Short Communication

A PERVASIVE TYPOGRAPHICAL ERROR IN AN EQUATION FOR CALCULATING NECTAR DENSITY IS LIKELY TO HAVE LIMITED CONSEQUENCES

Hamish A Symington[1,]*, Joris Rockx[2]

[1]*Department of Plant Sciences, University of Cambridge, UK*
[2]*School of Agriculture, Policy and Development, University of Reading, Reading, UK*

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*Corresponding author: has27@cam.ac.uk

Abstract—Analysis of floral nectar reward often involves converting nectar volume to sugar mass. Nectar density depends on nectar sugar concentration, and has been empirically measured. A quadratic equation which accurately models sucrose density over a range of concentrations was published in a book in 1987. This equation was restated in a publication in 2001, but with a typographical error transposing two digits in the coefficient of the linear term. The incorrect equation has been used in numerous studies since its publication, including in the generation of large datasets. However, the error in density introduced by the incorrect equation is never more than 0.5%, which is greatly smaller than the standard deviation in published floral measurements of nectar volumes and concentrations. The error is therefore likely to have limited consequences, but we recommend using the more accurate equation for future studies. While exploring this error we found several others, some of which affect reported data and some of which are simple typographical errors introduced while preparing a manuscript. We caution authors to be scrupulous in reporting units and equations relating to nectar measurement.

Keywords—Density, nectar, sucrose, refractometer, typographical error

INTRODUCTION

The mass of sugar available to nectar-feeding insects is an important metric for quantifying floral resource. This is because nectar sugar mass directly correlates to nectar energetic content; sugar mass can therefore be thought of as a currency in the 'economic payroll transaction' of pollination (Willmer 2017, p235). The sugar available in flower assemblages can be calculated by referring to large datasets which give empirical data on nectar sugar production for assorted plant species (e.g. Baude et al. 2016; Flo et al. 2018; Tew et al. 2023).

Nectar sugar mass depends on the volume, density and sugar concentration of the nectar in question. The relationship between sucrose concentration and solution density is not linear. The density of numerous concentrations of sucrose solution has been experimentally measured (Rumble 2024) and modelled as a quadratic equation (see Equation 1, from Prŷs-Jones & Corbet 1987, p74, republished in 1991 and 2011) which between concentrations of 0 and 84% w/w 'gives an estimate of density to within 0.05% of the values given in Weast (1978)'. This equation has been used by ecologists and pollination researchers to convert nectar volume and concentration measurements to sugar mass.

In 2001, a temporal and species-based catalogue of nectar production in British plants was published (Corbet et al. 2001). In this study, the authors restated Equation 1, but two digits were transposed in the coefficient of the linear term (see Equation 2).

$d = 0.0037291C + 0.0000178C^2 + 0.9988603$ [Equation 1; d = solution density (g cm^3); C = sucrose concentration (% w/w)]

$d = 0.0037\mathbf{92}1C + 0.0000178C^2 + 0.9988603$ [Equation 2]

Various studies use either Equation 1 (e.g. Tan 2008; Pattrick et al. 2023; Zhou et al. 2024) or Equation 2 (e.g. Baude et al. 2016; Tew et al. 2023). Clearly, one equation will give results closer to the empirical data than the other; this study aims to identify which equation should be used in future studies, and the extent of the issues introduced by use of the incorrect equation in historical studies.

MATERIALS AND METHODS

Concentration-specific densities were calculated according to Equation 1 and Equation 2, then the percentage errors from empirical data (Rumble 2024) were calculated using R (v4.4.2, R Core Team 2024) and plotted using ggplot (Wickham 2016) (see Fig. 1). The percentage error of the results of Equation 2 was then modelled as a cubic equation (Equation 3) using the lm function in R, and plotted (see Fig. 2). This model was used to quantify errors as described below.

To identify studies using the incorrect equation, a systematic literature search was conducted in Google Scholar and Scopus. Search terms were either a) a citation of Corbet et al. 2001, b) the phrase 0.0037921C, c) the phrase 0.9988603. Results were limited to peer-reviewed studies; books, theses and technical reports were filtered. The resulting 101 studies were then inspected and those which made reference to findings of Corbet et al. 2001 but not to the calculation of nectar density, or which used the correct version of the equation (i.e. Equation 1) were removed.

Data from Tew et al. 2023 were used to quantify the effect of the error. Because individual volumetric measurements for each flower were not reported in that study, we were unable to use the correct equation to calculate individual nectar sugar masses for each measurement; instead, Equation 3 was used to calculate the percentage error in nectar density for species for which a mean nectar sugar concentration was reported. These percentage errors were used to calculate absolute values for the error in nectar sugar.

RESULTS

A plot of concentration vs percentage error in predicted density values from empirical clearly shows that Equation 1 is correct and that Equation 2 is a poorer fit to the empirical data (Fig. 1).

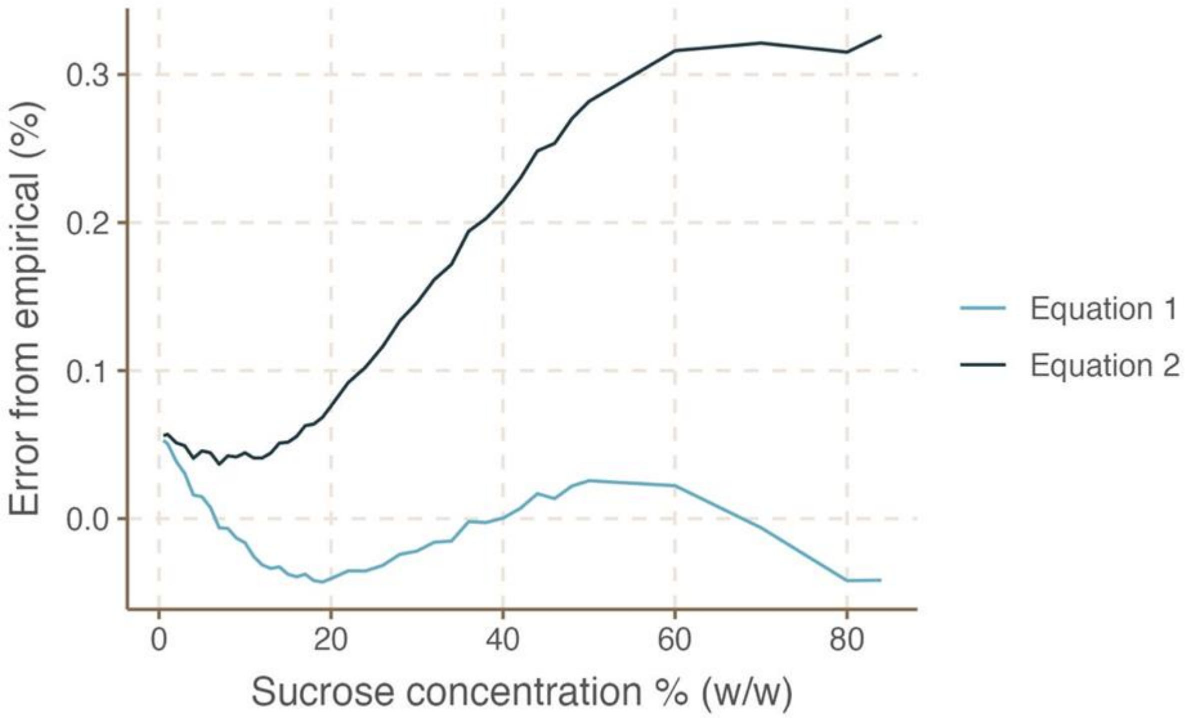

Figure 1: Line plot of percentage error from empirical values vs concentration (% w/w) for density values predicted by Equation 1 (pale blue) and Equation 2 (dark blue). Equation 1 (from Prŷs-Jones & Corbet 1987) is closer to the empirical values for all concentrations. While Equation 1 is, as stated by the authors, within ±0.05% of empirical values, Equation 2 always overestimates density, to a maximum of 0.326% of empirical observations at 84% w/w sucrose.

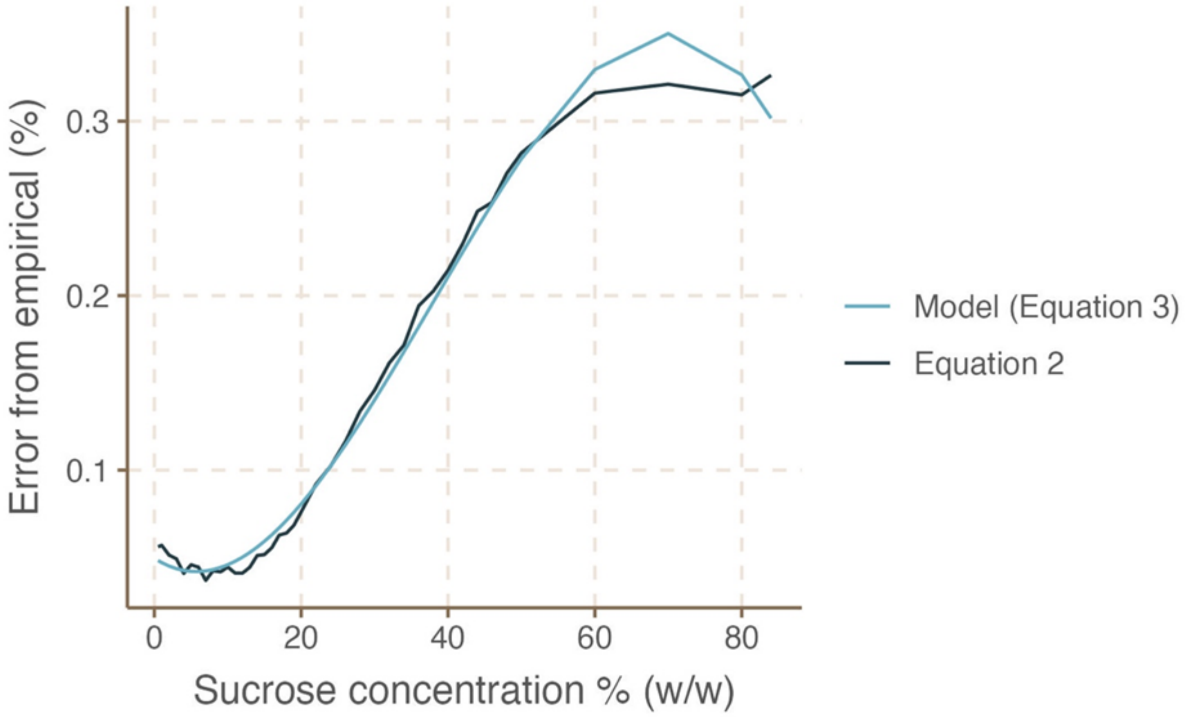

Figure 2. Line plot showing percentage error in density values vs concentration (% w/w) for densities calculated using Equation 2 (pale blue), and those predicted by Equation 3, a cubic model of those errors (dark blue).

Equation 3 models the error between Equation 2 and empirical data with an adjusted R-squared value > 0.99 (see Fig. 2).

error = 0.0004951 – 0.00002762C + 0.000002619C^2 – 0.00000002301C^3 [Equation 3; C = sucrose concentration (% w/w)]

It was not always possible to identify studies which used the incorrect equation for calculating nectar density, as some (e.g. Chittka & Schürkens 2001) stated sugar mass without stating the method by which it had been calculated. In such studies, it cannot be assumed that such an equation was used: some measure nectar sugar by other methods, such as liquid chromatography-mass spectrometry (as clearly described by e.g. Pavlik et al. 2018). However, the incorrect equation was stated in 14 studies (listed in Table 1). Additionally, four studies stated incorrectly copied versions of the incorrect equation, which could introduce a different error (see Table 1).

To identify the potential effects of the transposition error we used data from Tew et al. 2023, which reports nectar concentration and nectar sugar mass (calculated using the incorrect equation) for 102 taxa. Because individual volumetric measurements were not reported in that study, we could not use the correct equation to individually calculate nectar sugar content. Instead, we used Equation 3 to estimate the errors in mean nectar sugar mass. We estimated the largest absolute error in mean nectar sugar mass per flower as 21.43 µg (*Iris virginica*). For this species, the mean nectar sugar concentration is 25.95% (w/w), and the mean sugar mass given by the authors is 18799.40 µg, with a standard deviation of 8732.63 µg: the estimated error in sugar mass due to the use of the incorrect equation is 0.11% of mean, and less than 0.25% of standard deviation. Across all species in this study for which concentration was empirically measured, the mean estimated error in sugar mass was 0.30% of standard deviation, with the maximum estimated error in sugar mass being 0.90% of standard deviation (*Phacelia tanacetifolia*; reported mean sugar mass 469.27 µg; standard deviation 176.26 µg; reported mean nectar sugar concentration 62.05% w/w; standard deviation 8.22% w/w). It is therefore reasonable to conclude that variation in

Table 1: studies which report the use of an incorrect equation to calculate nectar sugar mass. As described in this manuscript, these errors are likely to be negligible, or are unlikely to affect the broad conclusions of these studies. We do not call the methodology of these studies into question, only the reporting of nectar sugar mass.

Authors	Year	DOI	Notes
Comba et al.	1999	10.1006/anbo.1998.0798	Introduces the same typographical error but is rarely cited for the equation.
Suzuki et al.	2007	10.1007/s11284-006-0010-3	Incorrect linear coefficient (0.0037821)
Suzuki et al.	2009	10.1007/s00265-009-0789-3	Incorrect linear coefficient (0.0037821)
Eberle et al.	2014	10.1371/journal.pone.0113556	
Baude et al.	2016	10.1038/nature16532	
Hicks et al.	2016	10.1371/journal.pone.0158117	
Villamil et al.	2018	10.3389/fpls.2018.01093	Incorrect linear coefficient (0.003791)
Broyles	2019	10.26786/1920-7603(2019)541	Incorrect linear coefficient (0.00379201)
Goulnik et al.	2020	10.1016/j.agee.2020.107033	
Garbuzov et al.	2020	10.1111/icad.12420	
Tew et al.	2021	10.1111/1365-2745.13598	
Torices et al.	2021	10.3389/fevo.2021.589781	
Nicolson et al.	2022	10.1038/s41598-022-20626-5	
Tew et al.	2022	10.1111/1365-2664.14094	
Carisio et al.	2022	10.1111/1365-2435.14210	
Egawa et al.	2023	10.1002/ece3.10441	
Genty et al.	2023	10.1111/oik.10219	
Quinanzoni et al.	2024	10.1016/j.baae.2024.04.006	

measurement dwarfs the error introduced by using the incorrect equation, and therefore that this error is likely to be negligible.

While identifying studies which use the incorrect equation, we discovered that some reported a conversion of nectar volume and sugar concentration to sugar mass using a single equation which models the sugar mass in 1 μL nectar of a given concentration (see Equation 4). This appears to originate in Dafni et al. 2005 (sometimes cited as 'Galetto & Bernadetto 2005', as the authors of the relevant chapter), and has different variations from empirical data from those of Equations 1 and 2. Plotting the percentage error from empirical data of the sugar mass calculated using Equations 1, 2 and 4 (see Fig. 3) shows that Equation 1 is the best fit of the three. For accuracy, we therefore recommend a methodology of calculating nectar density using Equation 1, then using that to calculate sugar mass.

Sugar mass = $0.00226 + 0.00937C + 0.0000585C^2$ [Equation 4; C = sucrose concentration (% w/w)]

We found one study (Guerra et al. 2010) which states the use of a version of Equation 4 with a typographical error in the quadratic coefficient, changing it from $0.0000585C^2$ to $0.000585C^2$ and thereby increasing the contribution of the quadratic component by an order of magnitude. This results in overestimates of sugar mass of 49% at 10% w/w, 96% at 20% w/w, and 214% at 50% w/w. However, this study also reports mean sugar mass calculations consistent with the use of a *correct* version of Equation 4. We therefore believe that this error is purely typographical and does not affect the study's conclusions, but the existence in the literature of an equation which produces highly inaccurate calculations of sugar mass provides a pitfall for other researchers. This incorrect version is also specified in Guerra et al. 2014, but again the reported mean sugar mass calculations are consistent with a *correct* version of equation 4. After an exhaustive literature search, we believe that the only other uses of this incorrect version of Equation 4 have been by Castro et al. 2023 (citing both Dafni et al. 2005 and Guerra et al.

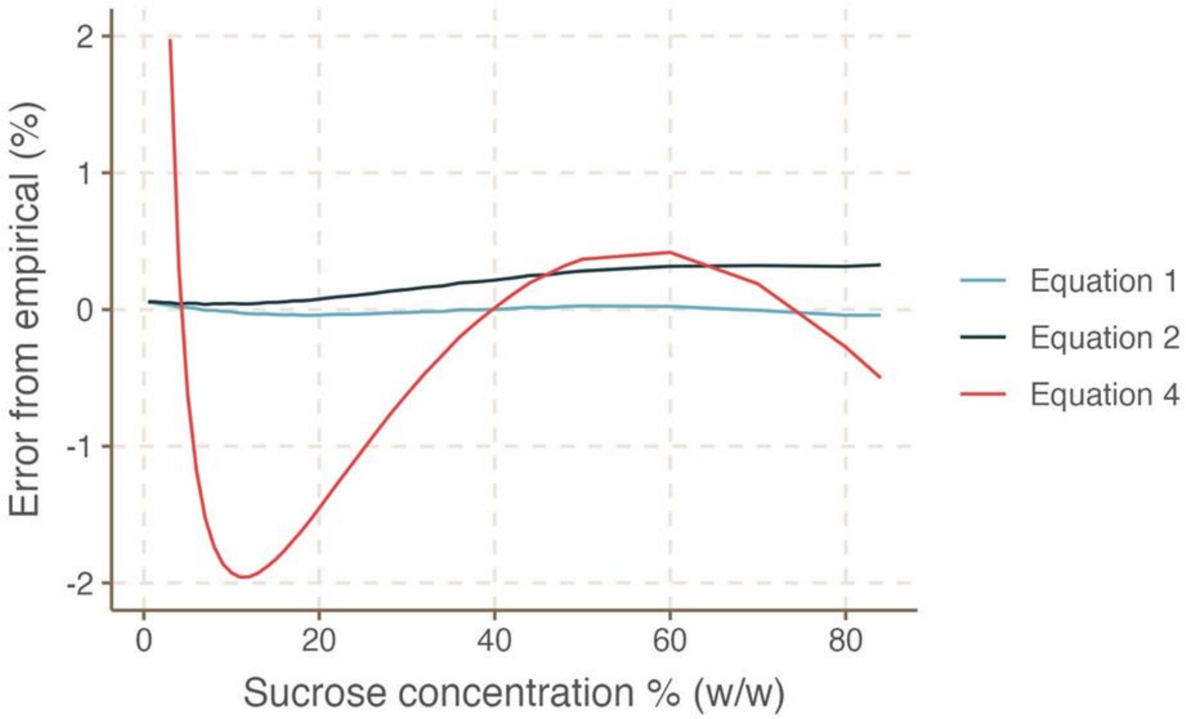

Figure 3. Line plot showing percentage errors in sugar mass vs concentration (% w/w) of Equation 1 (Prŷs-Jones & Corbet 1987), Equation 2 (Corbet et al. 2001) and 4 (Dafni et al. 2005).

2014) and Rogalski et al. 2023 (citing Dafni et al. 2005 and making the same typographical error as Guerra et al. 2010). We do not call the methodology of these studies into question, only the reporting of nectar sugar mass.

Individual nectar measurements were not reported by Castro et al. 2023, so it is impossible to determine whether the error affects the published results; reported percentages in that study ranged from 16.5% (w/w) to 29.4% (w/w), implying that nectar sugar masses could be overestimated by a factor of between 1.8 and 2.4. However, in that study, the pattern of decrease in nectar standing crop appears to be strongly driven by nectar volume, so the effect of any error on the conclusions of this study is likely to be small.

Rogalski et al 2023 similarly do not report individual nectar measurements, so it is impossible to determine whether the error affects the published results; this study reports larger mean nectar volumes and higher mean nectar concentrations. Again, nectar sugar mass appears to be strongly driven by nectar volume, so the broad conclusions of this study are unlikely to be affected.

Some studies compare landscape-scale nectar production at different timepoints (eg Baude et al. 2016). In these cases, because species richness (and therefore the distribution of nectar sugar concentrations) will differ over time, sugar production sums for different timepoints are likely to have different percentage errors. Baude et al. 2016 present England and Wales-scale total nectar data of the order of hundreds of thousands of tonnes; the maximum 0.326% overestimation of nectar sugar mass (from Equation 2) would give a maximum potential error of the order of hundreds of tonnes. Again, standard deviations of nectar measurements of the order of those reported by Tew et al. 2023 will dwarf this error, as will assumptions made while performing calculations to scale up nectar production to landscape scale.

Discussion

We have shown that use of an equation featuring an unfortunate typographical error introduces errors in the calculation of the density of nectar solutions, but that those errors are likely to be negligible. While studies using the incorrect equation will slightly overestimate available reward, it is our opinion that this error does not necessitate a recalculation of these large datasets or reconsideration of conclusions.

Nectar volume and sugar concentration display large variation between flowers on the same plant, between flowers on different plants, and at different times of day (e.g. Bailes et al. 2018; Symington & Glover 2024; and explored in Pacini & Nepi 2007). Variation between samples and inherent error within the sampling processes will be greatly larger than the error introduced by the use of the incorrect equation. Additionally, throughout this manuscript we have assumed a constant temperature of 20 °C. Density is dependent on temperature; the density of a 50% w/v sucrose solution has been empirically measured as 1.19168 g cm^{-3} at 15 °C and 1.18926 g cm^{-3} at 25 °C (Darros-Barbosa et al. 2003). This represents a difference of 0.20% – a similar order of magnitude to the error introduced by use of the incorrect equation. When working in the field to gather measurements of nectar volume and concentration, standardising temperature is impractical, so it is likely that comparable errors will have been introduced due to sampling conditions.

In this report we have not addressed variation in sugar mass caused by differences in the sugar composition of nectar. Refractometer-based studies generally report sugar content as mass-based percentage (% w/w), which amalgamates the sugars glucose, fructose and sucrose, and which does not take into account other metabolites or sugars within the nectar. A given volume of a 40% (w/w) sucrose solution has a different energy content to the same volume of a 40% (w/w) glucose or 40% (w/w) fructose solution (Pattrick et al. 2025), with a % w/w sucrose solution containing nearly 6% more energy than the equivalent volume of glucose or fructose solution. There exists great variation in nectar sugar composition, often linked to pollination syndrome or phylogeny (reviewed by Nicolson 2022). Failing to take the sugar composition of floral nectars into account will therefore introduce further error into nectar sugar mass calculations.

While exploring this particular error, we have encountered other typographical errors in equations, some of which affect calculations and some of which have been introduced during manuscript preparation. The field of nectar biology is not unusual in this regard: a search for 'equation typographical error' in Google Scholar finds about 2,970 studies published since 1 January 2024 contain these words. Many of these are corrigenda, but some are more pervasive, such as (for example) errors in a set of coefficients used to compute unsteady aerodynamic forces (explored by Bueno & Gonçalves 2016). As these authors note, "these errors have contributed to an increased in time wasted by comparing different bibliographical references"; some researchers "might even be wasting some part of their time with incorrect computational implementations".

To improve accuracy and consistency in future studies, we recommend that researchers should use Equation 1 to calculate density, and should then use measured volume to calculate sugar mass. We also echo the suggestions of Pattrick et al. 2025 and encourage researchers to clearly specify methods used for nectar measurement and calculation of sugar mass.

Additionally, while responsible authors work with journals to correct errors in published articles, those corrections are often not recorded in open data repositories used for the circulation of preprints or for authors to self-archive their own work (Bordignon 2025). This creates situations where different versions of the same article exist in different places. When errors in a manuscript are corrected, it is vital that authors ensure that all repositories containing the article are updated.

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AUTHOR CONTRIBUTION

Concept and design HS and JR, data collection HS, data analysis HS and JR, writing HS, edits and approval for publication HS and JR.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available at as supplementary material in the online version of this article: JPE841_Data.csv

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