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Reply to: A caveat about the use of trigonometric functions in statistical tests of Nutritional Geometry models

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REPLYING TO: A. Senior et al.; Scientific Reports https://doi.org/10.1038/s41598-025-90267-x (2025).

Over the past decade, analytical models leveraging the experimental power of the Geometric Framework for nutrition (GF) have advanced significantly in extracting insights from multidimensional data^{1–5}. In a recent study⁶, I introduced the use of Thales' theorem to analyse experimental data on appetite and nutrient intake. While supportive of the concept, Senior et al. (2025)⁷ critiqued my model, highlighting potential misestimations of the standard error and confidence intervals for the angle β . This angle was used to statistically test whether nutrient arrays align with the closest distance optimization (CDO) rule of dietary compromise (see^{6,8} for details).

Using simulations and a reanalysis of the *Drosophila melanogaster* data from my study, Senior et al. $(2025)^7$ demonstrated two key points: (1) heteroscedastic models are required instead of the homoscedastic models I used, and (2) estimates of standard error and confidence intervals for the angle β depend on the proximity to the intake target (IT), that is, the nutrient balance animals select when given a choice. Senior et al. $(2025)^7$ offered heuristic explanations for these findings and suggested that the delta method could improve accuracy when using trigonometric functions. They also emphasised the need for further theoretical development to address these issues comprehensively.

I welcome the engagement of Senior et al. $(2025)^7$ and endorse their call for more theoretical work in nutritional ecology. I was delighted by the delta method's ability to accurately estimate standard errors and confidence intervals, enabling correct statistical inferences with my proposed model. However, an important question remains: why are the angle β estimates influenced by the distance to the IT? While Senior et al. $(2025)^7$ heuristic argument offered valuable insights, I believe further formalisation is needed, and I aim to address that here.

Recall from Morimoto⁶ and the law of cosines that the angle β is calculated as:

$$\beta = \cos^{-1}\left(\frac{s^2 + t^2 - h^2}{2st}\right)$$
(1)

Where *s* is the length between the origin and the average intake of an unbalanced diet *U*, *h* is the length between the origin and the IT, which is also the diameter of the Thales' circle in the method, and *t* is the Euclidean distance between the IT and the intake in the unbalanced diet. Senior et al. (2025) claimed that standard errors are wider as the intake of an unbalanced diet *U* approaches the IT (Fig. 1a). In the GF framework, this happens if diet *U* was designed (purposefully or serendipitously) and used in no-choice experiments with PC ratios near that of the $IT^{8.9}$.

The inverse cosine function $\cos^{-1}(x)$ used in Eq. (1) has domain [-1, 1]. Notice that this function is non-linear in its domain and the absolute magnitude of its gradient increases as the input value x approaches the domain boundaries (i.e. $\frac{d}{dx}\cos^{-1}(x) = -\frac{1}{\sqrt{(1-x^2)}}$). This means that estimates of the angle β will vary proportionally more as x approaches the boundaries, that is, as $x \to \pm 1$. For the sake of argument, let's focus on the case where $x \to 1$, although the logic is the same when $x \to -1$. As the domain interval is closed, let x=1 which means that in Eq. (1), $\cos^{-1}(1)$ when $s^2 + t^2 - h^2 = 2st$. Simplifying this, we find that $\cos^{-1}(1)$ when h = s - t (see Appendix I). To show that estimates of the angle β are more variable, we therefore need to show that as the intake of a diet U approaches the IT, then $h \to s - t$.

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Let's consider a diet *U* that is some distance *y* to the IT as shown in Fig. 1a. With some geometric constructions and projections, we have the following relationships.

$$t^2 = x^2 + y^2$$
 using Pythagoras theorem (2)

$$x'^2 = x^2 + y'^2$$
 using Pythagoras theorem (3)

$$\sin(\alpha) = \frac{y'}{x}$$
 using similarity of triangles (4)

$$s = s' + \delta + x'$$
 by construction (5)

$$(s'+\delta)^2 = h^2 + y^2$$
 using Pythagoras theorem (6)

What happens to these equations when $U \rightarrow \text{IT}$? Another way of stating this is 'what happens when $y \rightarrow 0$?' (Fig. 1a) This means that:

- (a) $t^2 \rightarrow x^2$ which also implies that $t \rightarrow x$ (using Eq. 2)
- (b) $\alpha \to 0$ and $\sin(\alpha) \to \hat{0}$ such that $x' \to \sqrt{0+x^2}$ and $x' \to x$ using Eqs. (3) and (4).
- (c) $\delta \to 0$ as the distance between the horizontal line *y* becomes tangent to the Thales' circle at the IT. This also means that $s \to s' + x'$ in Eq. (5).
- (d) Note that $x' \to x$ (b) and $t \to x$ (a), then $s \to s' + x'$ is equivalent to $s' \to s + t$
- (e) As both δ (above) and y (by definition) \rightarrow 0, Eq. (6) then leads us to $h \rightarrow s'$

(f) Substituting this in (d), we have that as $y \to 0$ then $h \to s - t$, which is what we needed to show that estimates of the angle β become more variable as the intake of diet $U \to IT$.

To show how this looks like within the GF context, I used the software R version $4.3.2^{10}$ to run simulations showing how the standard deviation (which is related to the standard error) of the angle β changes across a GF landscape. For the simulation, I created a mesh which simulated the nutrient intakes across a range of 0 to 10 for both protein (x-axis) and carbohydrates (y-axis). For each point, I added a random noise from a normal distribution using the 'rnorm' function parameters of mean = 0 and standard deviation = 0.2. The IT was set at the coordinates (Protein = 6, Carbohydrate = 6) and as in Senior et al. (2025)⁷, was assumed to be known with perfect knowledge (i.e. no error associated with IT estimates). Figure 1b shows that standard deviation of the angle β indeed increases as the estimates approach the intake target. It also increases next to the origin for the same reasons as mentioned above (Fig. 1b). Having said that, neither I nor Senior et al. (2025)⁷ have a definitive solution to solve the instability of the estimates of the standard errors near the IT when using the Thales' method. While the delta method appears promising as shown by Senior et al. (2025), we still lack a formal study to ascertain its suitability. Thus, until this is done, I agree with Senior et al. (2025)⁷ advice to exercise caution when using the Thales method for statistical inferences. From the simulation, it appears that the effect is symmetric in both x and y-axis which may help approaches such as the multivariate approach of the delta method assuage the effect and improve statistical inferences.

Despite these criticisms, the Thales' method remains a valid even if as a qualitative tool for understanding dietary compromise rules. This is because animals following the CDO rule will by definition have average angle β estimates close to 90°. Figure 1c illustrates angle β estimates within the same noisy landscape, demonstrating the method's utility. As expected, average angle β values increase when the intake of an unbalanced diet (*U*) falls within the Thales' circle, while estimates near the circle approach 90°. Thus, the Thales' method continues to be a valuable approach for evaluating nutrient intake patterns.

An encouraging finding from Senior et al. (2025)⁷ is their reanalysis of the *Drosophila* dataset from Lee et al.¹¹. Using Welch's heteroscedastic models, they concluded that neither equal distance nor CDO fully explains macronutrient regulation in females. This aligns with my original conclusions using the Thales' theorem with a homoscedastic model, where I found that flies follow the CDO rule when diets are protein-rich but deviate from it as diets become carbohydrate-rich (see Figure 2a,b in the original paper)⁶. While this does not suggest fitting an incorrect model, it underscores the overarching value of the Thales' method.

Increased intake variance near the IT may not merely result from statistical artifacts but could reflect underlying biological mechanisms. GF studies suggest that performance landscapes for traits across diets often form 'plateaus' of maximum expression (see e.g.^{3,5,11-14} and others). This implies that individuals might tolerate deviations from their IT without significant fitness costs as long as these deviations remain within the plateau (Fig. 1a). In contrast, larger deviations from IT, taking individuals off the plateau, could act as filters that reduce variance in nutrient intake. Animals feeding closer to the IT might exhibit greater variability in nutrient intake without incurring fitness costs.

This idea aligns with Simpson et al.'s (2004)¹⁵ assumptions that fitness costs increase "continuously and smoothly" with distance from IT. Under these assumptions, animals would optimize their intake to minimize this distance, shaping their nutrient array and performance landscape geometry. Deviations from IT on costly diets (i.e., off of the IT) would be penalised, possibly non-linearly¹⁵, resulting in narrower feeding ranges for animals further from IT. Simpson et al.'s (2004)¹⁵ Figure 5a visually supports this, showing increased errors when dietary intakes neared the plateau. I reanalysed data from Lee et al. (2008)¹¹ which also supports this pattern, particularly for carbohydrates and, to a lesser extent, proteins (Fig. 2). This raises intriguing questions for future research and will certainly uncover new biological patterns, provided the field adopts stronger opendata policies to enhance experimental power and collaboration^{13,16}.

In sum, I agree with Senior et al. (2025)⁷ that further theoretical work is needed to formalise the sampling distributions and statistical inferences using angles and confidence intervals. Advancing our understanding of the hidden patterns in animal nutritional ecology will require a concerted effort combining new theoretical frameworks, analytical models, and empirical data.





Appendix I

$$s^{2} + t^{2} - h^{2} = 2st$$
$$s^{2} - 2st + t^{2} = h^{2}$$
$$(s - t)^{2} = h^{2}$$
$$s - t = h$$

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Author contributions

JM is the sole author of this article and therefore was responsible for analysing the data, generating the figures as well as writing and revising the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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