Latitude, local ecology, and hunter-gatherer dietary acid load: implications from evolutionary ecology[1,2]

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ABSTRACT

Background: Past estimations of the net base-producing nature of the Paleolithic "Diet of Evolutionary Adaptedness" derived primarily from interpretations of ethnographic data of modern historically studied hunter-gatherers. In our recent ethnographic analyses, we observed large variations in diet-dependent net endogenous acid production (NEAP) among hunter-gatherer diets.

Objective: We proposed to determine whether differences in ecologic environments influence estimations of NEAP.

Design: By using ethnographic data of plant-to-animal subsistence ratios and mathematical models established previously, we computed frequency distributions of estimated NEAP in relation to latitude in 229 worldwide modern hunter-gatherer societies. Four different models of animal fat density were used: models A (3%), B (10%), C (15%), and D (20%). In addition, we estimated NEAP by primary ecologic environments in those hunter-gatherer societies (n = 63) for which data were documented.

Results: With increasing latitude intervals, 0°–10° to >60°, NEAP increased in all 4 models. For models A, B, and C, the diets tend to be net acid-producing at >40° latitude and net base-producing at <40°; the same held for model D (>50° and <50°, respectively). For models A, B, and C, the diets of hunter-gatherers living in northern areas (tundra and coniforest) and in temperate grassland and tropical rainforests are net acid-producing. In all other ecologic niches, hunter-gatherers seem to consume a neutral or net base-producing diet.

Conclusions: Latitude and ecologic environments codetermine the NEAP values observed in modern hunter-gatherers. The data support the hypothesis that the diet of *Homo sapiens*' East African ancestors was predominantly net base-producing. *Am J Clin Nutr* 2010;92:940–5.

INTRODUCTION

Attempts to reconstruct the diets of ancestral and modern hunter-gatherers have a long history (1–5). However, only recently has the subject become a relevant field of discourse among nutritionists. In this context, the seminal 1985 article, "Paleolithic Nutrition," by S Boyd Eaton and Melvin J Konner (6), elicited a great deal of attention (7–16), some of which is controversial (17–23). Since then, some have claimed that the nutritional characteristics of hunter-gatherer diets—particularly those of our ancestors who lived in the Paleolithic age [Old Stone Age, roughly equivalent to the Pleistocene geologic epoch (≈2.5 million to ≈11,000 y ago)], before the emergence of agriculture about 10,000 y ago—represent a reference standard for the physiologically appropriate diet for modern humans (24). This claim is based on the hypothesis that because evolution via natural selection is a very slow process, the 10,000 y since the end of the Paleolithic was too short for the development of core physiologic adaptations to the drastically different postagricultural and postindustrial diet (6, 25, 26). Therefore, humans should still be adapted to Paleolithic conditions. Accordingly, various attempts (6, 27–30) have been made to characterize "The Diet of Evolutionary Adaptedness (DEA)," namely "common nutritional practices which typify" the Paleolithic period (31).

Because increasing evidence indicates that diet-induced disturbances in acid-base status have pathogenic effects (32–34), investigators have tried to estimate the DEA's net endogenous acid production (NEAP). Contrary to the modern net acid-producing Western diet, such studies estimated the DEA as net base-producing (24, 26). However, because of limitations in the archeologic record, our knowledge about the nature of "the" Paleolithic diet consumed by past hominids and the archaic *Homo sapiens* is only rudimentary (23, 35, 36). Consequently and coherently, assumptions about the net base-producing nature of the DEA (12) are based on interpretations (6, 28) of ethnographic data on modern hunter-gatherers (24, 37), which suggests that the average diet consisted of high energy intakes from plant foods, generally yielding net base when metabolized. However, more recently, Cordain et al (30) found, contrary to previous interpretations (6, 28), that most modern hunter-gatherers (73%) consumed higher amounts of animal food (>50% of energy)—a source of net acid production (38). Indeed, in a previous study (39), we found net acid-producing diets in a high proportion (≈50%) of forager diets when we computed the NEAP for all of the diets consumed by modern hunter-gatherers.

However, with respect to plant-to-animal subsistence ratios, one cannot assume that worldwide historically studied hunter-

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gatherers serve as "living fossils" (40) for hunter-gatherers who lived in the Paleolithic age—a time of different geographic, climatic, and ecologic conditions. The latitude and ecologic niche of hunter-gatherer living sites play an important role in determining the diet plant-to-animal ratio (30). Thus, the same might hold for NEAP. Here we examine that possibility.

SUBJECTS AND METHODS

Using recent ethnographic data of plant-to-animal subsistence patterns and quantitative estimations of the NEAP of 229 historically studied worldwide forager populations, we computed frequency distributions of NEAP in relation to latitude. Additionally, we calculated NEAP by primary ecologic environment in those hunter-gatherer societies for which data were documented (n = 63). The procedures were carried out as detailed below.

Ethnographic data

The data of plant to animal energy subsistence ratios (P:A ratios) in relation to latitude and local ecologic conditions came from an analysis of a revised version (41) of the *Ethnographic Atlas* (42), performed by Cordain et al (30). In their analysis, summarizing various ethnographic data of 1267 of the world societies, Cordain et al (30) identified 229 hunter-gatherer societies whose economic subsistence depended primarily on hunting (including trapping and fowling), gathering (wild plants and small land fauna), and fishing (including shell-fishing). In accordance with Cordain et al (30) and our previous analysis (39), we assumed in the present study that gathered food would only include plant foods, whereas Murdock (42) had stated that gathering activities could also include the collection of small fauna, although hunters would not have been expected to return empty-handed if they encountered lodes of plant foods. We also followed the assumption of Cordain et al (30), whereby the P:A ratio based on weight in the *Ethnographic Atlas* can be considered reasonably equivalent to the P:A ratios based on energy.

Computation of the NEAP in the current model

Estimations of the NEAP were based on our previous work (39), in which—based on the validated model of Sebastian et al (12)—we established a mathematical model for computation of the NEAP as a function of the P:A ratio of each of the hunter-gatherer diets. According to this model, we found a linear relation (r^2 = 1) between the energy ratio from plant and animal food and the measure of the NEAP, depending on the percentage body fat of the edible carcass that was consumed. Because the fat content of animal foods eaten by hunter-gatherers varied between 3% and 20% of whole-body fat (30), we generated 4 different NEAP models: model A (3% body fat of animal food), model B (10%), model C (15%), and model D (20%). The models were represented by the following 4 linear systems of equations, where x represents the percentage of energy from animal food (39):

$$f(x_A) = 422.8x - 241.7 \quad (1)$$

$$f(x_B) = 369.73x - 241.8 \quad (2)$$

$$f(x_C) = 355.35x - 244.22 \quad (3)$$

$$f(x_D) = 328.53x - 241.87 \quad (4)$$

Considering this and the P:A ratios of hunter-gatherer diets in relation to latitude and local ecologic conditions, we calculated the NEAP for the different diets.

Re-use of the same data set for the present manuscript as used in a previous article

Whereas this manuscript used the same data set as used in a previous article (39), it used previously unused data from that

TABLE 1
Effect of degree of latitude to the ratio of plant-food energy intake to animal-food energy intake (P:A ratio) and the corresponding net endogenous acid production (NEAP) for 229 historically studied worldwide hunter-gatherer diets with variations in the body fat of the hunted animal foods

Degrees of latitude from the equator	P:A ratio by class interval	Absolute frequency	Relative frequency	NEAP model A[1]	NEAP model B[2]	NEAP model C[3]	NEAP model D[4]
	%	*No. of societies*	*% of societies*	*mEq/d*	*mEq/d*	*mEq/d*	*mEq/d*
0–10	36 to 45:55 to 64	6	2.6	−9 to 29	−5 to –38	*See* Figure 1	−61 to –32
11–20	46 to 55:45 to 54	15	6.6	−51 to –13	−76 to –42	*See* Figure 1	−94 to –64
21–30	46 to 55:45 to 54	11	4.8	−51 to –13	−76 to –42	*See* Figure 1	−94 to –64
31–40	46 to 55:45 to 54	64	27.9	−51 to –13	−76 to –42	*See* Figure 1	−94 to –64
41–50	26 to 35:65 to 74	75	32.8	33 to 71	−2 to 32	*See* Figure 1	−28 to 1
51–60	16 to 25:75 to 84	38	16.6	75 to 113	36 to 69	*See* Figure 1	5 to 34
>60	≤5 to 15:85 to ≥95	20	8.7	118 to 181	72 to 128	*See* Figure 1	37 to 87
Median	—	—	—	33 to 71	−2 to 32	−15 to 19	−28 to 1

[1] Animal-fat energy = 26% of animal-food energy. Considering the cubic relation between the percentage of fat by weight and the percentage of energy from fat [$f(x) = 0.009x^3 - 0.403x^2 + 7.92x - 22.79$, where x represents percentage body fat by weight (39)], this is equivalent to ≈3% whole-body fat content.

[2] Animal-fat energy = 51% of animal-food energy. Considering the cubic relation between the percentage of fat by weight and the percentage of energy from fat [$f(x) = 0.009x^3 - 0.403x^2 + 7.92x - 22.79$, where x represents percentage body fat by weight (39)], this is equivalent to 10% whole-body fat content.

[3] Animal-fat energy = 62% of animal-food energy. Considering the cubic relation between the percentage of fat by weight and the percentage of energy from fat [$f(x) = 0.009x^3 - 0.403x^2 + 7.92x - 22.79$, where x represents percentage body fat by weight (39)], this is equivalent to 15% whole-body fat content. Data were omitted from the table and shown in Figure 1 to avoid repetition.

[4] Animal-fat energy = 72% of animal-food energy. Considering the cubic relation between the percentage of fat by weight and the percentage of energy from fat [$f(x) = 0.009x^3 - 0.403x^2 + 7.92x - 22.79$, where x represents percentage body fat by weight (39)], this is equivalent to 20% whole-body fat content.

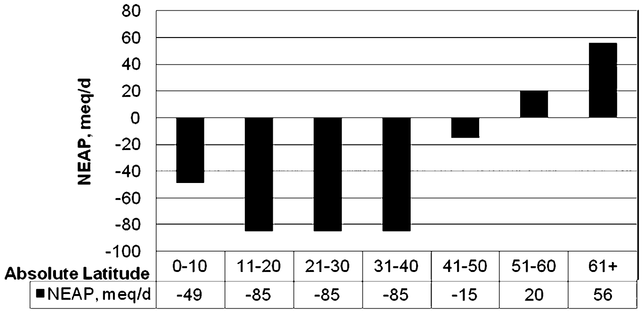

FIGURE 1. Relation of net endogenous acid production (NEAP) and absolute degrees of latitude from the equator. Representative data from model C (n = 229 hunter-gatherer diets).

data set to answer a separate question arising from the interpretation and implications of that previous article, namely, why did we find a wide distribution of NEAP values among the 229 historically studied hunter-gatherer societies? This question was alluded to by the authors of an editorial (43) that accompanied the previous article. Stimulated by this editorial, we then realized that the data set also included additional data enabling an ecologic/evolutionary approach to that new question, crystallized from the findings of the previous article.

RESULTS

Quantitative estimations of NEAP in relation to latitude

The findings of the computations of NEAP for different P:A ratios of each of the 229 hunter-gatherer diets in relation to latitude are summarized in **Table 1**. According to our calculations, NEAP markedly increased with increasing latitude >40° in all of the models (A to D). However, for a given latitude interval, there remained differences in NEAP in each model, and between models. For example, whereas the diets of hunter-gatherer societies located in the latitude interval from 0° to 10° north or south showed a neutral or even a small net acid-producing effect in model A (NEAP: –9 to 29 mEq/d), they were base-producing in models B (NEAP: –38 to –5 mEq/d), C (NEAP: –17 to –49 mEq/d), and D (NEAP: –32 to –61 mEq/d). Nevertheless, for models A, B, and C there was a threshold value at a latitude of 40° north or south: hunter-gatherer diets tended to be net acid-producing at >40° latitude and net base-producing by <40° (Table 1, **Figure 1**). The same held true for model D at latitudes >50° and <50°, respectively.

Quantitative estimations of NEAP in relation to local ecologic conditions

In addition to computing frequency distributions of the NEAP in relation to latitude, we calculated NEAP estimations in relation to primary living environments in 63 hunter-gatherer societies for whom appropriate data were available. The results are summarized in **Table 2**. Independent of models A to D, the data showed that the diets of hunter-gatherers living in northern areas (tundra and coniferous forest) were net acid-producing: model A (75–155 mEq/d), model B (35–106 mEq/d), model C (22 –to 90 mEq/d), and model D (5–67). In models A, B, and C, only 2 additional ecologic environments—temperate grassland and tropical rainforest—showed a similar net acid-producing effect of the hunter-gatherer diets. In all other ecologic niches, hunter-gatherers consumed a diet characteristically neutral or net base-producing.

DISCUSSION

The nutritional characteristics of hunter-gatherer diets have been the focus of several studies, various attempts having been made to "develop a model hunter-gatherer diet" (6, 27–30, 24, 43), which, as Jenike (44) stated, should be "a valid description of the central tendency of Paleolithic hunter-gatherer diets." Assumptions about such "a model hunter-gatherer diet" (44) are primarily based on ethnographic records of modern Holocene (current geologic epoch, beginning ≈11,000 y ago) foragers. However, contrary to popular belief, there is high dietary diversity within individual modern hunter-gatherer societies (3, 45, 23). For instance, we observed plant-source energy intakes as low as 0–5%, and animal-source energy intakes as high as 86–100% when we systematically analyzed the economic subsistence data for all 229 historically studied hunter-gatherer societies in a previous study (39). This variability was further expressed by the great variations in the NEAP (−185 to 120 mEq/d) for the different historically studied hunter-gatherer societies

TABLE 2
Effect of different ecologic environments on the ratio of plant-food energy intake to animal-food energy intake (P:A ratio) and the corresponding net endogenous acid production (NEAP) for 63 worldwide hunter-gatherer diets with variations in the body fat of the hunted animal foods

Characterization of the ecologic environments	P:A ratio by class interval	Absolute frequency	Relative frequency	NEAP model A[1]	NEAP model B[2]	NEAP model C[3]	NEAP model D[4]
	%	*No. of societies*	*% of societies*	*mEq/d*	*mEq/d*	*mEq/d*	*mEq/d*
Tundra, northern areas	6–15:94–85	6	9.5	118 to 155	72 to 106	90 to 58	37 to 67
Northern coniferous forest	16–25:84–75	14	22.2	75 to 113	35 to 69	22 to 54	5 to 34
Temperate forest, mostly mountainous	36–45:55–64	6	9.5	−9 to 29	−38 to −5	−49 to −18	−32 to −61
Desert grasses and shrubs	46–55:45–54	11	17.5	−51 to −13	−75 to −42	-84 to −52	−94 to −64
Temperate grassland	26–35:65–74	11	17.5	33 to 71	−1 to 32	−13 to 19	−28 to 1
Subtropical bush	36–45:55–64	2	3,2	−9 to 29	−38 to −5	−49 to −18	−61 to −32
Subtropical rain forest	36–45:55–64	4	6.3	−9 to 29	−38 to −5	−49 to −18	−61 to −32
Tropical grassland	46–55:45–54	4	6.3	−51 to −13	−75 to −42	−84 to −52	−94 to −64
Monsoon forest	36–45:55–64	2	3.2	−9 to 29	−38 to −5	−49 to −18	−61 to −32
Tropical rainforest	26–35:65–74	3	4.8	33 to 71	−1 to 32	−13 to 19	−28 to 1

[1–4] Body fat of the hunted animal foods: [1]≈3%, [2]≈10%, [3]≈15%, and [4]≈20% by weight.

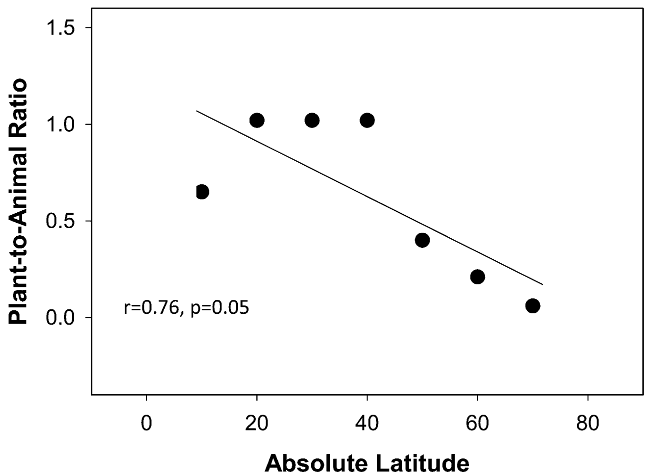

FIGURE 2. Plant-to-animal ratio in relation to absolute latitude (r = 0.76 and r^2 = 0.57, P = 0.05; n = 229 hunter-gatherer diets).

(39). Given the fact that modern worldwide foragers lived under different geographic, climatic, and ecologic conditions than did our Paleolithic ancestors for millions of years (44, 46), it would not be surprising to find that those factors play an important role in codetermining dietary variability among them (23, 45). Given this background, the analysis presented here is based primarily on the question of how latitude and variable ecologic environments influence the quantitative estimations of NEAP in all of the 229 worldwide hunter-gatherer societies.

NEAP in dependency on latitude

As our results showed (**Figure 2**), we found a significant, although not highly significant, inverse relation between plant-to-animal subsistence ratios and increasing latitudes, consistent with the finding of positive NEAP values at the higher latitudes (Table 1, Figure 1). Over a wide range of latitude intervals from 11° to 40° north or south, forager diets had identical and notable net base-producing effects in each of the models. These findings need to be considered in light of the results of ethnographic data (30, 45) that show that hunted animal food remains relatively constant with latitude, whereas plant food declines with increasing latitude and fished animal food replaces hunted animal food with increasing latitude. Therefore, P:A ratios, the main predictors of NEAP, are identical in latitude intervals from 11° to 40° north or south (*see* Figure 2). Our evaluation of the ethnographic database showed further that the threshold above which hunter-gatherer diets became net acid-producing emerged at >40°. This finding reflects the fact that modern hunter-gatherers who lived in higher latitudes consumed high amounts of animal foods (P:A ratio ≤26:≥65) (30, 45).

However, in light of evolutionary ecology, it should be noted that settlement of higher latitudes took place relatively late in human evolution (46) (**Figure 3**). Actually, as Snodgrass et al (48) have rightly pointed out, "most Eurasian Arctic sites, such as those in Scandinavia, were not permanently occupied until the Holocene, and much of the North American Arctic was not inhabited only in the past 7000 years". Accordingly, if we are interested in the NEAP values of diets consumed by Paleolithic hunter-gatherer living 200,000–50,000 y ago in Africa, most of the diets of modern Holocene hunter-gatherers (those lived in latitudes >30°) can be not taken as to be representative. Given this, only NEAP associated with latitude intervals from 0° to 30° north (N) or south (S) might serve as a model for NEAP values of our African ancestors. With respect to our results presented in Table 1, it seems evident that a near neutral or net base-producing diet was the norm of those African Paleolithic hunter-gatherers on average – an interpretation that is in accordance with the findings from Sebastian et al (12). However, there was a remarkable dietary change (23) when *H. sapiens sapiens* colonized higher-latitude environments (>40°) ≈46,000–7000 y

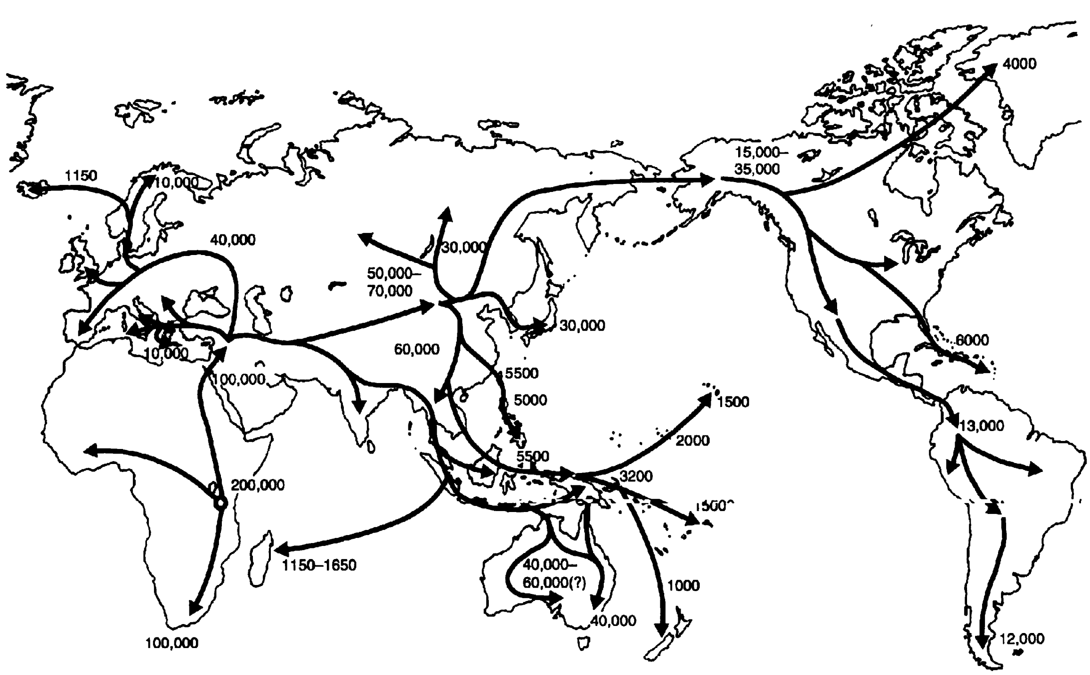

FIGURE 3. Geochronologic worldwide expansion of *Homo sapiens* during the past 200,000 y. Reprinted with permission from reference 47.

ago (48, 49). Indeed, as stable-isotope values indicate, Upper Paleolithic humans in Europe consumed an animal-based diet (23), whereby the P:A ratio might be located in the range of $\leq$26:$\geq$65, as our findings in Table 1 indicate. Consequently, that change switched the diets of our ancestors from net base- to net acid-producing, reflecting a reduction in endogenous bicarbonate production rates and an increase in both sulfuric acid and organic acid production rates (12).

NEAP in dependency on local ecologic conditions

An alternative manner in which the NEAP values of modern hunter-gatherer diets could be examined is by the ecologic niche in which the group resides—this potentially would be more revealing, because many of the historically studied hunter-gatherers live in the least desirable habitats, occupied not before the end of the last glaciation and only few settled in very productive environments (3, 40). As our results showed, there were only 2 northern and 2 temperate ecologic environments characterized by net acid-producing diets, whereas all other ecologic niches were associated with neutral or net base-producing effects. Again, these results should be interpreted in the context of evolutionary ecology, showing that much of hominin evolution and the origin of modern humans took place in woodland and grassland (50, 51). Therefore, if we are interested in the NEAP values of the diets consumed by members of the archaic modern *H. sapiens* who lived 200,000–50,000 y ago in Africa, most of the ecologic environments we have analyzed in this work seem irrelevant (45). Indeed, from the background stated above, only NEAP values associated with desert grasses and tropical grassland should serve as a model for NEAP values of our direct African ancestors. As our results presented in this article clearly show, it seems most likely that those Plio-Pleistocene foragers had consumed net base-producing diets. Again, this result agrees with the findings of Sebastian et al (12). However, the expansion into new ecologic environments, especially those located in northern latitudes, occurring during the Upper Paleolithic (48, 49) changed the P:A ratios (23) and thus the NEAP values of the diets considerably.

In conclusion, our data presented here showed that latitude and/or ecologic environments are important factors that codetermine the wide intercultural ranges of NEAP values found in modern hunter-gatherer diets. These high intercultural variations impressively demonstrate the high dietary flexibility and metabolic plasticity of humans (52). Indeed, it might be this "plasticity in many aspects of phenotype" (52) that accounts for the evolutionary success of *H. sapiens* all over the world.

With respect to the DEA concept of "evolutionary health promotion" (53), our results are of relevance because they showed that it is difficult to characterize common nutritional practices that typify the Paleolithic period (31). Actually, lasting $\approx$2.6 million years, the Paleolithic era covers a long period of time in which the geographic, ecologic, and climatic conditions were highly variable (46, 54). Thus, the same variability may have been the case for the hominin diet (23). Therefore, if researchers were to use ethnographic data of modern hunter-gatherers to model the DEA, they have to be careful to identify only those forager societies that can be appropriately considered to be representative of a particular Paleolithic time period and a particular geographic and ecologic environment (55). Only then might the diets of contemporary foragers provide some credible information about the DEA of humans.

The authors' responsibilities were as follows— A Ströhle and A Sebastian: designed the research and wrote the manuscript; A Ströhle: analyzed the data; AH: generated ideas that were incorporated into this manuscript; and A Sebastian: had primary responsibility for final content. All authors read and approved the final manuscript. None of the authors had a conflict of interest.

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