcohol concentrations below 1 part per

million (Laska and Seibt 2002). Alcohols with less carbon require higher concentrations in order to be noted, and neither squirrel monkeys nor pig-tailed macaques can recognize ethanol when diluted lower than 1:300 – a concentration akin to the relationship of scent sensitivity and molecular properties in humans and rats (Laska and Seibt 2002). Interestingly, both species were more sensitive to aliphatic esters as opposed to aliphatic alcohols (of which class ethanol belongs), which constitute the majority of the aliphatic components in the odors of fruit during ripening (Laska and Seibt 2002). Evidence suggests *Drosophila melanogaster* follow vapors as a means of locating ripe fruits to lay their eggs (Gibson et al. 1981), though it so far remains unproven that volatized ethanol serves as a signal for nutrition in primates.

The adaptability of primate olfactory detection of ethanol may run counter to the apparent adaptive nature of ethanol production by yeasts (Levey 2004). Competition for scarce fruit resources occurs not only among vertebrates, but also between vertebrates and microbes and yeasts. A ripened fruit quickly attracts yeasts that colonize and begin to consume the fruit. However, if a primate or other vertebrate were to find the fruit, it would quickly eat the fruit and the nascent population of yeast along with it. In order to ward off this form of competition, it has been hypothesized that yeasts have developed the ability to produce ethanol as part of an adaptive strategy to protect its resources (Levey 2004). Further, the primary reason yeasts produce alcohol is to "render ripe fruits distasteful or unacceptable to wild vertebrates" (Janzen 1977:60). If primates instead used the scent of ethanol as a method of more quickly and efficiently finding the ripe fruit, the yeasts' strategy of producing ethanol would actually be maladaptive. The two strategies – ethanol production as a defense mechanism in yeasts and ethanol detection as a food

locating mechanism in primates – may seem to be mutually exclusive. If the Drunken

Monkey Hypothesis is correct, perhaps an alternative explanation for yeasts' ethanol

production should be offered.

For natural selection to have favored primates' ability to detect and follow ethanol

to reach ripe fruit, it must have conferred a nutritional advantage. On Barro Colorado

Island Stephens observed a howler monkey sniffing and then "bingeing" on *Astrocaryum*

standleyanum fruits while hanging precariously from branches (Stephens and Dudley

2004). The fruit the monkey was quickly consuming contained an estimated ethanol

content of about 1 percent (Stephens and Dudley 2004) – slightly more than a ripe fruit

that contains 0.6 percent and many times less than the overripe fruit that contains more

than 4 percent (Dudley 2000). The Drunken Monkey Hypothesis proposes that in

monkeys' predilection towards ethanol-laced fruits, they avoid unripe fruit that has no

alcohol and overripe fruit that has too much (and consequently, too little sugar), drawing

comparisons of a monkey's consumption of alcohol being similar to that of a human

beginning a meal with an aperitif (Dudley 2004). For the connection of alcohol with

nutritional reward to work in the evolutionary sense, Dudley asserts that alcohol use is

beneficial in humans, citing hormetic advantages that ethanol may confer on frugivores

(2000; 2014). Hormesis is a phenomenon where seemingly toxic substances may actually

be beneficial at low levels (Gerber et al., 1999; Parsons, 2001; Calabrese and Baldwin

2003). In this framework, human alcoholism is suggested to result when ethanol,

potentially healthy at lower concentrations, is readily available in modern times at very

high concentrations. Hormesis is considered by some to be widely applicable to many

toxins (Calabrese and Baldwin 2003). Alcohol – a toxin – is thought to have positive

impacts on health at low concentrations, but it can be quite damaging at high doses.

Vital to the Drunken Monkey Hypothesis are the varied genes related to the

consumption of alcohol that evolution would have selected for. The presence and

variation of human genes that regulate the efficiency with which humans process alcohol

and its by-products is evidence to support alcohol's long-term presence in the human diet

(Stephens and Dudley 2004). Frugivory has comprised an ample portion of the diet of

ancestral humans and primates since at least 40 million years ago (Stephens and Dudley

2004) and persists as the predominant diet of many of our closest living relatives today.

Because of the concentrations of alcohol found in ripe fruit, ethanol is and has been a

component of the diets of frugivorous animals, as it cannot be avoided (Levey 2004).

This has necessitated the development of genes to respond to the ethanol and breakdown

its products. After being metabolized in the liver, ethanol is converted to acetaldehyde by

the enzyme alcohol dehydrogenase, or ADH. The acetaldehyde is then converted into

acetate by the enzyme aldehyde hydrogenase, or ALDH. There is variance among the

human population in respect to these gene-encoded enzymes and their efficiency of

removing alcohol or ADH from the bloodstream. Due to uncomfortable symptoms such

as nausea, headaches, and flushing, those without effective enzymes are expected to be

less likely to imbibe and perhaps be protected against the development of alcohol abuse

and dependence. Studies of East Asian and Jewish populations have shown this to be the

case (Enoch 2006).

Indeed, the genetic expression of alcoholism has long been debated. There are

numerous variables, including developmental and environmental that place individuals at

risk for alcoholism (Gerald and Higley 2001). The heritability of alcoholism, or the

proportion of variance among traits due to genetic factors, based on meta-analysis of twin

studies, has shown to be about 50 percent, with non-shared environmental factors being

approximately as important (McGue 1999; Enoch 2006; Sommer et al. 2005). The

genetic factors associated with alcoholism are likely to be due to multiple gene-

environment interactions, and it is unlikely that a single gene could render one genetically

vulnerable (Enoch 2006; Sommer et al. 2005). Important environmental factors are

clearly necessary to the equation of genetics in the study of alcoholism and ultimately

how the phenotypes of genetic vulnerability will be expressed. Genotype environment

models advance the notion that alcoholism can occur when individuals have multiple

contributing genes that are predisposed to or favor alcoholism, and are raised in

environments that can be particularly challenging (McGue 1999).

     To date, the Drunken Monkey Hypothesis has received relatively little attention in

the anthropological literature, though there appears to be an uptick in publications that

offer evidence that support its underpinnings. For example, the pen-tailed tree shrew –

which closely resemble the animals from which primates were thought to evolve –

chronically consumes ethanol via fermented fruits and nectars, and it does so in amounts

that would intoxicate humans (Wiens et al. 2008). Free-ranging vervet monkeys on the

Caribbean island of St. Kitts, who steal drinks from tourists, tend to exhibit drinking

behavior in controlled studies in percentages that are consistent with human populations:

for example, the majority are what she calls "social" drinkers, 15% are "regular"

drinkers, 5% "binge" drink, and 15% are "teetotalers" and do not consume alcohol at all

(Palmour et al. 1997), though quantitative behavioral data examining ethanol

consumption is derived from a captive population in-facility (Ervin et al. 1990; Juarez et al. 1993). Heavy drinkers that will drink to the point of liver, heart and gastric damage, and pregnant females with access to alcohol sometimes produce infants with features of fetal alcohol syndrome have also been observed (Palmour et al. 1997). A quantitative assessment has documented habitual ethanol-ingestion in wild chimpanzees (*Pan troglodytes)*, which use tools to retrieve fermented palm sap from trees that have been tapped by humans (Hockings et al. 2015). Further, paleogenetic reconstructions of ADH4 (ethanol-metabolizing enzymes) demonstrate that ape ancestors of humans, chimpanzees (*Pan* spp.), and gorillas (*Gorilla* spp.) obtained the capability to metabolize ethanol approximately 10 million years ago. The presence of this enzyme suggests that the apes' hominin ancestors' capacity to metabolize ethanol was an adaptive response to ethanol present in fermented fruit (Carrigan et al. 2014). In addition, ethanol has been found to be present in all stages of development of fourteen species of fruit from Southeast Asia, ranging from 0.005% to 0.48% Dominy (2004) showed. The ethanol content of these fruits also correlated positively with concentrations of soluble sugars, suggesting that it could provide a "valuable foraging guide" (Dominy 2004:295). Lastly, studies on the fruits of the palm *Astrocaryum standleyanum* on BCI – a fruit known to be consumed by the Barro Colorado spider monkeys (Campbell 2000) – indicate that ripe fruits contain on average 0.5% ethanol, and over-ripe fruits contain about 4.5% (Dudley 2004). Thus, there is indirect evidence that spider monkeys – the study species of the present work – are indeed ingesting ethanol. In addition, spider monkeys have been shown to have excellent scent sensitivity to alcohols, which may indicate that the sensitivity is an evolutionary adaptation to optimal foraging.

Methods

Study Site

Fieldwork was conducted at Barro Colorado Island, a dense lowland tropical rainforest that is located in the Panamá Canal Zone. The island was formed following the damming of the Chagres River to form the man-made Lake Gatun in 1913. At approximately 1500 hectares, Barro Colorado is the largest of the islands in the Canal Zone that were created due to the flooding of the mainland, and it receives an annual rainfall of 2600 mm (Dietrich et al. 1996; Leigh et al. 1996). The island, part of the Barro Colorado National Monument, is one of the best-studied sites in the world among lowland tropical forests (Leigh et al. 1996). In addition, the laboratory methods proposed to test fruits in the current study have been validated in this environment (Dudley 2004).

Study Group

Spider monkeys (*Ateles* spp.) are a logical choice of primate species to test the possibility of regular low-level ethanol consumption as they are consistently reported as being highly frugivorous during most months of the year (DiFiore and Campbell 2007) and are known to be "ripe fruit specialists" (Di Fiore et al. 2008; Takahasi 2008). In addition, spider monkeys have been shown to have excellent olfactory sensitivity to alcohols (Laska et al. 2006), which may indicate that the sensitivity is an evolutionary adaptation to optimal foraging (Hernández-Salazar et al. 2003).

The single community of black-handed spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, consisting of approximately 42 individuals (Campbell unpublished data 2013), is an excellent study group for this research for multiple reasons: they are fully habituated to human presence, their diet is well characterized, and, as

previously mentioned, previous work investigating the ethanol levels in the fruits of the palm *Astrocaryum standleyanum* (a fruit known to be consumed by the troop) was conducted on Barro Colorado (Dudley 2004). Thus, there is indirect evidence that the community of spider monkeys on Barro Colorado Island is ingesting ethanol; however, a test of the ethanol content of a fruit species more important to spider monkeys (such as *Spondias mombin*) will provide solid data concerning the importance of ethanol in their diet.

Data Collection

Data collection was conducted from June – August 2013 to coincide with the known fruiting activity of *Spondias mombin* (Croat 1978) – a mango relative of extreme dietary importance to the spider monkeys (Campbell 2000) with high sugar content (Di Fiore et al. 2008), thus making it a likely candidate for fermentation. During the data collection period the group was followed for as long as possible (from approximately 6:00am until approximately 6:00pm) once visual contact was made. When a field assistant was present, a data collection schedule was implemented that allowed for full-day (approximately 6:00am-6:00pm) or half-day (6:00am-12pm or 12pm-6:00pm) follows.

In order to ensure that the ethanol levels obtained reflect as closely as possible the levels being consumed by the monkeys, partially eaten ripe fruits were collected opportunistically only when individuals were actively feeding (placing fruit into the mouth) and when the dropped fruits were able to be traced visually to a specific individual. Additionally, in order to show that spider monkeys **prefer** ethanol-laden fruit, a "natural" baseline range of ethanol concentrations in uneaten dropped fruits was

compared to the range of ethanol concentrations in fruit eaten by the monkeys. The uneaten fruits were collected only during the same periods that partially eaten ripe fruits were being collected (at the same site of the active feeding bouts) and when they could be discerned from other fallen fruits on the forest floor. Fruits were visually categorized as ripe, and under- and over-ripe fruits were not collected.

Fruits were stored individually in small zip lock bags and kept in a cooler with ice packs to prevent subsequent fermentation prior to measurements, which were taken in a temperature-controlled laboratory (10˚C) at the end of each shift in the field (i.e. at approximately 12:00pm or approximately 6:00pm). Samples of the mesocarp (pulp) of individual fruits were obtained and blended using a small handheld blender to ensure homogeneity. Ethanol concentrations of the samples were determined from InfraSpec VFA-IR spectrometer readings (Wilks Enterprise) and carbohydrate concentrations were determined from refractometer readings (LW Scientific). The InfraSpec VFA-IR spectrometer and refractometer were calibrated using known standards. These have been validated in this environment (Dudley 2004). Statistical analyses (one tailed, independent-samples, t-test for comparison of means and linear regression) were performed using SPSS to determine whether spider monkeys exhibit a statistically significant preference for fruit with higher ethanol concentrations, and whether there is a significant correlation between ethanol concentrations and sugar levels. Seven samples analyzed were found to have ethanol percentages that exceed the amount possible in fruit (samples ranged from 10-40%) and were therefore excluded from the final analysis.

The present study sought to investigate the problem by testing the ethanol

concentration of *Spondias mombin* fruit, with close attention paid to the fruits monkeys at

least partially consumed. In total, 72 partially eaten and 31 uneaten *Spondias mombin*

fruits were collected between July and August 2013 and tested.
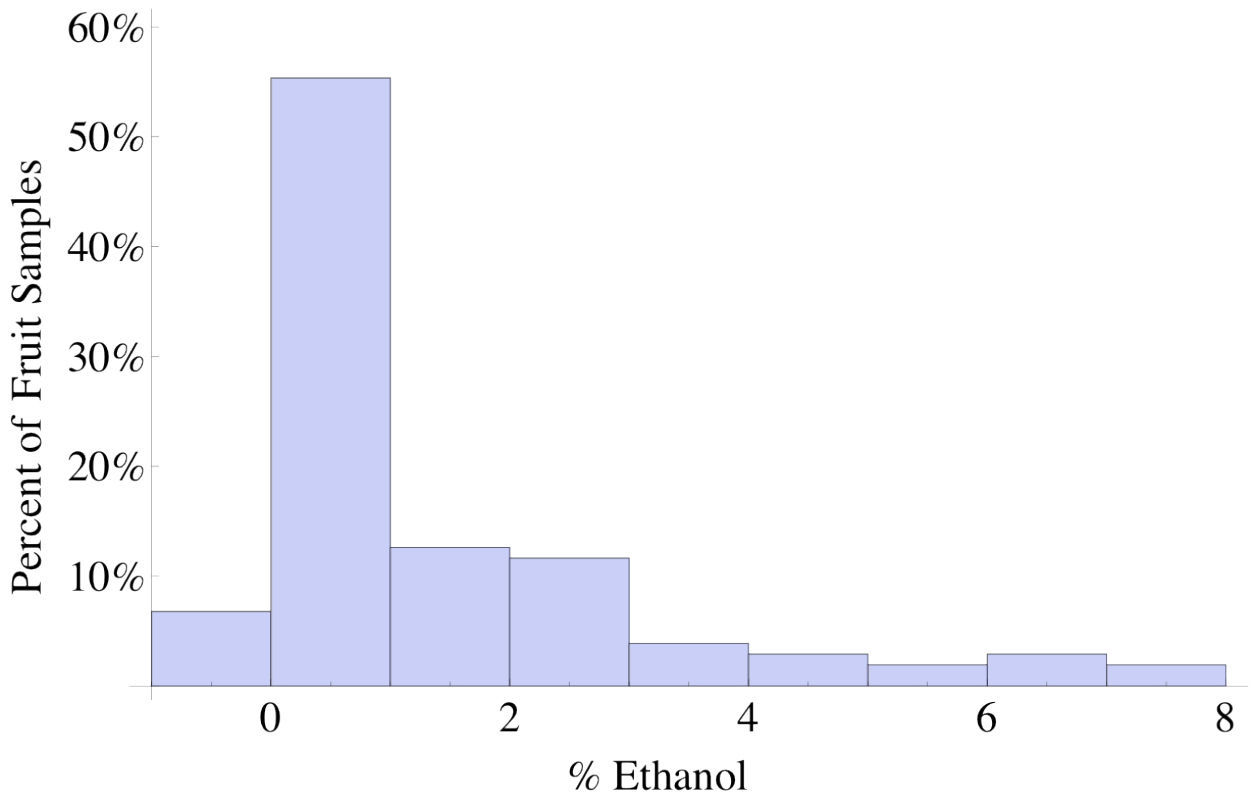

Figure 4.1: Fruit samples grouped by alcohol content

Data show the Barro Colorado Island spider monkeys consume fruits with

measurable ethanol content regularly (see Fig. 1). In this study, 85.7% of the *S. mombin*

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fruits that spider monkeys had at least partially eaten contained measurable ethanol content. Many of these fruits had low ethanol concentrations (<3% ethanol, 70.1% of fruits). However, some fruits had substantial ethanol content, comparable to alcoholic beverages such as beer (>3% ethanol, 15.6% of fruits). As *S. mombin* is an important component of their diet, spider monkeys appear to chronically consume low levels of ethanol during feeding.
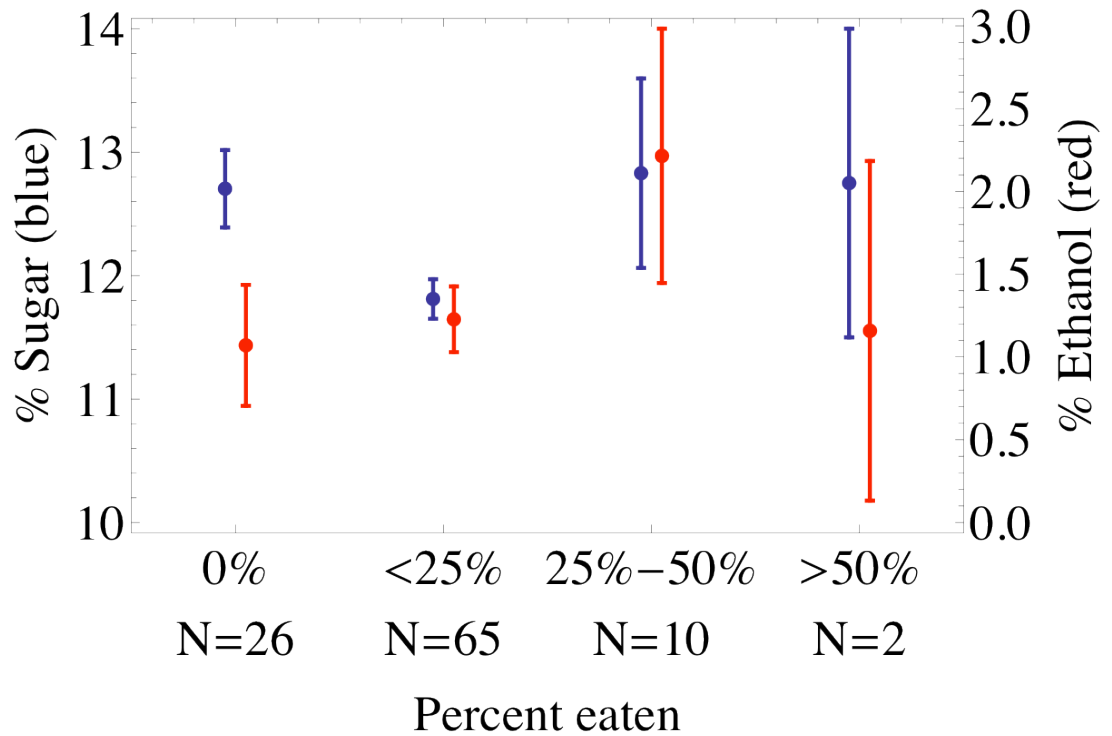

Figure 4.2: Average sugar and ethanol content grouped by percent of fruit sample consumed

Results from a *t*-test (one-tailed, independent samples) show the average ethanol contents of non-consumed (baseline) fruits and consumed fruits were 1.1% and 1.4%, respectively (Figure 4.2). However, this effect was not statistically significant; these results indicated a non-significant trend in the predicted direction ($p = 0.25$). There was a non-statistically significant trend towards spider monkeys eating a higher proportion of fruits that had higher ethanol content ($p = 0.12$). However, fruits that were fully consumed by spider monkeys were unable to be measured, as they consume the entire fruit, seed included. Thus, if spider monkeys consume higher proportions of fruit that have higher ethanol content, these crucial data points (100% consumed fruits) will necessarily be missing.
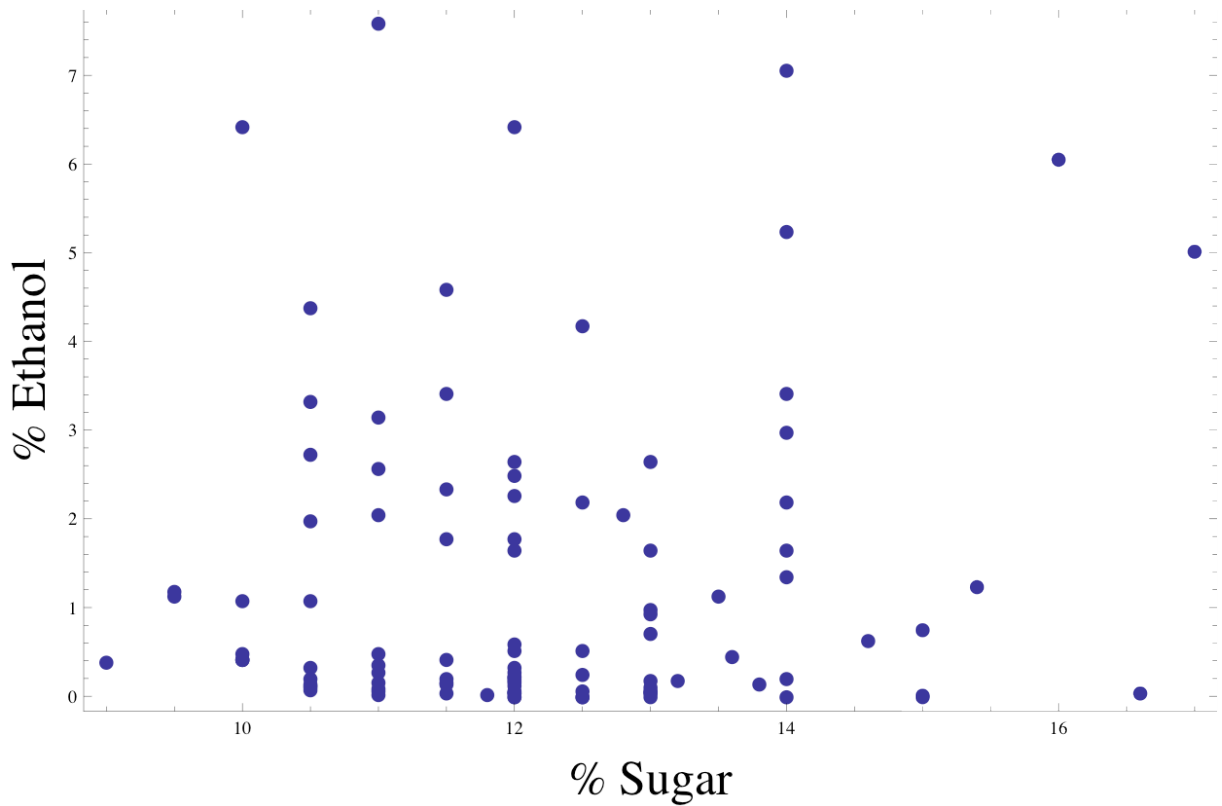

Figure 4.3: Relationship between sugar and ethanol content

It was expected that fruits with higher ethanol content would also have lower sugar content, as fermentative yeasts convert sugar into ethanol. However, as the linear regression in Figure 4.3 shows, there was no observed relationship between ethanol content and sugar content ($R = 0.11$, $p = 0.27$ with sugar amount taken as independent variable and ethanol amount as dependent variable). If anything, higher ethanol content was associated with higher sugar content, though the effect was insignificant and likely due to the small sample size. Ethanol content ranged rather dramatically, from 0.0% to 7.6% (Mean = 1.28, Std Dev = 1.76). Sugar content ranged from 9.0% to 17.0% (Mean = 12.15, Std Dev = 1.56).

This study demonstrates that Barro Colorado Island spider monkeys consume fruits containing ethanol. Additionally, it showed a non-statistically significant trend towards spider monkeys preferentially selecting – and consuming more of – fruits that contain higher levels of ethanol. There was no observed relationship between ethanol content and sugar content. Future studies investigating the role of ethanol in the diet of spider monkeys will extend data collection further into the fruiting season of *S. mombin* and sample additional fruit species. These fruit samples were collected between July 28 and August 29 – early in comparison to *S. mombin*'s full fruiting season of July to October (Croat 1978). Thus, the process of ripening, which produces the sugars necessary for ethanol production, was still ongoing. Later in the season overall ethanol levels may be higher, potentially further revealing a preferential selection for ethanol-laden fruits. The importance of these missing data points due to research design cannot be understated.

Conclusion

Spider monkeys may use the scent of ethanol for foraging. If this is the case, it is unknown whether they utilize ethanol plumes to locate ripe fruit or, further, to select ripe fruit. They may be able to follow an ethanol plume to locate a group of ripe fruit without being able to select the higher-ethanol fruits from within that group. This may obscure the importance of ethanol in their diet, as fruits ripen differentially. This is an important avenue for future research, both to further characterize the diet and foraging behavior of spider monkeys and to directly address the Drunken Monkey Hypothesis.

Lastly, though the data presented here are far too sparse to demonstrate that nonhuman frugivorous primates exhibit a proclivity to consume ethanol, they nevertheless suggest that this is an important avenue for future research. Future studies investigating the role of ethanol in the diet of spider monkeys will extend data collection further into the fruiting season of *Spondias mombin* and sample additional fruit species to further characterize the role of ethanol in the diet and increase the statistical power of the results. Locating the presence of an ethanol metabolite in urine samples may also serve to clarify the relative importance of ethanol in the spider monkey diet, and further investigation into the mechanism by which spider monkeys locate ethanol-laden fruits must be undertaken. Thus, an expansion of research in these areas may possibly show greater support for the hypothesis that evolutionary adaptation may partially explain the role, or the origins, of alcohol in the human diet. Such studies will not only illuminate primate foraging behavior, but may also give clues to humans' biological relationship with ethanol. If future results indicate that nonhuman frugivorous primates indeed exhibit an innate sensitivity and attraction to ethanol, then modern humans may have retained

such behavioral characteristics. This preliminary study may be the first step in establishing such an explanation.

Monkeys, Alcohol and Evolution: A Summary

One may ultimately wonder what use there is in testing a hypothesis for the origins of alcohol consumption and alcoholism in humans by studying the dietary preferences of spider monkeys, and in many ways, this is a fair criticism. However, as has been discussed in the preceding pages, decades of ethological and primatological research have rested upon just such a conceptual leap. These disciplines are built upon, and have developed theoretical frameworks that attempt to validate, comparisons of behavior across species – in the general form in the case of ethology, and specifically between primates and humans in the case of primatology. Both disciplines utilize a critical and biologically founded analysis of animal behavior to make conclusions about evolution, phylogeny, and adaptive strategies. The central tenet of primatology in particular – that the close phylogenetic relationship between humans and the rest of the primates, coupled with conservation of traits between species, allows us to make tractable comparisons across species lines – presents a framework through which a comparison between the dietary habits of spider monkeys and humans can be made and still carry weight.

An examination into the origins of alcoholism integrates the natural and social sciences in its attempt to address a complex question of human culture and biology. Although this work is by no means a comprehensive account of the role of alcohol, nor alcoholism, in the lives of modern humans – as it does not touch on the important and myriad social and environmental factors intimately tied with alcoholism – it is hoped that

the theoretical concepts and frameworks addressed herein ultimately demonstrate the use validity of animal behavioral studies, the use of nonhuman primates as homologues, and Darwinian perspectives of disease through a holistic anthropological framework. The distinct, yet often overlapping frameworks of ethology, primatology, Darwinian medicine – and indeed, the field of anthropology as a whole – combine to provide key insights into behavioral patterns, a greater understanding of which may shed light upon the inner workings of human and nonhuman primates and our relationship with the world around us – both in the past and in the present.

The ubiquity of alcohol consumption and production throughout humanity indicate alcohol's incredible informative power and its importance to our species. For this reason, the disciplines of primatology and anthropology must make greater efforts to engage with theoretical perspectives and methodologies that move beyond traditional approaches to alcohol studies with the aim of investigating the complex, enigmatic, and conceivably evolutionary components of humans' long and multifaceted relationship with alcohol, much as the present study has aimed to do. While only some major themes in anthropological investigations of alcohol have been addressed here, it is hoped that this examination of the Drunken Monkey Hypothesis engenders a greater understanding of the contributions of anthropology and primatology to alcohol studies and the multiple methods of examination that are able to be utilized in the search for a greater understanding of humans' – and indeed, nonhuman primates' – relationship with alcohol.

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