Pollinator ethanology: A comment on Bowland et al.

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A recent review by Bowland *et al.* [1] highlights increasing evidence that ethanol is frequently encountered in the wild, favouring mechanisms that enable its use across multiple animal lineages. The review also discusses the concept of hormesis in relation to ethanol consumption – where low to moderate doses of ethanol are linked to beneficial effects, while high doses have negative consequences. Ethanol hormesis underpins one of the most significant negative outcomes in humans: the tendency toward alcoholism, as proposed by the 'drunken monkey' or 'evolutionary hangover' hypothesis [2], which the review also examines. This hypothesis centres on the nutritional ecology of frugivorous human ancestors that consumed sugar-rich, ethanol-spiked ripe fruits, resulting in adaptations for ethanol consumption. Nowadays this predisposes modern humans to alcoholism in an environment with artificially increased ethanol availability, enabled by controlled fermentation and distillation techniques [3]. While Bowland *et al.* appropriately emphasises fleshy fruits as a key dietary ethanol source for vertebrates, particularly primates and other mammals, two points deserve more explicit focus. First, nectar is also an ethanol-bearing substrate, and nectarivores, including invertebrate pollinators, could be included within this framework [4]. Second, ethanology, a comparative study of ethanol exposure and response [5], could be expanded to test the scenario proposed in the 'evolutionary hangover' hypothesis across various organisms.

Flower nectar often contains ethanol due to yeast infestation [6], and bees and wasps routinely consume nectar in addition to juices from ripe and overripe fruits. Notably, the evolutionary split between bees and wasps coincides with the emergence of yeast-produced ethanol in the Cretaceous period [7], indicating a long, co-evolutionary history of ethanol in the diets of these pollinators and paralleling that of human ancestors within the context of the ‘evolutionary hangover’ hypothesis. Honeybees, for example, show striking affinities for ethanol, some of which are mentioned in the review [1]; moreover, they can display traits akin to alcoholism under conditions of excess ethanol access. The presence of withdrawal symptoms commonly defines alcohol addiction, and such symptoms seem to occur in honeybees [8]. Additionally, honeybees do not exhibit conditioned taste aversion to high ethanol concentrations up to 10 or even 20% [9]. Hornets, in turn, demonstrate extraordinary ethanol tolerance, consuming ethanol at concentrations as high as 80% without adverse effects on survival or behaviour [10]. This tolerance may result from multiple copies of the alcohol dehydrogenase gene and their generally high metabolic rate [10]. The consistent exposure to ethanol, historically and presently, in bees and wasps suggests their suitability as models for studying ethanol effects and abuse. These invertebrates may exemplify animals that align with the ‘evolutionary hangover’ hypothesis and offer opportunities to experimentally test its assumptions and predictions [4].

The outstanding questions highlighted in Bowland *et al.* [1] could be extended to address these additional issues. While further research is needed on natural ethanol levels, studies specifically measuring ethanol in nectar and identifying factors that promote its presence are even scarcer than those on fruit. Similarly, basic knowledge is lacking regarding the natural history of dietary ethanol exposure in many frugivores and nectarivores. Furthermore, there is limited understanding of the prevalence of ethanol hormesis and whether animals exposed to dietary ethanol over their evolutionary history are more susceptible to ethanol addiction than related species without such a history. Investigating this in animals, such as bees and wasps with demonstrated ethanol tolerance, could clarify whether altered environmental conditions foster dependencies similar to those hypothesised in humans. Currently, there is no consensus on the operationalisation of alcoholism, but research in the evolutionary ecology of ethanol could help address this issue. One might argue that amplified responses to adaptive, low concentrations of ethanol could indicate alcoholism, for example, through a pathological preference for ethanol-spiked foods. Insights into these symptoms could be gained across the nutritional, medicinal, health-related, and other aspects of ethanol consumption by studying ranges of concentrations and exposure periods in various organisms, including invertebrates. Questions posed by Bowland *et al.* can also be broadened to incorporate invertebrate pollinators. The question of whether gut microbiota produces ethanol is relevant not only to frugivores but also to nectarivores; in honeybees, for example, fermentation may likely occur within the organisms and in bee products stored in the hive [11]. Whether ethanol serves as a resource localisation cue for pollinators is also an open question; yeast volatiles, including ethanol, may be attractive due to their association with sugar [12]. This could reveal if ethanol in nectar or other plant-based resources functions as a signal for pollinators, potentially influencing their behaviour and foraging efficiency. Answering these questions may shed light on how historical ethanol exposure has shaped human evolution and the behaviour and physiology of other animals with long-term ethanol interactions.

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