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The Comparative Biology of Ethanol Consumption: An Introduction to the Symposium[1]

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In classical Greek, the word "symposium" signifies a drinking party held for the purposes of intellectual discussion. This symposium introduces a new evolutionary perspective on an ancient question: why are many animals, including humans, attracted to ethanol? Recent research has shown that behavioral responses to ethanol and molecular pathways of inebriation are shared among many taxa (Wolf and Heberlein, 2003), and that the preferences of modern humans for alcohol consumption may derive from the diets of our fruit-eating ancestors (*i.e.*, alcoholism as evolutionary hangover; Dudley, 2000, 2002). Placement of ethanol consumption within historical and comparative contexts may thus yield insight into contemporary patterns of human consumption and excessive use.

Ethanol and other alcohols originate naturally from the fermentation by yeasts of plant sugars. Yeasts can be found throughout the biosphere, and are common both on and within plant reproductive structures, including fruit (Spencer and Spencer, 1997). Competition among microbes for access to fruit sugars is intense, and may have elicited the initial evolution of ethanolic fermentation by yeast as a means of killing bacterial competitors (Ingram and Buttke, 1984). Suggestively, high glucose levels stimulate anaerobic fermentation by yeasts even in the presence of oxygen, a phenomenon known as the Crabtree effect (De Deken, 1966; Møller *et al.*, 2002). Well-studied at the molecular level, the Crabtree effect may also reflect an evolutionary outcome of intense competition among microbes within sugar-rich fruit substrates. Similar arguments pertain to the existence of killer yeast strains (Starmer *et al.*, 1987; Morais *et al.*, 1995). Frugivory by and competition among microbes likely arose contemporaneously with the Cretaceous origins of fleshy fruits. Consequently, plants express antimicrobial compounds within fruit to deter decomposition which might impede the desirable consumption and dispersal of fruits by vertebrates (Cipollini and Levey, 1997).

The natural occurrence of ethanol within ripe and fermenting fruit suggests that low-level ethanol exposure via dietary ingestion is characteristic of all frugivorous metazoans. Fruitflies live within ethanol-containing substrate as larvae, and moreover consume yeast spores as adults. It is therefore not surprising that *Drosophila* serves as a model system with which to evaluate both proximate behavioral responses (Frye *et al.*, 2003) and evolved metabolic and genomic outcomes (Fry, 2001) relative to ethanol exposure. Among the vertebrates, many birds and mammals are strongly frugivorous, although the relative importance of olfactory cues (including ethanol) to fruit selection and consumption is unclear (Korine *et al.*, 2000; Levey and Martinez del Rio, 2001; Dominy *et al.*, 2003). Primates in particular are a predominantly frugivorous lineage, and study of the diet of frugivorous human ancestors is accordingly of relevance to understanding the nutritional requirements of modern humans (Milton, 1993, 1999). The beneficial effects of low-level but chronic ethanol consumption by humans (Klatsky, 2003) mirror those in fruitflies (Parsons, 1980), and may indicate a common evolutionary outcome.

From fruitflies to barflies, diverse animal taxa exhibit profound behavioral responses to the alcohols produced within fermenting fruit. A common theme of historical ethanol exposure unites the otherwise disparate phenomena of microbial fermentation, fruit, frugivores, and the drinking behavior of modern humans. True to etymological origins, this symposium in New Orleans has provoked considerable questioning and comparative analyses of ethanol-related behaviors. Papers deriving from this symposium clearly demonstrate the potential for emergence of a comparative biology of ethanol ingestion, as well as for novel interpretations of modern-day alcohol consumption and its impact on human society.

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