Myth, Marula, and Elephant: An Assessment of Voluntary Ethanol Intoxication of the African Elephant (*Loxodonta africana*) Following Feeding on the Fruit of the Marula Tree (*Sclerocarya birrea*)*

Steve Morris[†]
David Humphreys
Dan Reynolds
School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom

Accepted 6/1/2005; Electronically Published 2/6/2006

ABSTRACT

Africa can stir wild and fanciful notions in the casual visitor; one of these is the tale of inebriated wild elephants. The suggestion that the African elephant (*Loxodonta africana*) becomes intoxicated from eating the fruit of the marula tree (*Sclerocarya birrea*) is an attractive, established, and persistent tale. This idea now permeates the African tourist industry, historical travelogues, the popular press, and even scholastic works. Accounts of ethanol inebriation in animals under natural conditions appear mired in folklore. Elephants are attracted to alcohol, but there is no clear evidence of inebriation in the field. Extrapolating from human physiology, a 3,000-kg elephant would require the ingestion of between 10 and 27 L of 7% ethanol in a short period to overtly affect behavior, which is unlikely in the wild. Interpolating from ecological circumstances and assuming rather unrealistically that marula fruit contain 3% ethanol, an elephant feeding normally might attain an ethanol dose of 0.3 g kg^{-1}, about half that required. Physiological issues to resolve include alcohol dehydrogenase activity and ethanol clearance rates in elephants, as well as values for marula fruit alcohol content. These models were highly biased in favor of inebriation but even so failed to show that elephants can ordinarily become drunk. Such tales, it seems, may result from "humanizing" elephant behavior.

* This paper was prepared as an overview of a symposium session presented at "Animals and Environments," the Third International Conference for Comparative Physiology and Biochemistry, Ithala Game Reserve, KwaZulu-Natal, South Africa, 2004 (http://www.natural-events.com/ithala/default-follow_2.asp).
[†]Corresponding author; e-mail: steve.morris@bristol.ac.uk.

Physiological and Biochemical Zoology 79(2):363–369. 2006. 1522-2152/2006/7902-5055$15.00

Introduction

Africa is intoxicating in its vistas and wildness and in its varieties of bottled liqueurs. First-time visitors frequently imagine ravenous beasts behind each bush, a fancy brought on by the undiluted and visceral attraction of wild Africa and, perhaps, by an indulgence with the liqueurs. Commercial brewing and distilling are important industries in South Africa, and among the more popular liqueurs is Amarula, made from the fruit of the marula tree, whose bottle is adorned with marula fruit and a rampant bull elephant. (The producers of Amarula [Distell Group Ltd., Stellenbosch, South Africa] make no claim as to marula intoxication of elephants but correctly describe the local folklore that elephants are insatiably attracted to the marula tree, known locally as the "elephant tree"; http://www.amarula.co.za/home.asp.) During the Third International Conference for Comparative Physiology and Biochemistry, in the Ithala Game Reserve, South Africa, we were prompted to reflect on these issues by the persistently related anecdote of drunken elephants. Even a superficial perusal of promotional material from the African safari and tourist industry reveals a widely held belief that evidence exists for ethanol intoxication in the African elephant and most especially that this elephant (*Loxodonta africana*) becomes intoxicated from eating the ripe and fermenting fruit of the marula tree (*Sclerocarya birrea*). This belief is persistent. For example, the French naturalist Delegorgue, describing his experiences in the vicinity of the iMfolozi River in present-day KwaZulu-Natal around 1839, reports how his Zulu guides told him of the strangely aggressive behavior shown by elephant bulls after feeding on marula fruits. He writes, "The elephant has in common with man a predilection for a gentle warming of the brain induced by fruit which has been fermented by the action of the sun" (Alexander and Webb 1990; p. 275). Naturally, at a meeting with physiologists, there were some attempts to calculate whether this was a likely phenomenon, most befuddled by attempts at empirical proof with the Amarula. In this paper, we explore and analyze the likelihood of natural intoxication in the African savannah elephant.

A recent symposium at the Society for Integrative and Comparative Biology New Orleans meetings ("In Vino Veritas: The Comparative Biology of Ethanol Consumption," January 5–9, 2004) examined the proposition of Dudley (2000, 2002) that the predilection of humans for imbibing ethanol may be inherited from frugivorous primate ancestors (Dudley and Dickinson 2004) who developed an attraction to the ethanol that may accumulate in overripe fruit (Dudley 2002). This intriguing idea remains to be fully tested (e.g., Dominy 2004; Levey 2004). Many of the accounts of "drunken animals" are anecdotal, mired in folklore and myth and possibly confused with other forms of intoxication. Monkeys apparently avoid overripe fruit, although this is based on human definitions of acceptable ripeness (Milton 2004). While bats seem to avoid fruit if it contains more than 1% ethanol, the attractiveness of fruit with an ethanol content close to that naturally within fruit has yet to be tested (Sánchez et al. 2004). Thus, while a pattern is hard to discern, frugivory in elephants may be similarly alcohol related.

A dearth of data has led to a tendency to recount anecdotes and a reliance on the few published accounts (see also Dennis 1987; Dudley 2000). There are almost no reliable studies on ethanol intoxication for wild mammals (Dudley 2004) and few for birds (e.g., Fitzgerald et al. 1990). Elephants clearly do have a taste for alcohol (Siegel and Brodie 1984), which can have deleterious effects on their behavior (e.g., http://news.bbc.co.uk/2/hi/south_asia/3423881.stm). There are numerous accounts of elephants becoming dangerously intoxicated after accessing stores of wine or beer in Assam and Bengal in India (e.g., "Elephants Rampage, Trample 5 in India," *Los Angeles Times*, January 1, 1985, sec. 1). The legend of the elephant and the marula fruit was explored by Siegel (1989) without a clear outcome. Yet the popular press seems convinced; for example, "What does it take to get an elephant drunk? Not much, apparently: A few bites of the fruit of the marula tree seems to do the trick … the fruit that leads elephants to shake down marula trees" (Graves 2002). Can marula fruit really drive elephants to such exertions? So compelling, it seems, is the idea of drunken elephants that the suggestion appears in scholastic works (e.g., p. 196 of Sukumar 2003) and embellishes press reports (Yoon 2004).

Nonetheless, various animals may seek out alcohol (Dominy 2004) and use it in sensing and selecting between different qualities of fruit. How likely, then, is it that African elephants can truly be intoxicated from eating marula fruit? Do elephants even eat the fruit of the marula tree, is an elephant capable of becoming intoxicated by alcohol, and is there sufficient naturally occurring alcohol in the fruit?

The Marula as an Elephant Food Item

The marula is a dioecious tree in deciduous savannahs of southern Africa and is a member of the mango family (Anacardiaceae) with an important role in local tribal cultures (Coates Palgrave 1993). The tree is considered to have healing qualities (e.g., Eloff 2001; Grace et al. 2003; Steenkamp 2003; Ojewole 2004), and the fruits are a source of protein and vitamins. These fruits are traditionally fermented by the local people to produce marula wines. The marula is of economic importance (e.g., Shackleton 2002), but what of the ecology? Many species rely on *Sclerocarya birrea* as a food source or as a host, in the case of some parasitic plants and the larvae of some species of Lepidoptera (Kroon 1999). Several herbivorous mammals browse the marula tree, including the giraffe and the rhinoceros, but the African elephant has a close affiliation with the species (Gadd 2002; Jacobs and Biggs 2002*a*, 2002*b*).

Elephants can both browse and graze (Clemens and Maloiy 1982). During the growing season, food is more abundant and, early on, of higher nutritional value, but during the dormant season, trees often shed their leaves. It is during the start of this period of lower-quality food that fruits and seedpods can become an important carbohydrate source (Owen-Smith 1988). The large extent to which elephants destructively feed on the bark and branches of marula (*S. birrea*) was a major limiting factor on the marula tree population in three South African reserves (Gadd 2002). Lewis (1987) similarly reported that elephants in Zimbabwe had marula as an important part of the diet and that the elephants were an important distributor of marula seeds.

Estimates of daily food intake of elephants range between 1% and 2% of the body mass (Table 5.1 in Sukumar 2003), and feeding requires as much as 60%–75% of the waking hours (Wyatt and Eltringham 1974; Poole 1997). In the dry season, browse makes up 58.6% of daily food intake, herbs (included as a browse material) are 12.8%, and forage is 28.6%. This changes in the wet season, with 20.7% of the daily intake made up of browse, 22.2% of herbs, and 57.1% of forage (collated by Sukumar [2003]). Fruits are normally not the only items that elephants consume in a day, and their availability will be seasonal. However, during fruiting periods, elephants may spend long periods at a particular tree or cluster of trees, literally gorging themselves with ripe fruit (Sukumar 2003). At these times, fruit could become the main constituent of their diet.

Digestive Anatomy and Physiology of Elephants

Anecdotal reports suggest that marula fruit may ferment to alcohol within the digestive system. Elephants are nonruminants and have a hindgut fermentation system consisting of an enlarged cecum and colon to facilitate cellulose digestion (Clemens and Maloiy 1982; for review, see Clauss and Hummel 2005). Sugars within the diet are metabolized by the microflora to volatile fatty acids (Church 1988), making them unavailable to alcoholic fermentation. Rees (1982) suggested a gut passage time of between 21.4 and 46 h and Sukumar (2003) an even shorter time of 12 h. These short times and the digestive efficiency of elephants (Clauss and Hummel 2005) would allow very little further alcoholic fermentation of the fruit sugars to take place. However, any endogenous marula yeasts (see next section) are also ingested and could, together with the endogenous flora, support continued fermentation of fruit sugars once the digesta enters the hindgut, although this would also be rapidly fermented to fatty acids and methane. Thus, some limited ethanol production may occur on diets rich in appropriately ripe fruit, although cecal fermentation also depends on diet (Maloiy and Clemens 1991). However, elephants drink up to 225 L of water each day (Poole 1997). Regular or recent drinking will dilute the gut contents, but elephants can go without drinking for up to 4 d. Elephants usually drink at night and at midday, directly after the peak feeding periods of early morning and late evening (Guy 1976; Clemens and Maloiy 1982, referring to Douglas-Hamilton 1973; Katugaha et al. 1999).

Can the Fruit of the Marula Become Sufficiently Alcoholic?

Elephant intoxication relies on the assumption that the marula fruits contain a significant amount of alcohol. If they do, yeast spores must find their way onto the skin of the fruits and begin the fermentation process while the fruits are still on the branch, because it is from there that the elephants feed upon them. Siegel (1989) appears in no doubt that the alcoholic content of the fruit can become as high as 7%, but there appear to be no other data to support this high level. Empirical studies of alcohol content in naturally fermenting fruit are surprisingly few (Levey 2004). Yeast, including *Saccharomyces*, occur in a variety of fruits (e.g., Tang et al. 2003) but will produce ethanol only when protected from O_2 within the body of large fruits (Levey 2004). Microorganisms isolated from ripe marula fruits include at least three species of *Hansenula* (Okagbue and Siwela 2002); the presence of members of the Saccharomycetaceae, and thus spontaneous fermentation, in marula fruit is at least possible. Eriksson and Nummi (1982), Dudley (2002), Dominy (2004, table 1), and Sánchez et al. (2004) report a range of ethanol from 0.04% to 0.72% in the fruit of 18 species, considerably below the 7% of Siegel (1989). However, Dudley (2004) reported the pulp of overripe palm fruits (*Astrocaryum standleyanum*) to contain up to 4.5% ethanol.

The brewing of marula beer requires leaving the juice to ferment naturally for 3–4 d with endogenous yeasts; no other strains are incorporated, as in commercial brewing, which may allow faster fermentation and higher alcohol content (Morrissey et al. 2004). Thus, on one view, it may be possible that the alcoholic content of a fallen marula fruit with naturally fermented sugars could perhaps reach the lower end of the range of alcohol of marula beer (3%). Temperature is important in the process of fermentation. *Sclerocarya birrea* is endemic to southern Africa (Nerd and Mizrahi 2000) and has a fruiting period from January to March (ambient temperatures of 26°–28°C). This range is at the high end of temperatures used in commercial fermentation, and preferential temperatures used for production of marula wines are around 15°C (Fundira et al. 2002).

Ethanol Intoxication in Wild Elephants

The amount of alcohol required to intoxicate an elephant can, potentially, be determined by extrapolation. In humans, approximately 20% of ingested ethanol is absorbed immediately in the stomach, with further and slower absorption in the stomach and duodenum, although this depends on fasting state (e.g., Cortot et al. 1986; Jones et al. 1997; Fig. 1). Ethanol quickly distributes itself throughout the body water space, reaching peak concentrations under fasting conditions at approximately 1 h after consumption (Fig. 1). The ethanol is metabolized over the next few hours. There appear to be no data for the relative activity of alcohol dehydrogenase (ADH) in elephants, but in three bird species, Prinzinger and Hakimi (1996) found the highest ADH activity in the frugivorous species. Further evidence that ADH activity is related to the propensity to frugivory is scarce, and consequently, Dudley (2004) cites evidence from *Drosophila*, in which the mechanisms of inebriation are similar to those in vertebrates (e.g., Moore et al. 1998; Wolf and Heberlein 2003). Flies lacking functional ADH are rendered drunk by an alcohol concentration of 5%, and there appears to be a correlation between developmental ethanol exposure, enzyme activity, and ethanol resistance (e.g., Ashburner 1998; Fry 2001; Fry et al. 2004). Given the evidence of elephants feeding on fruit likely to contain at least some ethanol, there is no reason to assume that their ADH levels are especially low. However, should ADH activity prove to be especially low, then there remains the possibility that relatively lower ethanol doses may

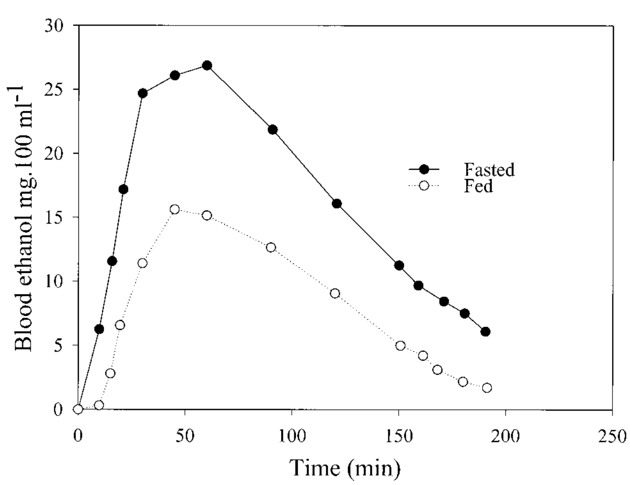

Figure 1. Blood alcohol content as milligrams per 100 mL in healthy human males when fasted (*solid symbols*) or fed (*open symbols*). Dosage was 0.30 g kg^{-1} body mass. Data abstracted from Jones et al. (1997). 10 mg 100 $mL^{-1} \approx 0.1$ g kg^{-1}.

be intoxicating; but this would necessarily contradict the required doses for elephant intoxication provided by Siegel and Brodie (1984; see next section). The likelihood of inebriation in elephants can also be interpolated from their ecological circumstances, and here we present models for both extrapolation and interpolation.

Model 1: Extrapolation by Scaling from Homo sapiens *to Ecophysiological Reality*

Adult African elephants range from 5,500 to 6,000 kg in males and from 2,500 to 3,000 kg in females (Owen-Smith 1988; Shoshani 1992; Poole 1997). In humans, a blood alcohol content (BAC) of approximately 0.15 g 100 mL^{-1} is likely to produce overt intoxication effects. Thus, a 70-kg human would need to consume approximately 90 mL of ethanol (12 mL of ethanol results in a BAC of 0.02 g 100 mL^{-1}) to acquire this level of BAC (Garriott 1988, 2003). Proportional scaling to the mass of elephants would produce a figure of 3.87 L of ethanol, or >55 L of 7% ethanol. However, human and elephant metabolism should scale to a power of ~0.75 ($M^{0.738}$; Kleiber 1961). Failure to account for scaling contributed in part to the controversial massive overdosage and death of an elephant into which West et al. (1962) injected 297 mg of LSD (Spinage 1994). Scaling from humans and accounting for metabolic rate would have reduced this to less than 4 mg. Thus, on the basis of cellular metabolic rate, the amount of alcohol required to intoxicate elephants may be relatively less, reducing the 55 L of 7% ethanol to closer to 10 L. There are no directly relevant data for rates of alcohol metabolism.

Inebriation of elephants was determined by Siegel and Brodie (1984) to occur at a BAC of 0.05–0.1 g 100 mL^{-1}. The highest likelihood for intoxication can be estimated using blood volume alone, since in humans the degree of impairment is directly proportional to BAC (Garriott 1988, 2003). With an approximate blood volume of 7% of body mass (Cameron et al. 1999), a 70-kg person possesses 4.9 kg of blood. In elephants, the blood mass is less, approximately 3.5% of body mass (Shoshani 1992), and thus a 3,000-kg elephant circulates 105 kg of blood. A 90-mL dose of ethanol raises human BAC to 0.15 g 100 mL^{-1}, a level for which an elephant would proportionately require 1,900 mL of ethanol (cf. 0.05–0.1 g 100 mL^{-1}; Siegel and Brodie 1984).

Marula trees produce up to 8,000 fruits, each 42 g and approximately 3.5 cm in diameter (Lewis 1987). Elephants are capable of consuming around 1%–2% of their body mass per day (Clemens and Maloiy 1982; Owen-Smith 1988). Thus, a 3,000-kg elephant might therefore eat at least 30 kg of fruit in one day (assuming it consumed only marula fruit; see next section), or approximately 714 individual fruits.

Thus, accepting that the unlikely estimate of 7% ethanol in marula fruit (Siegel 1989) can be achieved, if the required 1.9 L of ethanol were diluted to a concentration of 7%, the resulting volume would be ~27 L. Further assuming, rather unrealistically, that the alcohol remained in the bloodstream throughout the day, then each fruit would need to contain 38 mL of the 7% ethanol solution to produce intoxication. This volume is impossible to accommodate inside the average fruit, which has a volume of ~22 mL, including the large kernel (~1.7-cm diameter; Glew et al. 2004). Local marula wine production requires at least 200 fruits to make 1 L of alcoholic beverage (Mathonsi 1999).

These calculations were highly biased in favor of "drunken" elephants. Any alcoholic effects would be mitigated by the metabolism of the alcohol during the day, and the model also assumed all the fruits ingested would be overripe and in an advanced stage of fermentation (cf. Dudley 2004). Because of the bias in the model toward inebriation, it seems impossible that all, if any, of these conditions can be met; thus, drunken elephants seem highly improbable.

Model 2: Interpolating from Ecological Reality to Elephant Mass

Relative densities of the marula tree *Sclerocarya birrea* ranged from 2% to 35% over 28,000 hectares in three game reserves in South Africa (Gadd 2002); of these, 38% were fruiting. Together with data for likely elephant movement, these values allow a projection of the number of trees and fruit an elephant will be able to access. This model requires a solitary animal, maximizing the marula fruit component of the diet but having drunk little or no water for a number of days.

An approximate density of marula trees can be derived as 13.66 ha^{-1} (Gadd 2002). A complete understanding of the elephant foraging strategy has yet to be attained (see factors listed by Sukumar [2003], p. 217), but assuming equal distribution of trees at ~13 ha^{-1}, an optimized model can be devised. In this scenario, the elephant can visit homogeneously spaced trees within that 1 ha by covering a distance of approximately 430 m. Guy (1976) suggested that elephants spend between 16.4% and 19% of the day walking, and employing the average distance traveled (~11.5 km d^{-1}; maximum 38.6 km; Wyatt and Eltringham 1974), an elephant could visit up to 345 trees a day. Of these trees, 38% could potentially be in fruit (Gadd 2002), giving a figure of 131 trees that the elephant visits being in fruit. Fruit production by the marula tree gave an average yield of 36.8 kg (Shackleton 2002). Thus, if just 1% of this fruit were accessible (i.e., ripe), the elephant could access 48 kg of fruit in one day, which is close to the 1%–2% of body mass that the elephants must consume each day. If an elephant consumes 2% of its body mass in fruit, and assuming 3% of this fruit to be alcohol, the model grants access to an ethanol dose of 0.6 g kg^{-1}. In fed humans, a dose of 0.3 g kg^{-1} resulted in a maximum BAC of 15 mg 100 mL^{-1}, and even accounting for scaling, the 0.6 g kg^{-1} is insufficient to permit inebriation based on the 50–100 mg 100 mL^{-1} estimate of Siegel and Brodie

(1984). To achieve this dose estimate, this model omits the time required for actually harvesting the fruit, assuming instead that this occurs while the elephant is slowly moving. In addition, elephants eat a varied diet and not entirely alcoholic marula fruit.

Ethanol assimilation is not 100% efficient or instantaneous. Furthermore, should an elephant consume purely fruit as its forage material in addition to browse (43%), which is unlikely (Sukumar 2003), the fruit would constitute approximately half the total daily diet. With a 3% ethanol content and assuming 100% absorption efficiency with zero ADH activity, this would result in ~0.34 g kg^{-1} body mass assimilated. Furthermore, the kernel of the marula would occupy 2.6 cm^3 (Glew et al. 2004). Thus, the potential ethanol entering the elephant is reduced by a further 11%, to ~0.3 g kg^{-1}, and is substantially less than that required to reach the figure of Siegel and Brodie (1984). On this basis, it is highly unlikely that an elephant would become inebriated.

Conclusion

Both the extrapolative and interpolative models were constructed to maximize the likelihood of inebriation, but neither was able to convincingly support this conclusion. When fruit are available, elephants may feed on them to the exclusion of other items (White et al. 1993) and feed to excess (Sukumar 2003), but even so, inebriation is highly unlikely. Other variables include access to fruit and the rate of alcohol clearance in elephants. Lone individuals (usually bulls; Katugaha et al. 1999) will have relatively greater access to marula fruit. While it must be concluded that elephants likely cannot become sufficiently intoxicated by the fruits of the marula, physiological knowledge of how elephants deal with alcohol is practically nonexistent. Unregulated behavior of elephants in the field and as featured in Zulu accounts may be due to an intoxicant other than alcohol. For example, the bark of marula is home to beetle pupae traditionally used by the San people to poison their arrow tips (e.g., Mebs et al. 1982). Marula fruit are extraordinarily high in some vitamins, including nicotinic acid (niacin/vitamin B_3; SEPASAL [Survey of Economic Plants for Arid and Semi-Arid Lands], Royal Botanic Gardens, Kew, http://www.rbgkew.org.uk/ceb/sepasal/birrea.htm), and large doses may cause overt effects. Furthermore, unexpectedly aggressive behavior is most often reported for bull elephants, and if the marula fruit is a prized food item, then the observed behavior may simply be defense of that valued food source.

Field data are few, but a study by Mathonsi (1999) found that approximately 90% of the marula fruits were passed without being "squeezed, squashed or processed in any way." While keeping the fruit whole might allow fermentation to persist, protected within the fruit body, it seems very unlikely that the elephants truly access all of the fruit content. Furthermore, elephants show a distinct preference for fruit still on the tree rather than those ripening on the ground. It is improbable that enough of the fruit on the tree could simultaneously achieve sufficiently alcoholic status, although an elephant may select those that do. Assuming that all other model factors are in favor of inebriation, then intoxication would minimally require that the elephant avoids drinking water and consumes a diet of only marula fruit at a rate of at least 400% normal maximum food intake and with a mean alcohol content of at least 3%. On our analysis, this seems extremely unlikely.

Elephants display many behavioral characteristics viewed as positive traits in humans, often causing us to identify with them in anthropocentric ways. Thus, like beauty, it seems that the tipsy pachyderm may exist in the "eye of the beholder," a view bolstered perhaps by a mutual desire for the fruits of the marula tree?

Acknowledgments

We thank the reviewers, who helped straighten up some befuddled points and kindly pointed us in the direction of further historical anecdotes. We also thank the delegates to the Ithala 2004 meeting in Africa, who further fermented the tale of drunken elephants and stirred us to this analysis, and the many hundreds of elephants we have observed throughout Africa, some very angry but not one of which has ever appeared to be intoxicated.

Literature Cited

Alexander S. and C. de B. Webb, eds. 1990. Adulphe Delegorgue's Travels in Southern Africa. Translated by F. Webb. Vol. 1. University of KwaZulu-Natal Press, Pietermaritzburg.

Ashburner M. 1998. Speculations on the subject of alcohol dehydrogenase and its properties in *Drosophila* and other flies. Bioessays 20:949–954.

Cameron J., R. Grant, and J. Skofronick. 1999. Physics of the Body. 2nd ed. Medical Physics, Madison, WI.

Church D.C. 1988. The Ruminant Animal: Digestive Physiology and Nutrition. Prentice Hall, Englewood Cliffs, NJ.

Clauss M. and J. Hummel. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. Mammal Rev 35:174–187.

Clemens E.T. and G.M.O. Maloiy. 1982. The digestive physiology of three East African herbivores: the elephant, rhinoceros and hippopotamus. J Zool (Lond) 198:141–156.

Coates Palgrave K. 1993. Trees of Southern Africa. Struik, Cape Town.

Cortot A., G. Jobin, F. Ducrot, C. Aymes, V. Giraudeaux, and R. Modigliani. 1986. Gastric emptying and gastrointestinal absorption of alcohol ingested after a meal. Dig Dis Sci 31: 343–348.

Dennis J.V. 1987. If you drink, don't fly: fermented fruit and sap can inebriate birds! Birder's World 1:15–19.

Dominy N.J. 2004. Fruits, fingers, and fermentation: the sensory cues available to foraging primates. Integr Comp Biol 44:295–303.

Douglas-Hamilton I. 1973. On the ecology and behaviour of the Lake Manyara elephant. E Afr Wildl J 11:401–403.

Dudley R. 2000. Evolutionary origins of human alcoholism in primate frugivory. Q Rev Biol 75:3–15.

———. 2002. Fermenting fruit and the historical ecology of ethanol ingestion: is alcoholism in modern humans an evolutionary hangover? Addiction 97:381–388.

———. 2004. Ethanol, fruit ripening, and the historical origins of human alcoholism in primate frugivory. Integr Comp Biol 44:315–323.

Dudley R. and M. Dickinson. 2004. The comparative biology of ethanol consumption: an introduction to the symposium. Integr Comp Biol 44:267–268.

Eloff J.N. 2001. Antibacterial activity of marula (*Sclerocarya birrea* (A. rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro) (Anacardiaceae) bark and leaves. J Ethnopharmacol 76:305–308.

Eriksson K. and H. Nummi. 1982. Alcohol accumulation from ingested berries and alcohol metabolism in passerine birds. Ornis Fenn 60:2–9.

Fitzgerald S.D., J.M. Sullivan, and R.J. Everson. 1990. Suspected ethanol toxicosis in 2 wild cedar waxwings. Avian Dis 34: 488–490.

Fry J.D. 2001. Direct and correlated responses to selection for larval ethanol tolerance in *Drosophila melanogaster*. J Evol Biol 14:296–309.

Fry J.D., C.M. Bahnck, M. Mikucki, N. Phadnis, and W.C. Slattery. 2004. Dietary ethanol mediates selection on aldehyde dehydrogenase activity in *Drosophila melanogaster*. Integr Comp Biol 44:275–283.

Fundira M., M. Blom, I.S. Pretorius, and P. van Rensburg. 2002. Selection of yeast starter culture strains for the production of marula fruit wines and distillates. J Agric Food Chem 50: 1535–1542.

Gadd M. 2002. The impact of elephants on the marula tree *Sclerocarya birrea*. Afr J Ecol 40:328–336.

Garriott J.C. 1988. Medicolegal Aspects of Alcohol Determination in Biological Specimens. PSG, Littleton, MA.

———. 2003. Medical-Legal Aspects of Alcohol. 4th ed. Lawyers and Judges, Tucson, AZ.

Glew R.S., D.J. VanderJagt, Y.-S. Huang, L.-T. Chuang, R. Bosse, and R.H. Glew. 2004. Nutritional analysis of the edible pit of *Sclerocarya birrea* in the Republic of Niger (daniya, Hausa). J Food Compos Anal 17:99–111.

Grace O.M., H.D.V. Prendergast, A.K. Jager, and J. van Staden. 2003. Bark medicines used in traditional healthcare in KwaZulu-Natal, South Africa: an inventory. S Afr J Bot 69: 301–363.

Graves E. 2002. Spirits: out of Africa. Food and Wine (June). http://www.foodandwine.com/articles/spirits:-out-of-africa.

Guy P.R. 1976. Diurnal activity patterns of the elephant in the Sengwa area, Rhodesia. E Afr Wildl J 14:285–295.

Jacobs O.S. and R. Biggs. 2002*a*. The status and population structure of the marula in the Kruger National Park. S Afr J Wildl Res 32:1–12.

———. 2002*b*. The impact of the African elephant on marula trees in the Kruger National Park. S Afr J Wildl Res 32:13–22.

Jones A.W., K.A. Jonsson, and S. Kechagias. 1997. Effect of high-fat, high-protein, and high-carbohydrate meals on the pharmacokinetics of a small dose of ethanol. Br J Clin Pharmacol 44:521–526.

Katugaha H.I.E., M. de Silva, and C. Santiapillai. 1999. A long-term study on the dynamics of the elephant (*Elephas maximus*) population in Ruhuna National Park, Sri Lanka. Biol Conserv 89:51–59.

Kleiber M. 1961. The Fire of Life: An Introduction to Animal Energetics. Wiley, New York.

Kroon D.M. 1999. Lepidoptera of Southern Africa: Host Plants and Other Associations: A Catalogue. Lepidopterists' Society of Africa, Jukskei Park.

Levey D.J. 2004. The evolutionary ecology of ethanol production and alcoholism. Integr Comp Biol 44:284–289.

Lewis D. 1987. Fruiting patterns, seed germination, and distribution of *Sclerocarya caffra*. Biotropica 19:50–56.

Maloiy G.M.O. and E.T. Clemens. 1991. Aspects of digestion and *in vitro* fermentation in the caecum of some East African herbivores. J Zool (Lond) 224:293–300.

Mathonsi S. 1999. The myth of intoxication by marula fruit in the diet of the African elephant. Ecol J 1:56.

Mebs D., F. Bruning, N. Pfaff, and H.D. Neuwinger. 1982. Preliminary studies on the chemical properties of the toxic principle from *Diamphidia nigroornata* larvae, a source of Bushman arrow poison. J Ethnopharmacol 6:1–11.

Milton K. 2004. Ferment in the family tree: does a frugivorous dietary heritage influence contemporary patterns of human ethanol use? Integr Comp Biol 44:304–314.

Moore M.S., J. DeZazzo, A.Y. Luk, T. Tully, S.M. Singh, and U. Heberlein. 1998. Ethanol intoxication in *Drosophila*: genetic and pharmacological evidence for regulation by the cAMP signaling pathway. Cell 93:997–1007.

Morrissey W.F., B. Davenport, A. Querol, and A.D.W. Dobson. 2004. The role of indigenous yeasts in traditional Irish cider fermentations. J Appl Microbiol 97:647–655.

Nerd A. and Y. Mizrahi. 2000. Introduction of marula, an unexploited fruit tree from southern Africa, to the Israeli Negev. Isr J Plant Sci 48:217–222.

Ojewole J.A.O. 2004. Evaluation of the analgesic, anti-inflammatory and anti-diabetic properties of *Sclerocarya birrea* (A. rich.) Hochst.: stem-bark aqueous extract in mice and rats. Phytotherapy Res 18:601–608.

Okagbue R.N. and M. Siwela. 2002. Yeasts and related microorganisms isolated from ripe marula fruits (*Sclerocarya caffra*) in Zimbabwe. S Afr J Sci 98:551–552.

Owen-Smith R.N. 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge.

Poole J. 1997. The Elephants. 2nd ed. Colin Baxter Photography, Grantown-on-Spey.

Prinzinger R. and G.A. Hakimi. 1996. Alcohol resorption and alcohol degradation in the European starling *Sturnus vulgaris.* J Ornithol 137:319–327.

Rees P.A. 1982. Gross assimilation, efficiency and food passage time in the African elephant. Afr J Ecol 20:193–198.

Sánchez F., C. Korine, B. Pinshow, and R. Dudley. 2004. Possible roles of ethanol in the relationship between plants and frugivores: first experiments with Egyptian fruit bats. Integr Comp Biol 44:290–294.

Shackleton C. 2002. Growth and fruit production of *Sclerocarya birrea* in the South African lowveld. Agrofor Syst 55:175–180.

Shoshani J. 1992. Elephants: Majestic Creatures of the Wild. Rodale, Emmaus, PA.

Siegel R.K. 1989. Intoxication: Life in Pursuit of Artificial Paradise. Dutton, New York.

Siegel R.K. and M. Brodie. 1984. Alcohol self-administration by elephants. Bull Psychon Soc 22:49–52.

Spinage C. 1994. Elephants. Poyser, London.

Steenkamp V. 2003. Traditional herbal remedies used by South African women for gynaecological complaints. J Ethnopharmacol 86:97–108.

Sukumar R. 2003. The Living Elephants: Evolutionary Ecology, Behaviour and Conservation. Oxford University Press, Oxford.

Tang A.M.C., K.D. Hyde, and R.T. Corlett. 2003. Diversity of fungi on wild fruits in Hong Kong. Fungal Divers 14:165–185.

West L.J., C.M. Pierce, and W.D. Thomas. 1962. Lysergic acid diethylamide: its effect on a male Asiatic elephant. Science 138:1100–1102.

White L.T.J., C.E.G. Turin, and M. Fernandez. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. Afr J Ecol 31:181–199.

Wolf F.W. and U. Heberlein. 2003. Invertebrate models of drug abuse. J Neurobiol 54:161–178.

Wyatt J.R. and S.K. Eltringham. 1974. The daily activity of the elephant in the Rwenzori National Park Uganda. E Afr Wildl J 12:273–289.

Yoon C.K. 2004. "Of drunken elephants, tipsy fish and scotch with a twist." *New York Times*, March 23, late edition–final, sec. F.